THE UNIVERSITY OF HULL

SOME ASPECTS OF VARIATION IN
TAXUS BACCATA L.
IN ENGLAND.

being a Thesis submitted for the Degree of

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CONTENTS.

Page No.

PLATES.

TEXT FIGURES.

Page No.

TABLES.

The yew: Taxus baccata L.

Typical spreading crown form. (Butser Hill, Sussex).

CHAPTER 1.

Introduction.

Classification.

There are five orders in the class Gymnospermae; the Cycadales, Gnetales, Ginkoales, Coniferales and Taxales. Mitchell (1974) has noted that the last three orders are loosely referred to as 'conifers'. In the order Taxales is the family Taxaceae within which there are only three genera; they are *Austrotaxus* *Torreya* and *Taxus* (Pilger, 1916; Domin, 1940). Bugala (1975) has noted that the only endemic species of the genus *Austrotaxus*, *A. spicata*, grows in the humid forests of New Caledonia and is not cultivated in Europe and that the genus *Torreya* includes five species, of which three exist in Eastern Asia and two in North America. He went on to say that the genus *Taxus* includes seven species occurring in the temperate zone of the entire northern hemisphere, i.e. Europe, Asia and North America. Pilger (1903, 1916) noted that yews look very much alike and suggested the existence of one collective species; giving names to the various geographic types, he listed seven subspecies as follows:

a) *T. baccata subsp. eubaccata* Pilger - Europe, Western Asia, North Africa;

b) *T. baccata subsp. wallichiana* (Zucc.) Pilger - Himalayas;

c) *T. baccata subsp. cuspidata* (Sieb. et Zucc.) Pilger - Japan;

d) *T. baccata subsp. brevifolia* (Nutt.) Pilger - Western North America;

e) *T. baccata subsp. canadensis* (Marsh.) Pilger - Eastern (Atlantic) part of North America;

f) *T. baccata subsp. floridana* (Nutt.) Pilger - Florida; and

g) *T. baccata subsp. globosa* (Schlechtd.) Pilger - Mexico.

However, in more recent works, for example, Redher (1951), Dallimore & Jackson (1954), and Krussmann (1972), these subspecies of the yew are recognised as separate species and this opinion prevails. Only one species of the genus *Taxus* exists naturally in Europe, this being *Taxus baccata L.* (Bugala 1975).

Although all agree that the common name for Taxus baccata L. is 'the yew', there seems to be confusion as to what adjective best describes it. Coutts (1944) calls this species 'the common yew', while Keen (1958) suggests 'the English yew', and Edlin (1965) both 'the English yew' and 'the common European yew'; many other authors simply call it 'the yew' (Nisbet, 1893; Johns, 1892; Howard, 1944; Tansley, 1939; Mitchell, 1974). For the purposes of this dissertation it will be referred to as 'the yew'.

Edlin (1956) noted that the word itself derives from Yw in Welsh and Iubhar in Gaelic, (pronounced and Anglicised as 'Ure'), both of which are common elements of place names. This same author also comments that it is the only tree in Britain to have retained a Celtic name in English speech, the Anglo-Saxon name, Heben, not having survived past Elizabethan times.

Morphology.

Although small in height, in relation to other conifers, it stands out among other trees as it has a deep green foliage which is easily seen (Plate 1.1 and Plate 1.2). It is one of only two tree conifers native to Britain, the other being Pinus sylvestris, the Scots pine (Clapham, 1975). Its general morphology has been described most recently by Mitchell (1974), Clapham (1975) and Bugala (1975). It is a short-trunked tree which can reach twenty metres in height, but usually does not grow that tall. As Bugala (1975) has noted, "in general the tree attains a height of eight to twelve metres". The bark is reddish-brown which scales away to leave dark-red or brown patches. The branches are stout and level, although some can be upturned. The inner branches of the tree are denuded of shoots due to the deep shade cast by the outer foliage layer. The short-stalked leaves, which are 2 to 4 cm. in length and 3 mm. wide according to Mitchell (1974), or 3 cm. in length and 2 to 2.5 mm. wide according to Bugala (1975), are narrow and abruptly short-pointed, being dark glossy green above (Plate 1.3), and distinctly paler beneath (Plate 1.4). They are borne all round the green shoots but are twisted into two horizontal rows, pointing forwards to the point (Plate 1.5). The terminal

Plate 1.1. *Yew wood at Butser Hill, Sussex.* The deep colouration of the yew tree is clearly seen in comparison to the whitebeam (*Sorbus aria* (L.) Crantz) and ash (*Fraxinus excelsior* L.).

Left foreground, hawthorn (*Crataegus monogyna* Jacq.).

Plate 1.2. Close-up of a yew tree showing its deep colouration in comparison to ash (*Fraxinus excelsior* L.).

Plate 1.3. Dorsal, glossy-green side of the yew leaf.

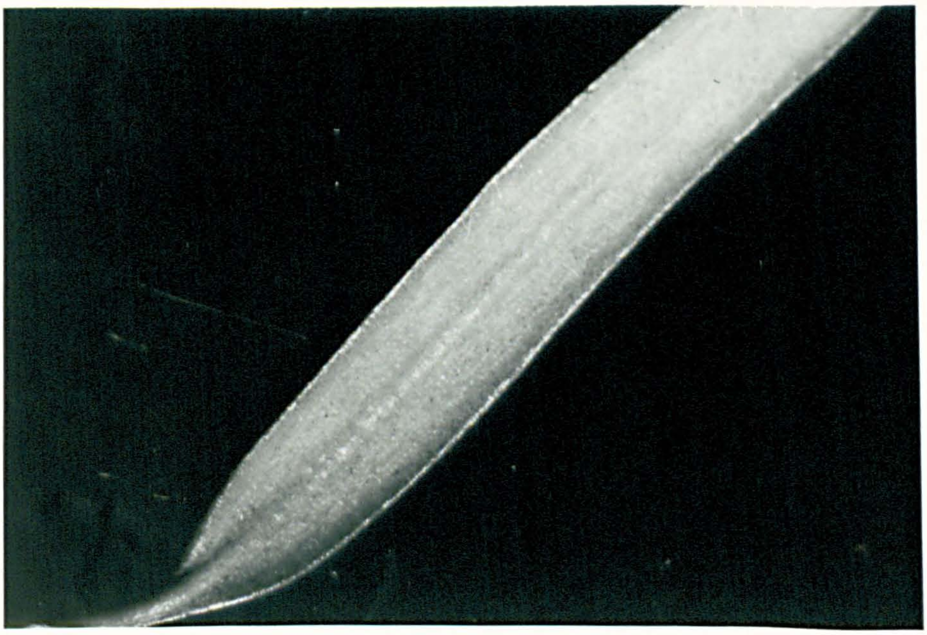


Plate 1.4. Ventral side of the yew leaf, which is paler than the dorsal side.

Plate 1.5. The horizontal rows of leaves.

Plate 1.6. The minute terminal bud.

bud is minute, ovoid and green (Plate 1.6), with most trees having some greatly enlarged buds forming a leafy rosette-shaped gall (Plate 1.7), caused by the yew gall midge (Taxomyia taxi Inch). The species is dioecious with the male flowers being globular (Plate 1.8), each bearing five to nine pollen sacs, hanging in heavy clusters on the tree. In contrast, the female flowers are minute and solitary, looking very much like axial buds until March to April when they ripen and push out an open-ended funnel to receive the wind-borne pollen (Plate 1.9). Both male and female flowers are borne on the underside of shoots of the previous year. After fertilisation, the berry, called the aril (Plate 1.10), slowly forms; it is at first green and tight, but by October will have swollen and become bright red, holding a solitary, olive-brown seed (Plate 1.11). Nurserymen call it 'a two year seed' because after falling from the tree it will take eighteen months before germination takes place. The yew is the only common conifer to bear only two seed leaves; these are strap-shaped and short-lived (Plate 1.12), disappearing at the end of the first season (Edlin, 1965). All the other leaves are as in the adult (Plate 1.13 and 1.14), as described above.

Economic and aethetic usage.

Howard (1944) described the fully grown tree as "romantic but rather sombre" in appearance. There are, however, two more practical characteristics of the tree that made it important as far back as Greek and Roman times. Authors of the time referred to the quality of the wood for making bows, and to its effectiveness as a poison (Coltman-Rogers, 1920). Loudon (1844) pointed out that Ceasar told of a king who poisoned himself with the juices of the yew. But although the yew's poisonous properties are undeniable, they become grossly exaggerated. Loudon (1844) credited Plutarch with the statement that it is fatal to sleep in the shade of the yew when it is in flower, with Pliny adding, "that the berries of the male yew are mortal poison particularly in Spain". Johns (1892) refers to Pliny's description of the yew, "neither verdant, nor graceful but gloomy, terrible and sapless",

Plate 1.7. The rosette-shaped gall caused by the yew gall midge (Taxomyia taxi).

Plate 1.8. The male flowers of the yew hanging in heavy clusters.

Plate 1.9. The minute, solitary, and ripe female flower of the yew with its open-ended funnel.

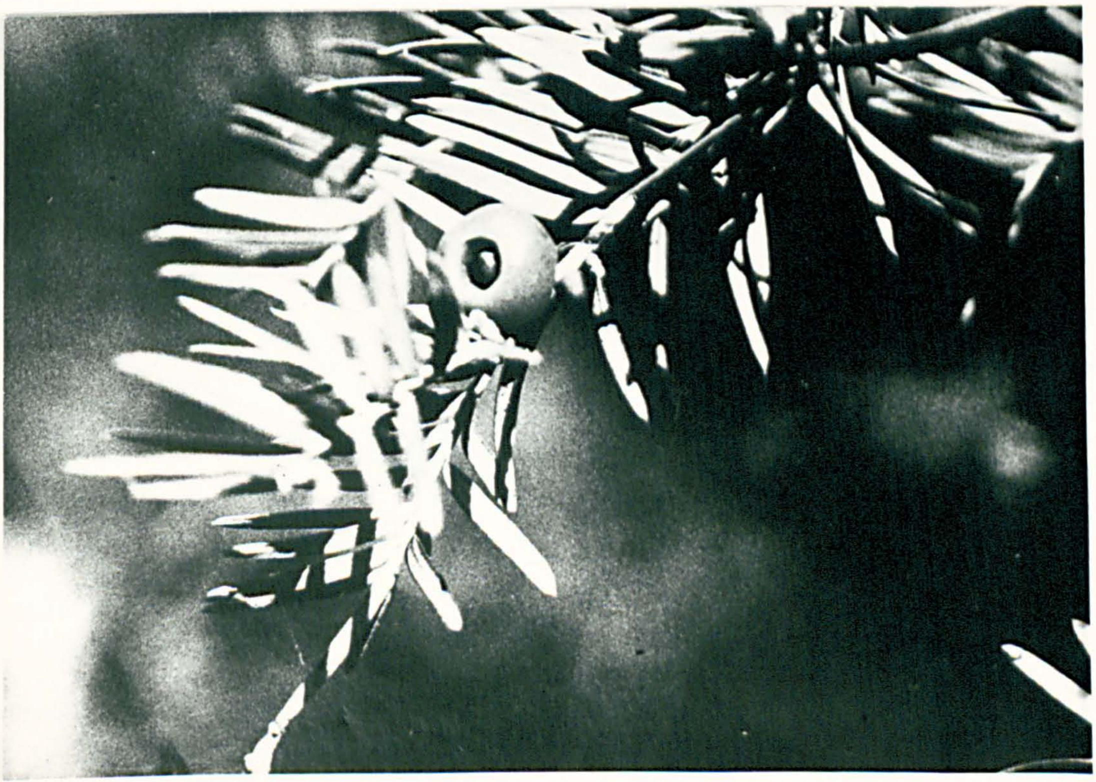


Plate 1.10. The aril, with a solitary seed housed inside.

Plate 1.11. The yew seed.

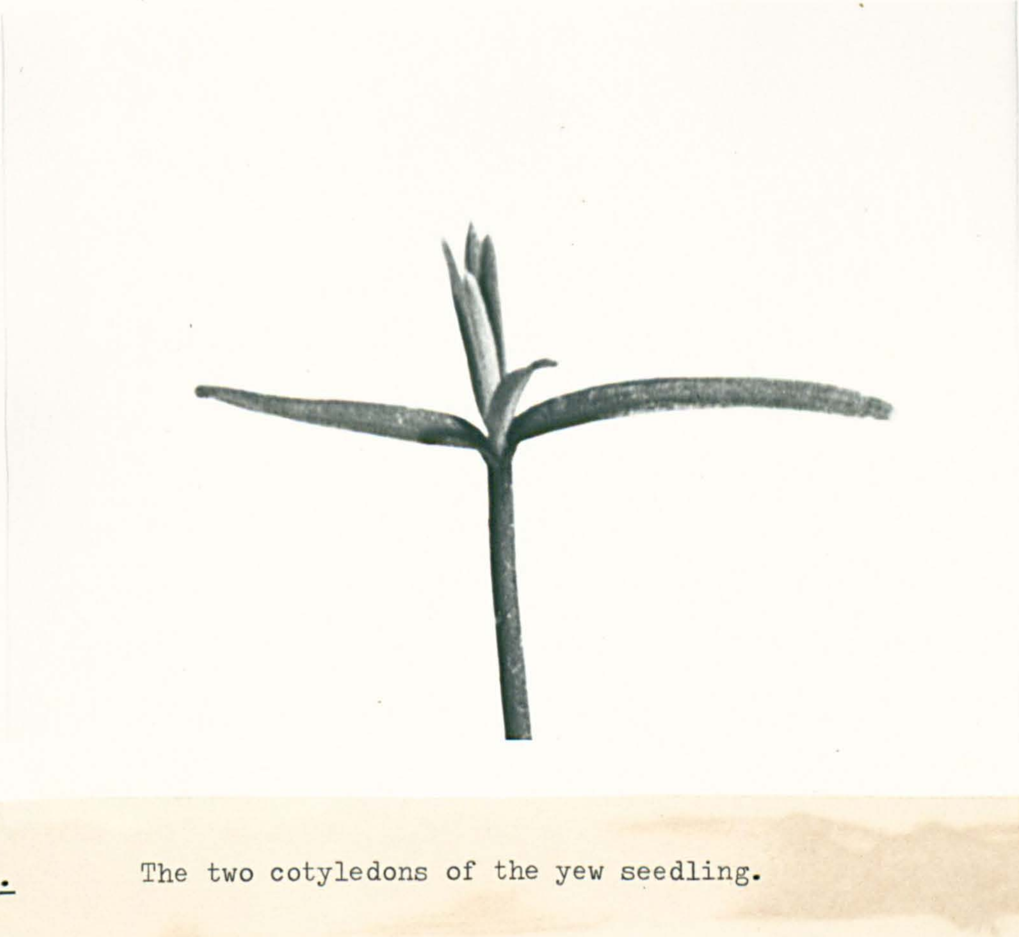


Plate 1.12. The two cotyledons of the yew seedling.

Plate 1.13. A side view of a two-month-old yew seedling.

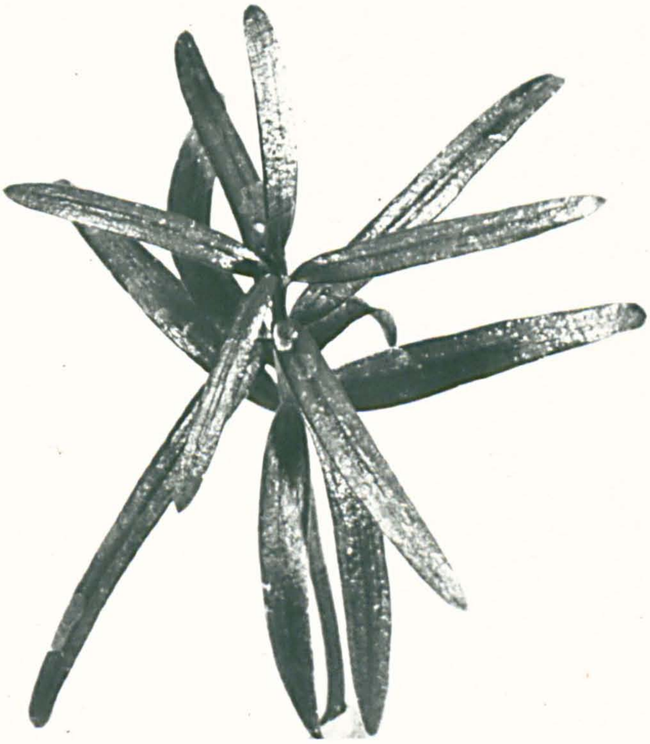


Plate 1.14. A plan view of a two-month-old yew seedling.

remarking that to judge from these words it is a tree of evil omen. In view of these and other comments about the tree, it is not surprising that the yew lived out its life with little help or encouragement, and moreover that it has been used as an emblem of death and burial. The intentional planting of yews in churchyards and graveyards is well known; however, the reasons for this are less well understood (Johns, 1892). In general, three main reasons have been advanced, namely: (1) to secure its continued cultivation for the making of bows; (2) to safeguard cattle from its poisonous leaves; and (3) its sombre evergreen branches made a fitting symbol of death and immortality. Howard (1944) discounts the first of these, as the best bow wood was imported from Spain and, moreover, in past days "the parsons' revenue partly consisted of the licence to feed cattle in the churchyard". This leaves the third as the most likely reason, Johns (1892) summarises: "generation after generation might be gathered to their fathers, the Yew tree proclaiming to those who remained that all like the evergreen unchanging Yew were yet living in another world, the life which had been the object of their desire".

The yew has been present in Britain from Hoxnian and Flandrian interglacial times (Godwin, 1975). The earliest prehistoric records for its use as spears in Britain have been recovered from Meare Heath and Ashcott Heath in the Somerset levels and have been respectively dated 2690 ± 120 B.C. and 2665 ± 120 B.C. Withies of yew wood were also employed as stitches, fastening the main timbers of the 'sewn' boats at North Ferriby, Yorkshire, referred by radiocarbon dating to a period about 1600 and 750 B.C. (Wright & Churchill, 1965).

However, the yew's best known traditional use was for archers' bows, because of its exceptional elasticity and suppleness (Edlin, 1956). A quotation from Homer tells of the inhabitants of ancient Crete being "dreadful with the bended Yew" (Loudon, 1844). According to Lowe (1897), the English long-bow owes its introduction to the Normans, "who, chiefly by its means, won the battle of Hastings". However, English yew wood seems generally to have been considered of inferior quality to that obtained from the continent. Statutes were passed by many English sovereigns obliging European merchant ships to import "ten bow staves with every butt of wine" (Johns, 1892). Howard (1944) quoted Boulger who said, "it was to bows of yew that we mainly owed the victories of Crecy (in 1346) and Poitiers (in 1356); and Edward 1V decreed that every Englishman should have a bow of his own height. English yew-wood, however, for this purpose, only fetched one-third the price of that which was imported". To an Englishman the yew was formerly what the Oak is now, the basis of our strength. "Of it the old English yeoman made his long-bow, which, he vaunted, nobody but an Englishman could bend. In shooting he did not, as in other nations, keep his left hand steady, and draw his bow with his right; but keeping his right upon the nerve, he pressed the whole weight of his body into the horns of his bow" (Loudon, 1844).

Although the use of yew wood for bows died out with the advent of firearms, its neglect was deplored by some. Evelyn (1664) wrote that "since the use of bows is laid aside among us, the propagation of this tree is quite forborne. But the neglect of it is to be deplored; seeing that the barrenest grounds, and the coldest of our mountains, might be profitably replenished with it". As far as it is known they were not planted in the sites Evelyn suggested, but they did find favour, and were grown, on estate land. Hummel & Lewis (1955) wrote of The Closewalks Yews on the Cowdrey Estate, Midhurst, in Sussex that they are "one of the most remarkable yew groves in Great Britain or elsewhere", because of their extraordinary height. They measured the tallest tree in the grove to be 92 feet (approx. 28 metres) and the mean height of all the trees being 81 feet (approx. 25 metres).

Mans' striving for aesthetic beauty did not stop at growing the yew tree in its natural state, for he has clipped it into all sorts of strange shapes. Evidence of topiary work can be seen in estates and gardens all over Great Britain although it has not always been seen as a desirable practice. Evelyn (1664) commented that "the yew tree has been generally cultivated for the pleasure garden, to be clipped into the shape of beasts, birds, etc., or for hedges. Whoever is pleased with such figures can raise no tree more proper for the purpose, as the branches and leaves may be clipped and fashioned into almost any form or shape. But as this method is justly exploded, and as everyone who has the least pretension to taste, must always prefer a tree in its natural growth to those monstrous figures..." Coutts (1944) remarked that "it is doubtful that there is any other plant that would stand yearly clipping and remain in good health over such a great number of years. As a hedging plant it has a long history. Howard (1944) noted that it is not only very decorative but it makes a "formidable barrier, impossible to climb and very difficult to destroy", although it takes a long time to reach perfection.

The toxin in yew, which has been known about for centuries (see above), is now understood to be an alkaloid called Taxine (Dallimore & Jackson, 1954). In fact the very name of the genus, Taxus, Loudon (1875) suggested, could have been derived from taxon, a bow; taxis, the arrangement of the leaves like the teeth of a comb; or from the Greek word for poison, toxicum. An opposite view was taken by Coltman-Rogers (1920) who said that the Greek word taxon (a bow) was evolved from another Greek word, taxos (a yew). Whatever the case, this alkaloid can be found in the bark, foliage and seeds of the tree (Edlin,1956), and is thus a danger to livestock, which must be kept well away from yew hedgerow. It has also been said that the dried shoots are more deadly than fresh material (Coutts, 1944). Although the seed is said to be poisonous it seems that some creatures find it to be a valuable food source, as hundreds of empty seed husks have been observed, by the author, below yew trees with the insides totally removed. It is not known which animals eat the seeds, although mice have been suggested by Watt (1926) and Tittensor (1979) suggested the bullfinch and hawfinch as well. By October, the fruit of the yew tree, the aril, in which the solitary seed is housed, has become bright red. Its colour is considered to be attractant to birds, especially to thrushes (Ridley, 1930). Edlin (1965) mentioned a yew in the New Forest that he knows to have been regularly visited by "flocks of fieldfares from Scandinavia, which gorge themselves on the scarlet berries". Ridley (1930) noted that the birds, when eating the yew berries, swallow them whole with the seed intact, and either regurgitate the seed or let it pass through the digestive system. He also noted that when the seed does pass through the bird, it can be seen to be unharmed, and he ~~finally~~ suggest~~ing~~ed that it is owing to the birds that the yew tree is so widely distributed.

Distribution and general ecological considerations.

The yew has been described by Szafer (1964) as a tertiary relic of fossil range, which agrees with the comment made by Tansley (1939) when he described its present distribution as being very local throughout its range.

The yew indeed has a large distribution area, being described as having Mediterranean-Montane and west and central European distribution range by Godwin (1956); the species area covers Britain, Europe, Algeria, Asia Minor to Persia (Iran). The eastern limit of the range of the yew in Europe runs from the Gulf of Riga, through Bialowieza to the Carpathians, and from the East Carpathians southeast (Bugala, 1975), Fig. 1.1.

In a more recent distribution map of the yew in Britain and Northern Europe, Fitter (1978) indicated in greater detail the places within this range where the tree could be found (Fig. 1.2). It can be seen from this figure that there are large gaps in its distribution in the more northerly countries, e.g. France, Belgium and Denmark, although it is not at its northern limit in these countries. The explanation suggested is that the

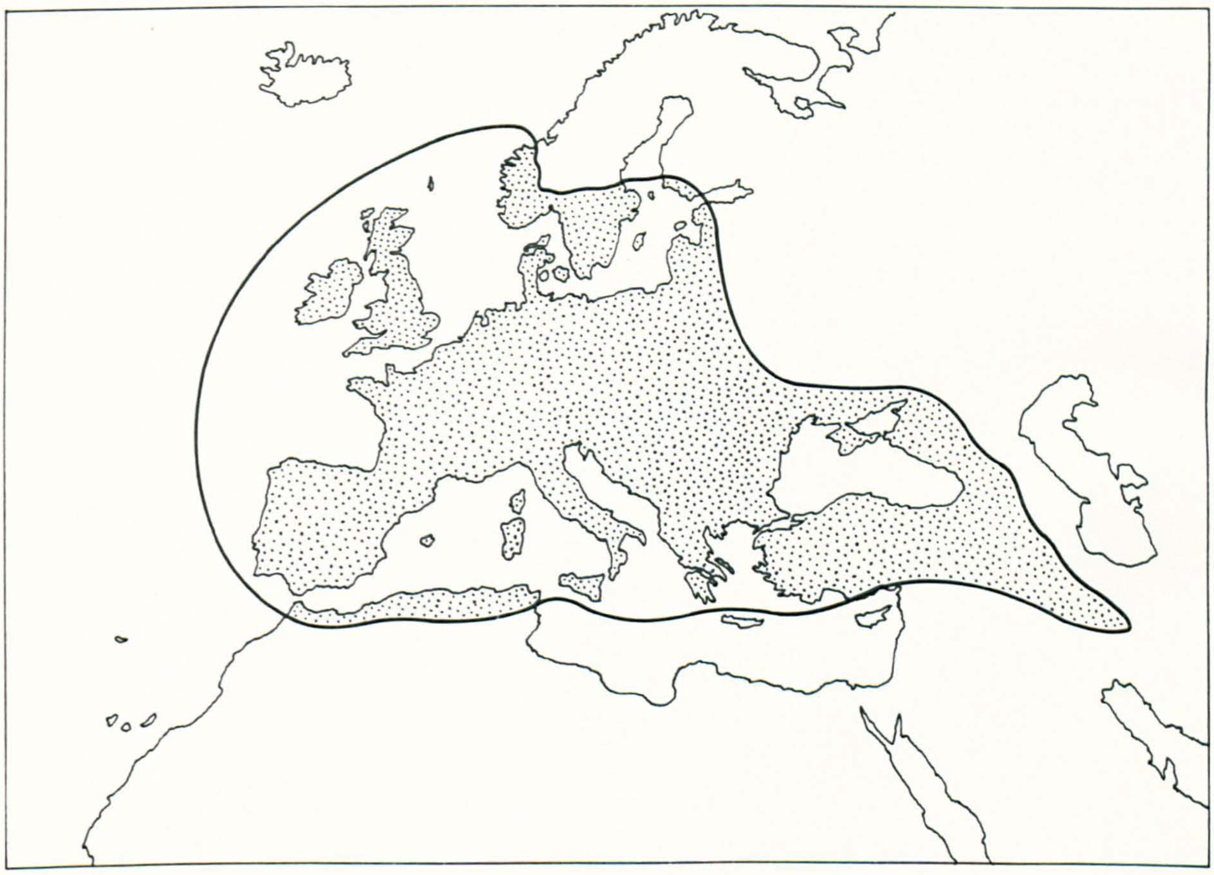


Fig 1.1. The geographic range of the yew tree (Taxus baccata L.) (after Bugala, 1975).

Fig 1.2. The geographic distribution of the yew tree (Taxus baccata L.) in Britain and northern Europe.

(after Fitter, 1978).

tree has been felled by man in these areas and has not replaced itself (pers. comm. R. Bunce).

Godwin (1956) noted that in the British Isles the tree extends north to Perth and Argyll, 56°N, and in Scandinavia to 63°N on the Norwegian coast and to 61°N in Sweden. Considering this northerly distribution, he went on to suggest that the northern limit to the tree's distribution is set, perhaps, by its intolerance to winter cold. Within the British Isles the 'probable native distribution' of the yew has been mapped out by Perring & Walters (1962), (Fig. 1.3), showing that it is present in the south of England, the Welsh border country, the southern tip of the Pennines, and the northwest and that towards the northeast naturally occurring populations become increasingly rare. Michell (1974) comments that it is found mainly over limestone soils although it does grow "in oakwoods on other soils" in the north of England. It should be pointed out that many of the yew trees in Britain, even in the chalk area, are isolated individuals, growing in chalk or limestone scrub or in ash or beechwood. It is interesting to note that individuals growing under beech take on a shade habit and will not flower (Tansley, 1939). It can tolerate extremely shallow soil and can even be seen growing out of crevices of pure limestone bedrock although in these situations the growth is stunted.

Tansley (1939) pointed out that the yew does not dominate "any considerable tracts of British woodland, but it does achieve local dominance..." He referred to the western Sussex Downs in the southeast of England as a place where it is "very abundant indeed". Here, on these chalk hills, the yew frequently colonises scrub especially on the South Downs of west Sussex and Hampshire and to a lesser extent on the North Downs of Surrey. This is the only area in Britain where yew forms pure local woodlands achieving this due to its dense foliage which effectively excludes other tree species; in fact little or no vegetation can exist under the shade of one of these closed yew woods. Watt (1926) commented that "the dominance of the yew is complete

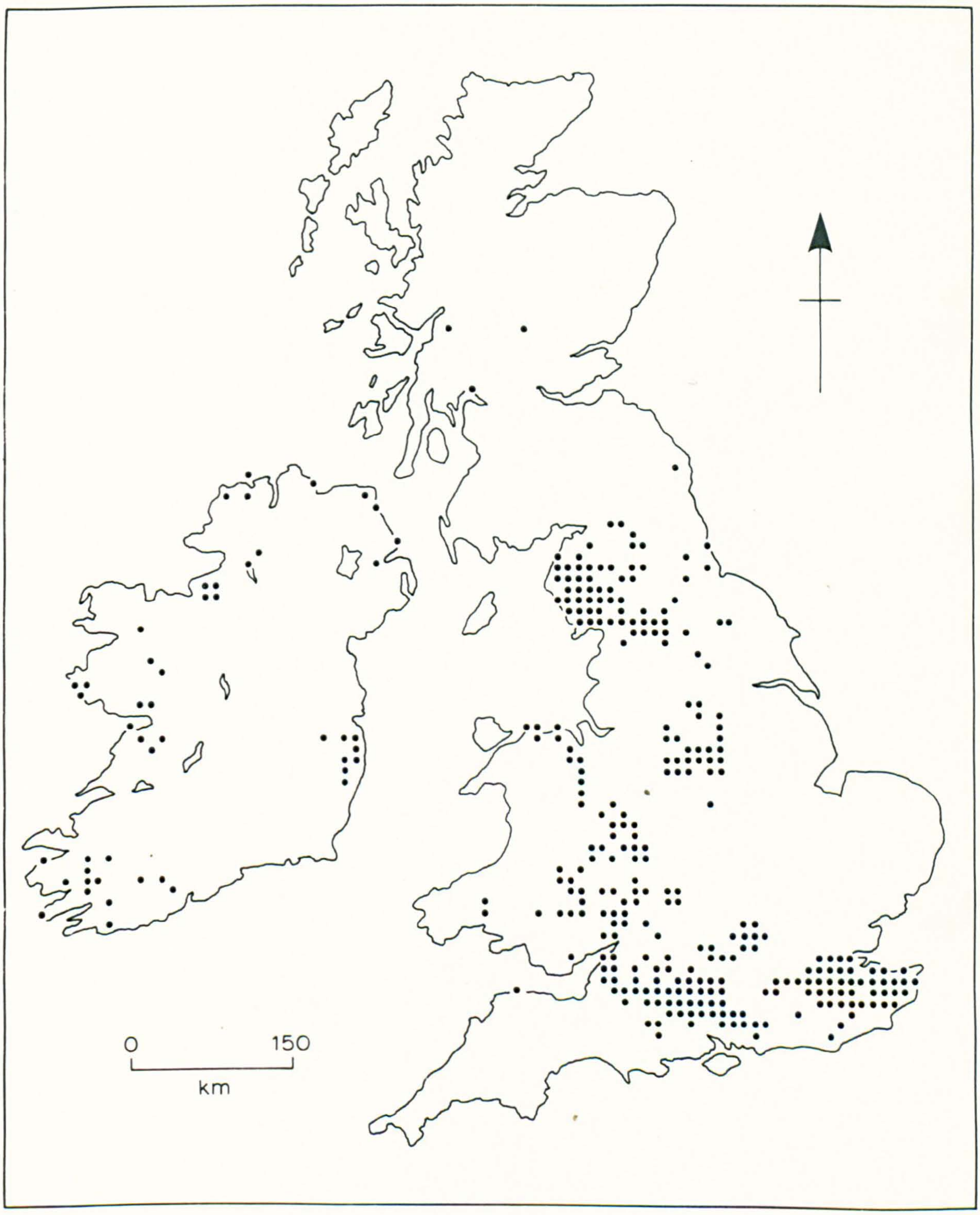


Fig 1.3. The 'probable native distribution' of the yew tree in Britain.

(after Perring & Walters, 1962).

to a degree found in no other British community: the shrub layer and ground flora are absent and mosses are rare". Indeed, I have observed yew seedlings around the circumference of a female yew but none in the shade of its branches suggesting that the yews' own offspring also cannot survive the conditions set up.

The pure yew woods of the South Downs have been closely studied by Watt (1926). He looked at the origin, structure, development and fate of ten South Down yew communities, looking at their relation to scrub, how ash (Fraxinus excelsior), the normal tree colonist of the chalk scrub in this area, affects yew wood formation. ~~and~~ He put forward evidence showing that the yew woods in question are migratory societies of scrub. He noted that new woods originate in chalk scrub under the protection of juniper (Juniperus communis), or hawthorn (Crataegus monogyna) scrub, although it is the juniper that provides the more efficient protection to the young yews from the wind and rabbit colonies that infest the area. In a closed juniper scrub, yew invasion may be general, culminating in a relatively quick transition into yew scrub. In an open juniper scrub, the invasion is more sporadic with the formation of clumps consisting of yew families encircled by scrub. These families consist of a central older yew, which has a richly branched spreading crown (the pioneer form) surrounded by younger yews whose cleaner stems and lopsided crowns are due to the shading effect of the pioneer tree. In the scrub, round these clumps, still smaller and younger yews establish themselves. These families can usually be distinguished even in the pure wood which eventually results after the destruction, by shading out, of the initially protecting scrub.

Hawthorn scrub on the South Downs develops on the less wind-beaten slopes and on deeper soils than those on which juniper is found, and is much richer in species. It is colonised by yew in essentially the same way but much less generally, since the hawthorn forms a less efficient protection than juniper. The yew families are usually fewer in number and enlarge more slowly so the process to yew domination will take longer.

When ash has entered the scrub, the development of the yew wood is halted for a time, i.e. the ash growing along side the yew forms an intermediate stage of yew-ash wood. As the yew has a much longer life than the ash, it will eventually form a pure yew wood, but this can take a very long time indeed. Relics of the original scrub, still surviving between yew trees, have been estimated to be five hundred years old.

These processes are summed up thus;

Juniper sere. Scrub (Juniper) → Yew scrub → Developing yew wood → Yew wood.
Hawthorn sere. Scrub (Hawthorn) → Yew scrub → Developing yew wood → Yew wood.
(without ash)
↗Ash scrub↘
Hawthorn sere. Scrub (Hawthorn)--------→ Yew-ash scrub → Yew-ashwood → Yew wood.
↘Yew scrub↗
after WATT (1926)

Watt (1926) also noted that both the nursing scrub and the yew wood which follows it first establish themselves in places least exposed to strong winds, and from there progress along and up and down the slopes, thus establishing a mature, uneven-aged yew wood in consequence. Therefore, the oldest yew woods will be found at the head of these dry, chalk valleys (coombes) and yews will get progressively younger as they are traced along the sides towards the mouth. Correspondingly, it is from the heads of the valleys that degeneration of the yews begins. Owing to the attacks of ground vermin (rabbits and mice) the trees cannot recolonise the gaps formed by the death of the oldest members, nor can scrub fit to protect young yews establish itself. Thus, the gaps increase by the progressive death of old yews and eventually the entire head may become bare, leaving a few isolated trees, the remains of the former wood. Watt (1926) summed up his study on the pure yew wood succession and Senescence ~~scenescence~~ thus: "During development the yew kills out the scrub and forms a community, which, like the elephant herd, is socially well developed because of the longevity of the individuals. The vast majority of the yew seeds and seedlings are destroyed and when old yews die the re-establishment of the scrub protective of the few yew seedlings is prevented;

the yew is unable to regenerate and the yew community dies out. This begins in the most sheltered part of the valley where colonisation first took place and spreads outwards leaving a gap where yew wood once stood". He concluded by saying that a yew wood is a single generation migratory community and owing to its dependence on scrub is best considered a society of scrub".

A recent publication on the natural history of the yew in England has been written by Williamson (1978). His book deals with Kingley Vale, Sussex, the site of "the finest yew forest in Europe" (a comment made by a Professor Drude from Germany when being shown around the site by Tansley, in 1911). In this book Williamson deals with his personal, casual observations of the plants, animals and insects of the forest and although it is a pleasant book to read it is not in essence a scientific work.

Finally, it should be pointed out that _Taxus baccata_, as other yew species, has been cultivated to produce a large variety of cultivars, for example _T. baccata 'aurea'_, the golden yew; _T. baccata 'adpressa'_ and many others. A full description of these varieties has been worked out by Keen (1958) and Chadwick & Keen (1976); however, an account of these is considered outside the scope of the present work.

Aims of this dissertation.

The work quoted above by Watt (1926) is the only scientific study found in the British literature that deals with the yew. Since this tree is a native conifer to our shores, this is a surprising state of affairs. It was therefore considered that a start should be made to redress this lack of knowledge. The following work is certainly the only one of its kind to have been attempted in England, and is possibly the only one of its kind throughout the entire range of this species.

As my specialised interest lies in the continued understanding of variation in organisms, the work presented here is a study of between-population and between-region variation of the yew in England (intraspecific variation), with respect to the morphological characteristics of the reproductively mature tree, the variation of seed weight, germination percentage, and seedling vigour, and the variation in cold hardiness of the leaf. It should be emphasised that this work is the beginning of what it is hoped will be an ongoing project to understand more about a tree which, in Britain, has been sadly neglected, and which deserves more attention than it has received thus far.

CHAPTER 2.

Review of the literature.

Most of the existing information about the yew can be found in the European literature, and especially from Polish and German sources. In Poland, the yew is a protected species and therefore highly cared for. Bialobok (1975) noted that the number of yew trees in Poland is rapidly dwindling, suggesting that this is connected with changes taking place in the forest environment. An English translation of the Bialobok (1975) monograph has recently been published, summarising much of the Polish work on the yew that has been carried out. This monograph has been used widely in the following literature review.

Ecology: a European perspective.

As mentioned in chapter 1, Taxus baccata is a Tertiary geographical relic of fossil range (Szafer, 1964). It is scattered in isolated stands from the Azores to Iran and from Algeria to 63°N latitude in Norway and Sweden (Browicz & Gostynska-Jakuszewska, 1969). Its vertical range also proves its wide ecological tolerance. As a montane species in North Africa, southern Spain and the Pyrenees it grows at 2500 m, 1948 m, and 1623 m above sea level respectively (Browicz & Gostynska-Jakuszewska, 1969), in Iran at 1400 m above sea level (Riedl,1965), in Turkey at 1400 m (Czeczotowa, 1938-1939) and 1900 m (Coode & Cullen, 1965), in the Caucasus at 2050 m (The Dendroflora of the Caucasus, 1959), in Macedonia at 1800 m (Em, 1967), in the Southern Carpathians at 1100-1450 m (Witting, 1935), and in the region of the Alps and Karawanken at 1330-1470 m (Rubner, 1952). As a non-montane species, the yew spreads across hill lands in Czechoslovakia, Poland and the two German republics (Szafer, 1930) to the lowlands in the north and to sea level in the Baltic countries (Beissner, 1907; Bjorkman, 1958).

The broad longitudinal and latitudinal range and considerable differences in the altitude of stands above sea level convey an idea of the diversity of climatic conditions prevailing within the range limits of the yew. However, stands at the ~~outermost~~ edge of its range testify that the fall in winter temperatures to below -30°C, and the severe continental climate east of the Baltic Soviet Republics and Poland (Kamppa, 1926), the long droughts during the year in large areas of Turkey and Sudan, and the drought and high temperatures in North Africa (Walter & Lieth, 1960), are impassable ecological barriers for the species (Krol, 1975). However, Krol went on to comment that at the southern boundary of its range there are sites where the climatic extremes are moderated by the microclimate of particular plant communities, thus creating conditions for the yew's continued existence. In the northern part of its range, extreme climatic conditions can be modified by the microclimate of maritime (oceanic) zones, which the yew can tolerate (Schonichen, 1933). Further, Krol (1975) has noted that on the Baltic coast, where the rainfall is below 750 mm per annum, as well as in areas with 500 mm per annum rainfall, the yew has stands only near marshes and peatbogs, which create a more humid local climate. On the other hand, in dry habitats, on steep and bare mountain slopes, the yew satisfies its moisture requirements by growing in rock crevices (Traczyk, 1953; Dallimore & Jackson, 1954; Hofman, 1948).

Lilpop (1931) stressed the adaptive capability of the yew, in terms of its existence on very humid soil, in a very shady forest, as well as in dry habitats, in shady and sunny places alike. Myczkowski (1957), describing the most elevated stand in the Tatras, noted the vigour of the yews in the upper zone of submontane spruces, where ecological conditions, an acid, podzolic soil with a thick layer of raw humus, are more severe than a typical tree stand of this elevation zone. Krol (1975) commented that among the montane stands in central Europe, this particular one must be considered exceptional.

Tschermak (1950) and Mitchell (1972), among others, consider the yew as a tree of the lower storey of high, polyspecific, deciduous forests with beech, or mixed forests with beech and fir, and in which it forms the under part of the tree stand as a shade-tolerant species. Svoboda (1953) and Sokolowski (1921) add that in their opinion, this relationship to the trees towering over it is a biological property which protects the yew against frost, and that shade is, for it, a condition of life and successful development. Krol (1975) adds that as it grows slowly, it does not compete with other tree species, and it does not form a distinct storey in the lower part because it grows singly or in small groups, neither does it form independent forests. Dallimore & Jackson (1954) noted that in the Atlantic climate of southern England, the yew does not really need the protection of taller trees. It often occurs among individually-growing trees and scrubs. Tansley (1911) noted the existence of a pure yew wood on the border between Sussex and Hampshire, which originated artificially after a high beech forest, with yew undergrowth, was felled. The yew grew so intensively that it protected the undergrowth against game and at the same time through its density and shade formed a community closed to other tree species. It is in this area of England, i.e. at Kingley Vale, Sussex, that the "finest yew forest in Europe" exists (Williamson,1978).

The Dendroflora of the Caucacus (1959) supplies information about the yew from the opposite side of its range. It noted that the yew occurs fairly frequently in the Caucasus and that it has its richest stands in Georgia, where there are areas of up to 10 hectares of yew forest on the hills of Alazania either as a dominant or exclusive, and growing to 25-30 metres in height. Near the Caspian sea, the yew exists without any admixture of other tree species. In Poland, as many as two hundred trees are growing in a pasture created by felling a forest near Przybynow (Pfabe, 1950). These examples are exceptions to the rule that, in general, yew grows individually or in small stands.

The requirements of the yew concerning soil and bedrock cannot be strictly determined as it grows within its range on different geological and pedological formations. However, it is a fact that the majority of natural stands in Europe grow on soil with a calcareous substratum of various origins (Krol, 1975). Yew is also found growing on quarztite, granite, and sandstones of different chemical composition (Schonichen, 1933). Traczyk (1953) wrote that in one area of Poland yew was seen growing above all on fertile soil rich in carbonates, while in the lowland part of its range it was found among diluvial formations on sandy, sandy-clay, loamy, and even peat soil (Szczesny, 1952). It also grows on chalk and limestone rendzinas (Mitchell, 1972; Hoffmann, 1958).

In general, the yew likes humid soil, as found in Atlantic climatic regions, but at low levels of ground water in regions with an oceanic climate any shortage of water supply is offset by the high humidity of the air from heavy rainfall. In mountainous regions, it grows mostly on less well-illuminated northwestern or northeastern slopes, where under deciduous or mixed stands, it finds an ecological climate similar to an oceanic one. Krol (1975) says that although the yew has a fairly extensive vertical range, the upper altitudinal limit is more or less consistent with the upper limit of the zone of deciduous and mixed forests.

Taxo-Fagetum forms major associations in the European centre of the yew's range in Germany and Switzerland, as noted by Hoffmann (1958). According to the same author, in central Germany, yew and beech (*Fagus sylvatica* L.) forests grow on the northern and western slopes of limestone mountains on moderately dry humus rendzinas, where the hornbeam (*Carpinus betulus* L.), mountain ash (*Sorbus aucuparia* L.), sycamore (*Acer pseudoplatanus* L.), and durmast (*Quercus petraea* (Mattuschka) Liebl.) grow together with the beech, and the yew forms the lower layer 5 to 10 m high.

The Dendroflora of the Caucasus (1959) gave a general picture of the optimum conditions for the yew in the east of its range, saying that the best conditions for its growth exist in a region near the Black Sea, 600-900 m above sea level. "Old trees and the younger generation feel most comfortable in conditions of light air humidity, small amplitudes of temperature, moderate shade provided by a 60-70% density of tree tops, soil with a low content of calcium, and annual rainfall above 800 mm". This is why the best yew stands exist in shady, deep ravines, on terraces and sides of depressions with a calcium substratum (Krol, 1975). The Dendroflora of the Caucasus (1959) noted that the yew is the most shade loving species of the Caucasus, but Krol (1975) has pointed out that the possibility of growth in full light must not be ruled out.

The Dendroflora of the Caucasus (1959) made five general points about the ecology of the yew as follows:

a) Considering that the yew develops successfully only in definite physical and geographical environmental conditions, the forming of a tree stand with the second storey of yew is possible only in a few suitable places.

b) The yew, as a tree with a fine, straight trunk, grows tall only when it grows for a long period of time in conditions of even, diffuse light and sufficient humidity of the air.

c) When yew crowns are not adequately protected against direct light by steep slopes, an indispensible condition for its normal growth, is the existence of the first storey of tall trees of other species. The crowns of those trees should not form a close canopy and this state should continue during the formation of yew trunks.

d) The formation of the second storey of yew under tall trees adds to the value of the stand, not only because it increases the resources of valuable yew wood but also because it helps the trees of the first storey to get rid of knots.

e) In numerous places in our forests, the yew regenerates fairly well in the form of self-sown plants, forming an undergrowth where even young trees can be found, and in exceptional cases up to 100 specimens per hectare. This testifies to the real prospects of increasing the number of trees of this valuable species in mountain forests.

It should be noted that recommendations concerning the best density of the first storey trees find confirmation in the work of Eichenberg (1929) from upper Bavaria where, in the largest yew reservation in Germany, one fifth of the stand was removed every five years to facilitate "the way of the air to the yews", conforming with the prevailing view that "...yew likes best to grow in side-shade or under a loose canopy of trees". Schonichen (1933) noted that older yews like a thin mixed forest, while Maly (1930) observed that young yews require shade but in older age they tolerate even open positions, In Traczyk's opinion (1953), intensive light is not harmful for the yew, provided that the tree grows on fertile, humid soil. He also said that he does not think yew "likes shade", but endures it, which is an adaptive trait compensating its somewhat negative properties to compete successfully with other trees. Other authors share this view (Koscielny & Krol, 1965; Sokolowski, 1973).

Growth.

An interesting fact mentioned by various authors is the hollowing-out of trunks of older yews. This has been commented upon by Izdebski (1956), when he noted that although a yew trunk may be hollow a healthy external appearance is preserved. The oldest yew in Poland in Henrykow (approximately 1230 years old) has a hollowed trunk (Stecki & Szule, 1957). In Britain the oldest yew tree is to be found at Fortingall; this is about 15 m in circumference, and its hollowed and cracked portion of trunk is only one tenth of the complete trunk (Mitchell, 1972). Mitchell (1972) also commented that all yews of the British Isles "...of more than 4.5 m in circumference have hollowed trunks and can exist for another 500 years while their circumference and crowns increase at an unslackened rate". Dallimore & Jackson (1954) noted that yews in England, which have reached an age of 1000 years and are notionally "in an advanced stage of decay", have not been showing any further sign of further decay for many years and have kept their branches and needles, although the trunks have been reduced to a shell.

Natural regeneration.

Bellegarde (1926) pointed out that there has been intensive natural regeneration of the yew north of Trieste, and Szczesny (1952) noted that, in a Causacan reservation, yew regenerates successfully, giving 3000 seedlings per hectare. Tansley (1939) reported after Watt that in southern England yew did not regenerate under the close canopy of old yews, but had numerous progeny in places from which individual trees have been removed. I have confirmed this observation in noting that seedlings were seen around the circumference of a female yew, but none were found growing in the shade of its branches. Fabijanowski (1951) found a site in Switzerland where natural regeneration of yew had taken place in an intermediary zone between a pine forest, and a yew and beech forest. Seedling development may not necessarily give rise to young trees however, and Krol (1975) noted that one- and two-year-old seedlings die under dense yew crowns due to lack of light.

Different conditions of natural regeneration are described by Hofman (1969). He cites two places on the eastern slope of a quarry, where in one, on loamy soil, twenty eight old yews are growing in a lower storey and in the other, thirty six are growing. He stresses that the density of the trees is high and in these conditions he found that self-sown plants, from young seedlings to fifteen-to twenty-year-old trees, were abundant.

Numerous Polish authors have noted regeneration in yew stands in Poland, e.g. Rygiel (1966), Bartkowiak & Zielinski (1973), and Koscielny & Krol (1970). However, there is also evidence of a lack of regeneration, and even the dying out of young seedlings in old yew stands, for example, in Czecholovakia by Hofman (1965), Hofman & Vackova (1969), Koscielny & Krol (1970), and from Germany by Schieferdecker (1925), and Hoffmann (1958). Various suggestions have been made as to the reason for this regenerative failure. Jasnowska (1957) proposed that the soil was getting too dry because of the lowering of the ground water; Hegi (1935) thought that this reflected a decreased vitality of the yew; and Gieruszynski (1961) suggested that there may be unfavourable phytosociological relations and too much shade. Other possible causes are the thick layer of leaf litter on the forest floor (Walas, 1964); deer and hare eating up young seedlings (Ostrowski, 1968); seed destruction by birds (Sybilski, 1952); and finally a vaguer suggestion from Fabijanowski (1951) of the adverse effects of little-known biochemical factors. Koscielny & Krol (1970) investigated the theory that lack of light adversely affected the seedlings. They measured the amount of light reaching the floor of the forest in relation to open space in three stands without any lasting regeneration, and in six stands where there was successful regeneration. The results suggested that the light factor, depending in forests on the prevailing phytosociological conditions, does not affect the regeneration of the yew. Comparative investigations of light, phytosociological relations, and soil as a definite complex of ecological factors did not show any correlation between the two categories of yew stands. Other experiments aimed at explaining this problem studied the effect of certain micro-organisms (Manka *et al.*, 1968a, Manka *et al.*, 1968b). Two stands were examined, one which showed successful regeneration and one which did not. The authors came to the conclusion that the soil conditions were microbiologically unfavourable, finding that a micro-organism called *Cylindrocarpon radicicola* was attacking the roots of yew seedlings and suggesting that this is a direct reason for the failure of the young plants.

Krol (1975) commented that the problem of regeneration of yews must be further investigated and solved, not only in order to preserve the existing stands but also to increase the number of yews in favourable habitats and forest associations.

Reproduction.

The forming and dispersal of yew seeds, as well as pollen shedding and fertilisation, takes place in the same vegetative season (Favre-Duchartre, 1962). Pollen is shed in the early spring, with fertilisation taking place about two months later. The growing seed is surrounded by a fleshy aril during maturation. The seeds themselves begin to mature in August and maturation continues until October, when in general they are ready for dispersal. During this time, the seed colour changes from green to olive-brown. Inside this hard seed coat, the seed is full of endosperm, which is rich in fats and in which there is a small embryo of 1.5 to 2.0 mm (Le Page-Degivry, 1973a), the seeds themselves being 5 to 6 mm long. Suszka (1975) noted that the yew embryos are in a deep state of dormancy, and germination can only take place when conditions enable them to break that dormancy.

According to Szczesny (1952), after cleaning about 150-200 g of clean seeds can be obtained from 1 kg of seeds in arils. The weight of 1000 seeds from Poland is 43-59 g, as compared to the same amount of seeds collected in Holland which weighed 77 g (Detz & Kemperman, 1968).

Birds are thought to be instrumental in the dispersal of seed, especially members of the thrush family, such as blackbirds, song thrushes, mistle thrushes, and fieldfares (Ridley, 1930), but also the nuthatch (Bartkowiak, 1970; Barkowiak & Zielinski, 1973).

Due to the deep dormancy of the embryos, yew seeds germinate very unevenly (Heit, 1969), and sometimes it can take a few years for this to be achieved (Suszka, 1975). According to Heit (1969), germination begins in the very early spring, soon after the soil has thawed.

Le Page-Degivry & Garello (1973) have investigated the reasons for the dormancy of the seed from a chemical point of view, by cultivating isolated embryos. They discovered that in cultivation on a liquid nutrient medium, inhibitors of growth are washed out and their presence can be later noted in the medium. The out-flow of the inhibitor from the tissues of the embryo into the liquid medium is a condition for the breaking of dormancy and the growth of embryos.

In further studies (Le Page-Degivry, 1973a) showed that when embryos are cultivated on liquid media, they begin to grow in large numbers or an even quicker growth response is achieved if gibberellin is added to the medium or if they are exposed to cold for two to three months before the cultures are placed in a temperature of 22°C. It was therefore concluded that the influence of lowered temperature can thus be replaced by a stimulator of growth, the effect on the growth of the embryo being the same.

Continuing her work, Le Page-Degivry (1973b) discovered that an inhibitor in the dormant embryo of yew was abscisic acid, which exists both in a free form, (ABA) and in a bound form (ABA-like substances). It was found that the free form must be removed from the embryo before it will begin to grow in suitable conditions, and that it is possible to inhibit the growth of embryos by treating them with abscisic acid, thus suggesting that ABA in the embryos is responsible for the dormancy of yew seeds.

Results from laboratory studies performed by Devillez (1976) indicated that a high percentage of germination of yew seed occurs when a warm-cold stratification is provided, with the germination occurring in the 4-5 month of the cold phase. He found that a constant temperature of 5-6°C is optimal in this phase, with a warm phase temperature of 10-15°C lasting for six months.

Suszka (1975) summed up the findings of dormancy breakage by suggesting that soaking the seeds in cold water is a necessary first step in breaking dormancy. This would lead to a migration of the inhibitor contained in the embryos into the endosperm. Warm stratification should follow, in order to increase the permeability of seed coats and remove the inhibitors from the embryos. A repeated period of cold (cool stratification) would be necessary after warm stratification to enable embryos to increase in length and to put an end to the dormancy. This would be followed by a period of moderately-increased temperature, which would not only enable the root to break through the seedcoat, but also encourage the hypocotyl and the cotyledons to grow at the expense of the gradually-used food reserves of the endosperm.

Cuttings.

Gordenko & Sapozhnikova (1974) have compared the rooting of Taxus baccata cuttings after different dates of preparation, and have found that it was better to take the cuttings in early spring than in the summer. They noted that the best time in spring was when the stock plants were in the development phase, which is characterised by an intensive growth of the roots while the shoots are still dormant. In their case this was twelve days earlier than the beginning of bud break. They got their best results when they applied root-promoting substances, such as potassium humate and indoleacetic acid (IAA), at this time. Yaroslavtsev (1968) drew similar conclusions from observing the growth of roots and shoots and the changes in the regenerative capability of roots after pruning. He noted that the temperature and humidity of the rooting medium should correspond to the humidity and temperature conditions prevailing in the soil during the period of most intensive growth of yew shoots. In contrast, Krussmann (1964) recommended that cuttings should be taken in the autumn, i.e. in August-September. He noted that cuttings planted in boxes in hot beds or a greenhouse take root without the application of growth regulators not earlier than the spring. However, yew cuttings can be taken in other seasons (Wells, 1956). This latter author noted that strong, thick cuttings with two-or three-year-old wood, often root better than one year old shoots, and even four-and five-year-old cuttings can be obtained in April.

Achterbarg (1959) noted that cuttings taken from younger parent plants rooted more successfully than those from older trees, commenting that cuttings from thirty-year-old trees, planted in the late spring, showed 100% rooting within fourteen months, whereas cuttings from trees "of probably 250-300 years of age" rooted in only 20% of cases in the same period of time.

Work using root promoting substances on cutting material has been undertaken by Gordenko & Sapozhnikova (1974), who noted that by adding a certain concentration of IAA (indoleacetic acid) to yew cuttings, there was an increase of 65% in the rooting capacity as compared to untreated cuttings. However, it has been suggested by Verleyen (1948) that naphthaleneacetic acid (NAA) is a better root-promoting substance than IAA. Grace & Farrar (1941) commented that NAA exerts influence not so much on the percentage of rooted seedlings as on the number and length of roots, which increases along with an increase of NAA concentration. Myhre & Schwartz (1948) got good results by applying NAA to cuttings and found that soaking the basal ends in indolebutyric acid (IBA) before planting gave good results, noting that a concentration of 60 p.p.m. was the most effective. However, it was pointed out that the treatment with NAA produced a considerably higher number of roots than did treatment with IBA; thus, approximately 8 to 11 roots were achieved from one cutting in NAA as compared to 1.3 - 1.5 in IBA.

Fungal diseases.

Damping off has been showed to occur in yew seedlings, causing rapid death. Various species of fungi have been identified, including *Rhizoctonia solani* and *Phytophthora cinnamomi* (Hepting, 1971) and *Cylindrocarpon radicicola* (Manka *et al*., 1968a; Manka *et al*., 1968b). Hepting (1971) pointed out that *Phytophthora cinnamomi* is a particularly dangerous damping-off fungus of *Taxus baccata*. He noted that yew seedlings growing on heavy, wet soil, which is insufficiently drained, are particularly susceptible to infection. When a seedling has this disease the root decays completely and dark brown necroses on short shoots extend a few centimetres above the root neck. Manka *et al*., (1968a) tried to find the reason for yew seedling death in a Polish national park. They determined that the reason was infection of seedlings by fungus, *Cylindrocarpon radicicola*, which they repeatedly found. However, they also discovered the fungus *Mycelium radicus atrovirens* in the roots of seedlings in another park in the absence of any Cylindrocarpon radicicola. Later, Manka et al., (1968b) suggested that one species of fungus tended to exclude the other.

In addition to infection by damping-off fungi, yew seeds can also be injured by parasitic nematodes, (Manka et al., 1968a; Hepting, 1971). It was pointed out by Manka et al.,(1968a) that the two pathogenic factors may act separately or together, making it difficult to isolate the real cause of seedling death. Hepting (1971) noted that bad yew growth was found on soil in which nematodes were isolated.

The most dangerous pathogen affecting yew needles and shoots is the ascomycetous fungus Sphaerulina taxi (Peace, 1962; Hepting, 1971 ; Morariu & Lundgescu, 1972). The symptoms are that leaves become brown and fall off quickly; a strong attack by the fungus will also cause shoots to die. It is suggested by the above authors that the fungus penetrates shoots from the tissue of infected leaves. It has also been pointed out by Peace (1962) and Hepting (1971) that other fungus species develop parasitically (although with little noxiousness) and saprophytically on yew leaves, shoots, and branches. A complete list of fungal species will not be given here; however, those mentioned above appear to cause most damage in this species.

Injuries caused by mites and insects.

Kapuscinski (1947) and Pfeffer (1964) observed the occurrence of two species of mites on the yew, with one, namely, Eriophyes psilaspis, causing excrescences and deformations, as well as a change of colour in new leaves and flower buds, and the other, Epitrimerus gemmicola, parasitising the buds deformed by the previously-named species. More recently, Bosenko (1971) noted injuries on yew trees being caused by Pentamerismus taxi. Kapuscinski (1947) has commented on the occurrence of Pseudococcus taxi, whose common name is the yew mealybug. This insect causes swellings on shoots; he observed a dozen or so such swellings on one-year-old twigs. Skuhrava (1965) noted that the most dangerous parasite of Taxus baccata in Europe is an insect, belonging to the order Diptera, called Taxomyia taxi.

Describing the symptoms, he said that as a result of the feeding of larvae of this insect, rosette-like growths appear in the buds of apical shoots, formed of twisted, shorter and broader leaves (Plate 1.7, Chapter 1). He continued by saying that short roots often grow at the base of affected buds. The rosette itself conceals a red larva, which after hibernation pupates in the spring, with the insects appearing in the early spring, usually before the development of the yew buds. When these insects occur in large numbers the development of attacked shoots is inhibited considerably, and even older yew specimens are greatly weakened. Jaufferet et al., (1970) looked in a preliminary way at certain metabolic processes that take place in the meristematic tissues of yew buds which have been parasitised by the larva of Taxomyia taxi, but there is much work to be done before this problem can be controlled.

Kapuscinski (1947) noted the presence of one other insect, Otiorhynchus sulcatus which causes damage to yew buds and young shoots. In this case the insect eats the bark off yew roots.

Physiology.

Atanasiu (1968) examined the variation in quantity of chlorophyll in the leaves of Taxus baccata during the winter. He noted that the curve for chlorophyll quantity diminished from November until the end of December, when it reached a minimum value. After this it increased strongly in January and diminished in February once again. In March, it increased again. However, Popov & Tsoneva (1966-1967) supplied contrary information. They found that the period of high concentration of chlorophyll in Taxus baccata continued from June to January, whereas from February to May the content of chlorophyll in leaves dropped to 50%. The authors also found a correlation between the age of leaves and the number of photosynthetic pigments; the concentration of green and yellow pigments in the plastids increased with the age of the leaves and decreased only in the last year of life. Tsoneva (1972) also found that in the yew the maximum concentration of chlorophyll occurred in spring and early summer. Fluctuations of the amount and activity of chlorophyase, connected with the age of the leaves, were also observed. He found that in the course of the first months after the production of a new leaf the activity of the chorophyllases increased and then dropped obviously after the leaf matured.

The yew does not belong to plants with a high photosynthetic capacity (Szaniawski, 1975). Larcher (1963) quoted the maximum intensity of CO_2 uptake by the yew from the Alps as being equal to 6.3 mg CO_2/g dry weight/hour. According to Atanasiu (1964), winter photosynthesis of the yew measured under natural conditions was about 1.0 mg CO_2/g dry weight/hour, and sometimes dropped to almost zero. Measuring the intensity of photosynthesis in five-year-old yew plants at the time of spring development of buds, Zelawski et al.,(1973), noted CO_2 uptake rates equal to 2.3 mg CO_2/g dry weight/hour. These results suggest that, under favourable conditions, yew photosynthesis may give values comparable to those of other conifers (Szaniawski, 1975).

It has been suggested frequently that the yew is a shade-tolerant plant. This was confirmed by work undertaken by Pisek & Rehner (1958) and Atanasiu (1964), when it was found that yew will assimilate CO_2 even when light intensities are relatively low, i.e. 2000-3000 lx. In the investigations conducted by Pavletic & Lieth (1958), the light compensation point, i.e. the light intensity at which net photosynthesis equals zero, changed from 175 to 3200 lx and more. These changes were correlated with the season and temperature. The authors observed that the highest values occurred in February, whereas, starting from March, the value of the light compensation point began to diminish. They suggested that these variations result primarily from different influences of temperature on the processes of photosynthesis and respiration.

Pisek & Rehner (1958) found that photosynthesis occurred in both the yew and Pinus sylvestris to a temperature of -4°C, when light of 3300 lx was provided. In his investigations, Atanasiu (1964) determined the minimum values of temperature for winter assimilation by the yew as -3°C. Pisek *et al*., (1967) quoted a temperature of -8°C as the minimum for net photosynthesis of the yew from the Alps. It seems that such a wide range of the minimum temperatures of net photosynthesis results from different methods of measurements, as well as from differences in the origin of the plants (Szaniawski, 1975). At the other end of the scale the maximum temperature of net photosynthesis varied from 38°C to 41°C (Pisek *et al*., 1968), with optimum temperature values from plants in the Alps of from 14°C to 24°C. The maximum value of assimilation was observed at a temperature of 19°C in samples gathered in summer and winter (Pisek *et al*., 1969). The authors in fact state that the optimum temperature of yew photosynthesis is distinctly higher than that in other ~~species~~ genera of conifers (*Pinus*, *Abies*, *Picea*, and *Larix*).

Atanasiu (1964) found that there were changes in the intensity of photosynthesis stemming from the seasonal variability of the external conditions. In midNovember, net photosynthesis rates decreased, reaching their minimum in December. From the second half of December to March, respiration was more intensive than the assimilation of CO_2 and when the air temperature was over + 10°C and light intensity reached 25 Klx, it was possible to observe positive values of net CO_2 uptake. From April, the intensity of photosynthesis increased systematically. Pisek *et al*., (1969) have stated that a few days with a temperature of 12°C to 15°C were sufficient for breaking assimilatory depression caused by continuing frost. In an attempt to explain this winter assimilatory depression, Atanasiu (1968) stated that the concentration of chlorophyll is not a factor limiting yew photosynthesis, provided it does not drop below 5 to 7 mg/g dry weight of the leaves.

Respiration.

Atanasiu (1964) indicated that CO_2 evolution in the dark, by yew twigs, takes place continuously, even when the temperature drops to -10°C and even -15°C. The intensity of respiration decreases along with the temperature; for example, at a temperature of -12°C, the intensity of CO_2 evolution was 50% lower than at -2°C. Pisek *et al.*, (1968) noted that it can be assumed that from +18°C to +25°C yew respiration increases linearly, and its intensity is similar to that in *Abies* but almost twice as high as in *Pinus cembra*. In high temperatures, the intensity of respiration is higher than photosynthesis, with the two processes compensating at a temperature of +41°C in *Taxus* (in comparison, in the case of *Abies* temperature compensation point is +38°C). Accordingly, the conclusion drawn was that this difference resulted from the higher sensitivity to high temperatures exhibited in the yew photosynthetic organs as compared to those of the fir.

Osmotic potential.

Atanasiu (1964) showed that the values of osmotic potential in yew leaves increased in winter. The highest value, 35 atmospheres, was noted in January, when the lowest temperatures were also noted. At the end of winter (February-March), osmotic pressure began to diminish and remained at the end of April at a constant level of about 20 atmospheres. This seasonal variation of osmotic potential does not differ from that observed in other conifers, in which the winter maximum and the drop to lower values at the beginning of the vegetative season are also marked (Szaniawski, 1975).

Resistance to air pollution.

Ilkun (1971) noted that the yew is capable of growing in areas subject to the "constant emission of phytotoxic industrial gases", and it is therefore suggested that it should be one of the species planted in such areas. According to Mez (1963) and Buck (1969), the yew is notably resistant to SO_2. They noted that concentrations of this gas at higher than 50 mg/cu m cause damage to yew needles, whereas much lower concentrations, amounting to decimal parts of mg/cu m, damage most species of both conifer and broad-leaf trees. Acatay (1968) noted that the yew was less sensitive to smoke from copper foundries than Pinus or Abies species. Guderian & Stratman (1962) wrote of the high resistance of the yew to hydrogen fluoride contained in industrial emissions.

Anatomy.

1) The shoot. Hejnowicz (1975) noted that the yew shoot develops from the formative tissues on its apex. At a certain distance from the apex, there are places in which leaf primordia are developing along with lateral shoot primordia on their axils. He continued; "at the time of the active development of the plant, three zones can be distinguished on the apex. Their cells differ in shape, distribution, plane of division, the degree of cytoplasm vacuolisation, the size of nuclei and nucleoli and the intensity of colour reactions. The apical zone has in its basal part a conspicuous group of cells, so-called mother cells, and a stratum of one or two layers of cells forms the peripheral meristem. The mitotic activity of cells is very weak. The peripheral and central inner zones border on the apical zone. The peripheral zone is often called the initiating ring, because leaf primordia form from it. The cells are smaller than in the apical zone, faintly vacuolated, with intensively colouring nuclei and large nucleoli about four times bigger in volume than in the apical zone. The mitotic activity of cells is very high. The cells of the peripheral meristem encircle the central part of the apex composed of pith mother cells, called the rib meristem. Cytologically, this zone is similar to the peripheral one, but the mitotic activity is less intensive. Their characteristic feature is that the division is exclusively perpendicular to the apical axis".

"...The leaf primordia initiating process begins in the layer of cells situated directly under the apical epidermis... procambial cells, i.e. the future vascular system, differentiate in the innermost layer of the peripheral meristem, at a distance of about 430 microns from the apex".

"The young shoot is covered with a unilayered epidermis the external walls of which, as well as in part radial walls, are strongly cutinized and coated with very thick cuticle. Stomata exist in the epidermis".

"The structure of the yew stem is connected with a characteristic setting of leaves. Their bases are grown together with the stem over considerable length. In cross section the stem has an irregular shape; it has swellings filled with parenchymal tissue rich in chloroplasts".

Esau (1969) and Den Outer (1967) have commented that the primary phloem functions for a very short time, being crushed by the developing secondary phloem. This phloem is composed of sieve and parenchyma cells, crystalliferous fibres and sclereids. Esau (1969) noted that the sieve cells are elongated in cross section, and that these cells along with the rest of the phloem elements do not have a secondary wall. He also noted that the new phloem does not have typical fibres. It has crystalliferous fibres, the internal walls of which are covered with tiny crystals of calcium oxalate, which originate as modifications of parenchyma cells.

Chang (1954) commented that the phloem rays are composed of one row of parenchyma cells, which abounds in starch and resinous substances.

2) <u>The wood.</u> Hejnowicz (1975) stated that yew wood consists of sapwood and heartwood, the colour of these being light brown and brown respectively. He continued: "the annual rings are distinct and trach~~ie~~eids form regular, radial rows, separated by single rows of rays. A characteristic feature of yew wood is spiral thickenings in the walls of trach~~ie~~eids existing in earlywood and latewood. As a rule, yew xylem has uniseriate rays, although in some sections the rays may have two rows of cells. They consist exclusively of parenchyma cells and do not have radial cells. The secondary wall does not form and the primary wall is unevenly thickened". Jane (1970) noted that rays are composed of one to fifteen cells, and rarely more.

Hejnowicz (1975) noted that the pits maintain continuous contact with various elements of the xylem. Bordered pit-pairs exist between two tracheids and pairs of mixed pits between the tracheid and the ray cell, with bordered pits in the tracheid wall and simple pits in the wall of the parenchyma cell. Timell (1978) studied the helical thickenings and helical cavities in normal and compression wood of the yew. He noted that the longitudinal trach~~ie~~eids in compression wood contained helical thickenings but no helical cavities, the thickenings being as frequent, well developed, and with the same ropelike appearance as in the normal wood. He continued: "except for the absence of cavities and the presence of thickenings, compression wood tracheids of *Taxus baccata* possess all the anatomical features typical of such cells..."

3) *The leaf.* Marcet (1948) described the leaf of the yew as a dorsiventral structure. Its surface consists of an epidermis, the thin walled cells of which, differing in size and shape, are covered with cuticle. On the lower, dorsal surface the cuticle forms irregular, papillary thickenings, above all near the stomata. The leaf has neither hypodermis nor resin ducts. A stratum of one to three layers of cells forming the palisade parenchyma lies under the epidermis, and loosely-arranged cells of the spongy parenchyma are situated under it. The relationship between the two strata depends on the light conditions prevailing when the leaf forms. The number of cell layers of palisade parenchyma is larger in leaves developing in the light. The spongy parenchyma is more compact and its system of intercellular spaces is less developed than in leaves developing in the shade. Hejnowicz (1975) added that the stomata are contained in depressions typical of xeromorphic leaves and that they only occur on the lower surface of the leaf. He also noted that a single vascular bundle composed of primary phloem and xylem is contained in the central part of the leaf, surrounded by large, thin-walled parenchyma cells and connected with the bundle by means of transfusion tissue. This tissue, he explained, is composed of live, thin-walled parenchyma cells and dead, lignified

tracheids, and acts as a link between the vascular bundle and assimilative parenchyma.

4) The root. Plaut (1910) wrote that the root meristem of the yew is covered with a cap. During the growth of the root the zone of elongation and the adjoining root hair zone are situated at a small distance from its apex. When the absorptive function ends, the external layers of cortex under the epidermis become suberised, forming exodermis. After the completion of growth, which is near the end of the vegetative season, the outermost parts of the cap and the innermost layer of cortex also become suberised. A sac, protecting the internal parts of the root against unfavourable influences of the environment during winter dormancy, originates, called the metacutis. Its thickest layer covers the root apex, and when the root resumes its growth, this layer of suberised cells falls off.

5) The generative organs. The yew is a dioecious plant. The male flower develops in the leaf axils. There are ten sterile decussate scales at the base of the flower and six to fourteen symmetrically-arranged peltate stamens on the axis. Each stamen has five to eight pollen sacs, which are also termed pollen chambers (microsporangia) (Konar & Oberoi, 1969). The female flower consists of a single, straight ovule and an aril. The ovule has a single integument, which at the apex forms a micropylar canal, which is closed by a drop of sticky fluid up to the time of pollination. The role of this micropylar drop is to catch pollen grains which are then sucked into the pollen chamber. This chamber originates as a small bulge in the nuclear tissue due to the degeneration of cells in its apical, micropylar zone (Hejnowski, 1975). In the early stages of development of the ovule, one or a few megaspore mother cells differentiate in the subepidermal layer. After two successive meiotic divisions, one of them produces four megaspores arranged in a line. All four megaspores can reach an advanced stage of development, but only one of them, usually the

innermost one, reaches full maturity and becomes the mother cell of the gametophyte. However, Dupler (1917) mentioned that, in the yew, two or more megaspores can function in one ovule, and thus several gametophytes can develop. Konar & Oberoi (1969) noted that the internal layer of the nucellus, enveloping the developing megaspore, acts as a tapetum; "a haploid tapetum, so characteristic of representatives of Coniferae, does not form (from gametophyte tissue) in the yew, and the developing gametophyte adjoins directly the nucellar cells".

The functioning megaspore grows, increasing considerably in volume, and its nucellus enters the stage of intensive division, forming a multinuclear, haploid prothalium (megagametophyte). Favre-Duchartre (1970) pointed out that the number of free nuclei in the prothalium in the yew, at the time when the first cell walls begin to develop, is 512, whereas in the pine it is over 2000. Archegonia develop in the prothalium, originating from some marginal cells of the gametophyte on the micropylar pole. The cell initiating the development of archegonia first divides into the neck and central cell. The repeated division of the neck cell gives rise to a neck of several cells and the central cell becomes the egg cell. The archegonium is enveloped in a coat of cells feeding the egg cell and after its fertilisation, i.e. when it becomes an embryo (Hejnowicz, 1975). Foster & Gifford (1959) have noted that the development of stamens begins in the summer of the year preceding pollination and fertilisation. Pollen sacs (microsporangia) develop on the lower surface of the stamen. In the yew, the microsporangial initials are in the hypodermal position, and for this reason the epidermis does not participate in producing microsporangia. Sax & Sax (1933) and Favre-Duchartre (1970) have indicated that, in the autumn, pollen mother cells are contained in the microsporangium, and are undergoing meiosis at this time. As the pollen mother cells develop, and then the pollen grains mature, plastids develop intensively and starch accumulates (Auger-Barreau, 1962).

The yew pollen grain is spherical, being 23-30 microns in diameter (Muller-Stoll, 1948). Its wall is composed of a two-layered, nonporous exine, an intermediate layer, and intine (Razmologow, 1963). The grain surface is rough. Its thickest intermediate layer has the consistency of gelatin, which helps in the germination of the grain by swelling and discarding the external layer (Ruguzov, 1972).

Having landed on the micropylar drop at the apex of the ovule, pollen is sucked into the micropylar canal and arrives in the hollow of the nucellus. Soon afterwards (ten or twelve days after pollination), the pollen begins to germinate (Dupler, 1917). Ten days after germination, the end of the pollen tube reaches the female gametophyte. Continuing to grow, the pollen tube increases in volume and destroys the tissues around it. Loze (1966) noted that the ovule-bearing branch of the yew consists of two successive axes. The primary axis is strictly vegetative and develops without any special characteristics. In the axil of one of its subterminal scales a very short lateral secondary axis is initiated, which bears the ovule. The primordium which initiates this dwarf branch is notably larger than the vegetative initials. It produces a series of bracts, then an apical zone, a ring initial and a medullary initial. The apical zone produces the terminal nucellus, and the integument is produced by the ring initial. The aril appears to be produced from the ring initial and is thus a secondary integument. Zenkteler & Cuzowska (1970) in studying the female gametophyte, found that all the cells were multinucleate, ranging from two to ten nuclei per cell. They found that these cells were rich in reserve materials. Lipids dominate throughout the tissue, and protein bodies of varying shape and volume are also present. Starch grains are not so abundant as lipids and proteins. Favre-Duchartre (1970) noted that the time between pollination and fertilisation is about three months, and that it takes another three months for the development of the embryo from the moment of fertilisation. In relation to the size of the seed, the embryo size is very small. It is not fully developed in the mature seed; it has two cotyledon primordia, but the plumule and the root are not identifiable. The cotyledons are covered with a fine cuticle, and stomata develop in their epidermis. The parenchyma is homogenous, and not differentiated into palisade and spongy parenchyma, as in the leaves of the yew. A single primary vascular bundle runs in the central part of the cotyledon.

Sax & Sax (1933), Dark (1932), and Love & Love (1961) have all noted that the yew has twelve pairs of homologous chromosomes, i.e. n=12. Sax & Sax (1933) described them thus: "Ten of them have the primary constriction more or less in the central part (metacentric chromosomes), and two have it closer to one of the arms of the chromosomes (submetacentric). In one of them, the smallest, the primary constriction occurs almost at its end (subterminally)".

Intraspecific variability of the yew.

Kulikov & Ruguzov (1973) studied the variability of anatomical features of the yew leaf in relation to the environmental conditions in the Crimea and Caucasus. They noted that both mesomorphic and xeromorphic structural features were found in the yew leaf, "which are evidently due to its history of development and origin". They concluded that, in the subarid conditions of growth in the Crimea and Caucasus an increase was noted in leaf thickness and the palisade-to-spongy tissue ratio of the mesophyll and a decrease of height of the cells of the upper and lower epidermis, as compared to wetter areas.

This chapter has attempted to cover all aspects of research into this species undertaken thus far, so as to give some idea of the extent of knowledge concerning this tree. Only one paper exists which deals with the geographic (intraspecific) variation of the yew, namely that by Kulikov & Ruguzov in 1973, which is concerned with the variability of anatomical features of the yew leaf in the USSR (above). This confirms the current lack of information on this theme throughout the range of this species.

Before introducing my own particular work on this theme, which aims to make a start in redressing this imbalance, a summary of the more important points on geographic variation within plant species that have been identified by other workers is required, and this is presented in the ensuing chapter.

CHAPTER 3.

Geographic variation in tree species: general considerations.

Of the many terms used in this chapter, perhaps three of overriding importance need to be immediately defined. *Geographic variation* is defined by Squillace (1966) as the phenotypic variation associated with locality. *Intraspecific variation* is phenotypic variation within a species. Therefore geographic variation within a species is intraspecific variation with respect to locality. The term *phenotype* (adj: phenotypic) refers to the observable properties of an organism.

Components of phenotypic variation.

The genetic constitution of an individual is called the *genotype.* But from the moment of fertilisation, the genotype is influenced by the plant's environment, this latter term including both the internal environment of cells, tissues, and biochemical reactions, and the external environment of temperature, moisture, light, and other factors. Thus, the resulting phenotype is produced by the interaction of the genotype in conjunction with the environment. Spurr & Barnes (1973) have expressed this relationship either for the entire organism, or for individual characters, by the formula $P=G+E$, where the phenotype or phenotypic character (P) is the sum total of the effects of the two components (G), the genetic information coded in the chromosomes; and (E), the non-genetic factors including those of the plant and its physical and biotic environment.

By examining three hypothetical situations involving individuals of a given species we can summarise the possible differences between phenotypes as follows :

Situation A.	Situation B.	Situation C.
$P_1 = G_1 + E_1$	$P_4 = G_1 + E_1$	$P_7 = G_1 + E_1$
$P_2 = G_2 + E_2$	$P_5 = G_1 + E_2$	$P_8 = G_2 + E_1$
$P_3 = G_3 + E_3$	$P_6 = G_1 + E_3$	$P_9 = G_3 + E_1$

The phenotypes in situation A illustrate the typical circumstances in the field, in that all phenotypes have different genotypes, and the environments are also different enough to contribute additionally to differences in the phenotypes. Situations B and C illustrate experimental conditions in which either the genotype is held constant (B), or in which different genotypes in a given environment are tested (C). Situation B illustrates plasticity, in which different phenotypes of a single genotype (G) are the result of environmental differences. In nature, the degree of plasticity of a character cannot be measured precisely because each individual has a different genotype, as in situation A. Thus, the extent of environmental modification can only be inferred. For example, individuals of an even-aged stand in rolling terrain may occur in locations ranging from a dry ridge top to a moist, fertile valley. When measuring the height of the trees in the field it may be shown that there is a marked increase of this character as one progresses from the ridge top into the valley. If it is unlikely that there are major changes in the genotypes along the gradient, we may infer that the environment is the major factor controlling the phenotypic differences in height. To determine the plasticity for representative genotypes we would then have to carry out experiments, based on situation B. In situation C, we see that if the environment is the same for all individuals, phenotypic differences are due to differences among genotypes, and the amount of genetic variation can be estimated directly from the phenotypes. In practice, however, the environment cannot be held constant, and we thus approach this ideal by using either growth chambers or relatively uniform field test plots, and a replicated experimental design.

Plasticity.

One of the major difficulties in the interpretation of geographic patterns within plant species is the great plasticity of many plant characteristics (Critchfield, 1957). For herbaceous species, Bradshaw

(1965) has said that, in general, the size of vegetative parts, the number of shoots, leaves and flowers, and the elongation rate of stems can all be considered as plastic, while leaf shape, serration of the leaf margin and floral characteristics are non-plastic. This is in agreement with the comments made by Stebbins (1950) to the effect that the most easily modified characteristic in plant species is the absolute size of the plant and its separate constituent vegetative parts, i.e. the roots, stems, or leaves. "Hardly less plastic", he indicated, "are the amount of elongation of the stem, the number of branches, and the number of leaves, inflorescences, or stems". On the other hand, many other particular plant species characteristics can be modified only slightly or not at all by the environment, and their appearance in the phenotype is almost entirely the expression of the genotype. For example in Potentilla the pinnate character of the leaves, the type of serration of the leaf margins, the shape of the inflorescence, and most of the floral characteristics, such as shape and size of the sepals, the petals, and the carpels are mainly genetically determined.

Spurr & Barnes (1973) have suggested that there is good reason to believe that these features hold true for most tree species, in noting, in general, that characters formed over long periods of meristematic activity, such as stem elongation, are more subject to environmental influences and are more plastic than rapidly-formed characters such as reproductive structures, or than traits such as leaf shape, whose pattern is impressed at a very early stage of development.

Genotypic variation.

The major sources of genetic variability are mutation, and recombination of the genes. Mutation is the ultimate source of variation, having the effect of adding to the pool of genetic variability by increasing the number of alleles, i.e. the different forms of a gene, available for recombination at each locus.

Continuous or polygenic variation is typical for most characters of tree species, this being due to the simultaneous and harmonious interaction of many genes affecting any one character, and the continuous variation arising from non-genetic causes. Wright (1962) has commented that only a few traits are controlled by a single gene, with major effects. An example of this was shown by Franklin (1970), who discovered that chlorophyll deficiency in seedlings of species of the Pinaceae and many other conifers and angiosperms was controlled by one or a few genes. He noted that albino and yellow seedlings usually died soon after germination, but that yellow-green types may turn green and survive in controlled environments.

Although mutation is the ultimate source of genetic variation, it is recombination that spreads mutations and extracts maximum variability from them. Recombination is regarded as being by far the major source of genetic variability of individuals in sexual systems (Spurr & Barnes, 1973; Stebbins, 1950).

The study of intraspecific variability.

Within the geographic range of a tree species, a particular location in which individuals are growing is called a provenance (Callaham, 1964; Wright, 1976). It is noted by Callaham (1964) that the term provenance may refer to either native or planted trees, but its common use is in reference to native trees; moreover, it should only be used in reference to populations of trees, and not to an individual tree. Callaham (1964) also pointed out that it is wrong to use the word in reference to major distributional regions, since trees from one local source might differ from all others, and refined research might show that any such region is made up of many provenances. So, provenance has a biological meaning which is roughly the same as that of the areal term local population. In this dissertation, therefore, the terms local population and provenance will be regarded as being essentially synonymous.

Provenance research aims at defining the genetic (genotypic) and environmental (plastic) components of phenotypic variability between populations of a given species of different geographic origins. Broadly, it involves all studies above the level of the individual and to the level of the species. Langlet (1962) has regarded the investigation of provenances as "...the study of ecological variability within a species, the relationship between this variability and the influence of environment, and the reactions of different populations to transfer to an environment foreign to them..." Callaham (1964) also noted that the scope of provenance research in its broadest sense should include both :

1) studies of inherent adaptive variation related to ecological variability within species; and

2) studies of the inherent nonadaptive differences that might result from isolation or other factors.

Provenance studies began with the comparative cultivation of seedling populations of forest trees originating from environmentally different sites which were pioneered by Duhamel du Monceau in about 1745 (Langlet, 1963, 1971), and the methods used were continued and refined by other workers such as de Vilmorin (1862), Kienitz (1879), Cieslar (1899), and Engler (1908), among others. Cieslar and Engler, whom Langlet (1962) considered to be the pioneers of modern provenance research, working independently in the Alps, determined experimentally that two species of forest trees, namely, Picea abies (Norway spruce) and Pinus sylvestris (Scots pine) were genetically adapted to the climatic conditions of their respective environments.

From his experiments Cieslar (1899) suggested a new term in botanical vocabulary when comparing seedlings of both species from different altitudes, calling them "physiological varieties". He noticed that seedlings from higher altitudes produced smaller plants, which flushed early in the spring and ceased growth early in the summer, whereas seedlings from lower altitudes flushed late and terminated their growth later. His general comment was that among the botanical species, and even among recognised morphological varieties, there are physiological varieties which for their existence have to thank hereditary characteristics acquired under the influence of special environmental conditions during an infinite space and time (Cieslar, 1899).

Engler (1908) expanded the size of area studied by including, in his work on Scots pine, seeds from different parts of Europe; he proceeded to test the material in a series of experimental plots at different altitudes. Using the term "climatic variety", which Cieslar suggested, to emphasise the relation between physiological variability and climate, Engler (1908) summarised the climatic variability of pine as follows:

"...the varieties of this species occurring from south to north, and from the lowlands of central Europe to the upper tree limits in the Alps, form two continuous series that are very similar, and the initial and ultimate sections of which are linked together by a large number of intermediate types. The north German pine can no more be distinguished from the south Swedish pine by any distinct morphological or biological characteristics than the latter can be distinguished from the Lappland pine, just as the Baltic and Livonian pines are nothing but climatic forms of transition between the east Prussian and the Finnish pines. The characteristics of all Scots pines in the different European regions vary always only in quantity. There are no sharply defined borders anywhere".

As Langlet (1962) later pointed out, Cieslar and Engler were the first to demonstrate physiological variability and the phenomenon of continuous change in the morphological characteristics of well-defined Linnean species. Both were working at a time when the Lamarckian theory of species evolution was prevalent; that is, the view was that environmental influences exerted on populations produced differences in hereditary characteristics over long periods of time. Their results suggested that this might be the case. This was the beginning of the debate between proponents of this theory, and those of the Darwinian theory of evolution. However they saw this problem as being a side issue, and Engler (1908) felt that the important thing was to fix the existing conditions of variability of species, noting that, "all available facts clearly indicate that the life functions of the pine and the spruce are minutely related to the climate in their natural habitats and that many of these adaptations are passed on to their offspring. However, we cannot state with certainty how these climatical varieties arose, whether by mutation as explained by Hugo de Vries and natural selection, or by selection of individual variability as per Darwin, or by direct adaption as indicated by Lamarck or even in some other way. But one thing is quite certain, and that is that the climate is the cause of a climatic variety dominating within its particular area".

Genecology.

Although work had already begun in the comparison of plant material from different locational sources in common plots, it was not until 1923 that a descriptive term was applied to it. Turesson, a Swedish ecologist,coined the term genecology in respect of such work, defining it as the study of the variability of plant species and their hereditary habitat types from an ecological point of view. Genecology has more recently been re-defined more precisely as being the study of adaptive properties of any sexually reproducing population race, species, subspecies, or local interbreeding population in relation to its environment (Langlet, 1971).

Turesson was primarily concerned with herbaceous species and, unlike his predecessors, transplanted whole individuals from markedly different habitats to grow them under standard conditions of cultivation. This method of comparative cultivation is often called the common garden technique (Spurr & Barnes, 1973). His technique was to select phenotypes that were usually different in habit and growth and in various morphological characters. He found that these differences were usually maintained in the garden, and therefore concluded that there were genetic differences between the populations studied.

For obvious reasons of practical difficulty, forest scientists engaged in such work cannot transplant whole trees and instead typically collect seeds from selected populations (provenances), and then raise the seedlings in a common garden so as to be able to study the differences between them. From this, they determine (a) whether there is any significant genetic difference between populations in the characters chosen for study; and (b) the amount of genetic differentiation among populations under the environmental conditions of the common garden. Their tests will not directly indicate what mechanisms caused the differences, although these may be inferred; nor will they indicate whether such differences would exist or be of the same magnitude, at another test site. Spurr & Barnes (1973) have commented that a wealth of evidence has been accumulated from such tests which confirms that genetically-based ecological differentiation, called genecological differentiation, is a recurrent feature in plants in general.

From the contemporary evidence available, Huxley (1938, 1939) introduced the term cline to designate a gradation in measurable characters of plant species. This was an important general term, as formerly there had been controversy about patterns of differentiation, and particularly whether they were discontinuous or continuous in nature. Clines, as Huxley described them, might be continuous, discontinuous, stepped, smooth or sloping in various ways (Huxley, 1939). The term does not only apply to genetically-fixed gradation in a character, but can be readily applied to a gradation of phenotypic characters observed along a natural gradient. A study of measurable characters undertaken in the field that is concerned with between-provenance differences of plants in their original habitats might indicate intraspecific variation along natural gradients. When studying the same characters in a common garden, an adaptive cline would have been demonstrated if this variation was found still to exist. If, however, the variation between characters was not repeated in the common garden, then it can be concluded that the clinal gradient was plastic in origin.

The ecotype.

The term ecotype also was first coined by Turesson (1922), who defined it as an ecological unit which represented the genecological response, of a species, to a particular habitat. Investigations of variability within many species soon demonstrated different patterns of variability, thus provoking controversy about the continuous or discontinuous nature of it (Langlet, 1962). The term ecotype also has been used in situations in which genetic differences have not been proved; and, further, each having a different genecological significance. All these usages have caused some confusion, and Spurr & Barnes (1973) have suggested that there are two features of Turesson's definition that are the cause of this confusion.

First, they noted that Turesson's definition referred to a genetic response of a species to a particular habitat. This has been interpreted to mean both local differentiation in specialised habitats, such as meadows and swamps, and large-scale differentiation, such as climatic races, embracing large portions of a species range. Turesson in fact used the term to characterise not only local differences but also in the wider sense, suggesting terms like alpine ecotype, coastal ecotype, and others. The possibilities for ambiguity are obvious: in this sense, the term can only be seen as being a useful concept where it relates to indications of general adaptation of plants to the environment. It has been used in this context by several recent authors. When discussing variation in ponderosa pine (*Pinus ponderosa*), Wells (1964) suggested that the species can be split into ecotypes occupying large geographic areas, within which local differentiation undoubtedly occurs. And Callaham & Liddicoet (1961) had demonstrated that for even a small part of the Californian ecotype, a marked clinal differentiation along an elevational gradient was demonstrated, when they studied the altitudinal variation of ponderosa pine (Pinus ponderosa) and Jeffrey pine (Pinus jeffreyi) after twenty years' growth along a narrow transect on the west slope of the Sierra Nevada, California. They found that the progenies of these two species showed inheritable differences in height and diameter growth associated with the elevation of the seed tree.

Secondly, Spurr & Barnes (1973) have pointed out that it was Turesson's sampling and cultivation methods themselves that culminated in his view of a species being a mosaic of populations, each adapted to distinct habitats. This led him to sample populations from distinctly different habitats, and the genetically-based differences led him to stress the discontinuity of ecotypes. Gregor & Watson (1961) have pointed out that subsequent investigations have indicated that the discreteness of ecotypes had been exaggerated. Because of these problems, the trend today is away from a classification of populations by ecotype and toward the study of the continuous patterns of genecological differentiation within a species (Spurr & Barnes, 1973).

Patterns of ecological variation.

Kozlowski (1971) has commented that shoot growth characteristics among provenances may show a clinal, ecotypic or random pattern of variation. The existence of clinal patterns has already been noted. Truly ecotypic variation, which is characterised by an absence of continuity, occurs only in species which have geographical isolation, and further, have been genetically adapted to a uniform habitat in regard to soil or exposure. The third type of variation is random variation, in which the real differences among stands of a species show no distinct trends at all.

Within the range of a species, combinations of patterns of phenotypic variation often occur. Pinus ponderosa, for example, can be found in isolated groups which show ecotypic variation. But the climate varies continuously throughout the extensive range of this species, and thus clinal variation also can be seen within and between the ecotypes. Combinations in patterns of geographic variation also occur in height-growth characteristics of Pinus elliottii (slash pine), with patterns being largely random in the northern part of the range, and clinal throughout Florida (Squillace, 1966).

In dealing with provenance studies in general, Langlet (1962) has cautioned against the use of the term "ecotype", unless discontinuity of an ecological adaptation has been clearly proved. He suggested that the ecotype concept be replaced by one of ecologic variability, which can be discussed in terms of clines. Taking as an example the International Provenance Tests (1938) on Pinus sylvestris, Langlet emphasised that the geographic variability of this species varied continuously with the variation of the determining ecological influences. He stated that as latitude always, and temperature usually, varied continuously, resulting in ecological variability within a species, geographic continuity also must exist. He did however concede that ecological variability was not always continuous. Discontinuities could arise from genetic or environmental isolation, abrupt environmental change, or radically-different edaphic conditions. Langlet (1959a) reanalysed data collected by Wright & Baldwin (1957), as he did not agree that Pinus sylvestris could be categorised into ecotypes through large parts of its European range, as they had proposed. His own conclusions on the reanalysed data was that the variability of this species was continuous to the same degree as that of the determining environmental influences, which varied continuously. Langlet (1959b) also criticised Sylven (1916) when he distinguished a subspecies of Norrland pine. He concluded that Sylven's data indicated continuous clinal variability and did not justify the subspecies distinction made by Sylven.

Langlet (1962) summed up his feelings quite unequivocally about the classification patterns of ecological variability into a rigid system. "There is no possibility of classifying the manifold patterns of ecological variability in the rigid system of acknowledged sub-divisions of a species. It seems just as futile to construct special terminologies in order to summarise, and at the same time discriminate between, the various patterns which may occur. The ecological variability and its pattern in different species of animals and plants vary in such a multitude of combinations and degrees that every effort to force them into one or another terminological system will inevitably result in violating the facts, and thus substituting artefacts for the real thing".

Langlet's views were supported by Callaham (1962), who wrote, "climate has a continuous and predictable variation, and tree growth is related to climate. The logical deduction follows: tree growth varies continuously in predictable patterns". He went on to say that "individuals of a widespread, uninterrupted species should show continuous variability (Langlet, 1934) or clines (Huxley, 1938) of inherent climatic adaptation. Interruptions in distribution of trees, as by water or mountains, might break such clines, of course. However, man should not come to the naive conclusion that patterns of genetic variation are discontinuous because he has limited perception. He can neither study all populations of a species nor visualise inherent adaptation to the multidimensional interaction of all environmental variables. Discontinuities in factors of the environment, like an abrupt change of soil type, may result in abrupt genetic change, producing ecotypes... However, discontinuities or abrupt changes do not negate the basic premise of continuous variation". He also put on record the evidence for continuous genetic variation, starting in the nineteenth century, and continuing through Langlet's experimental evidence (1934) to more recent studies (Irgens-Moller, 1957) on _Pseudotsuga menziesii_, and Olson _et al._, (1959) on _Tsuga canadensis_, noting that this has become overwhelming.

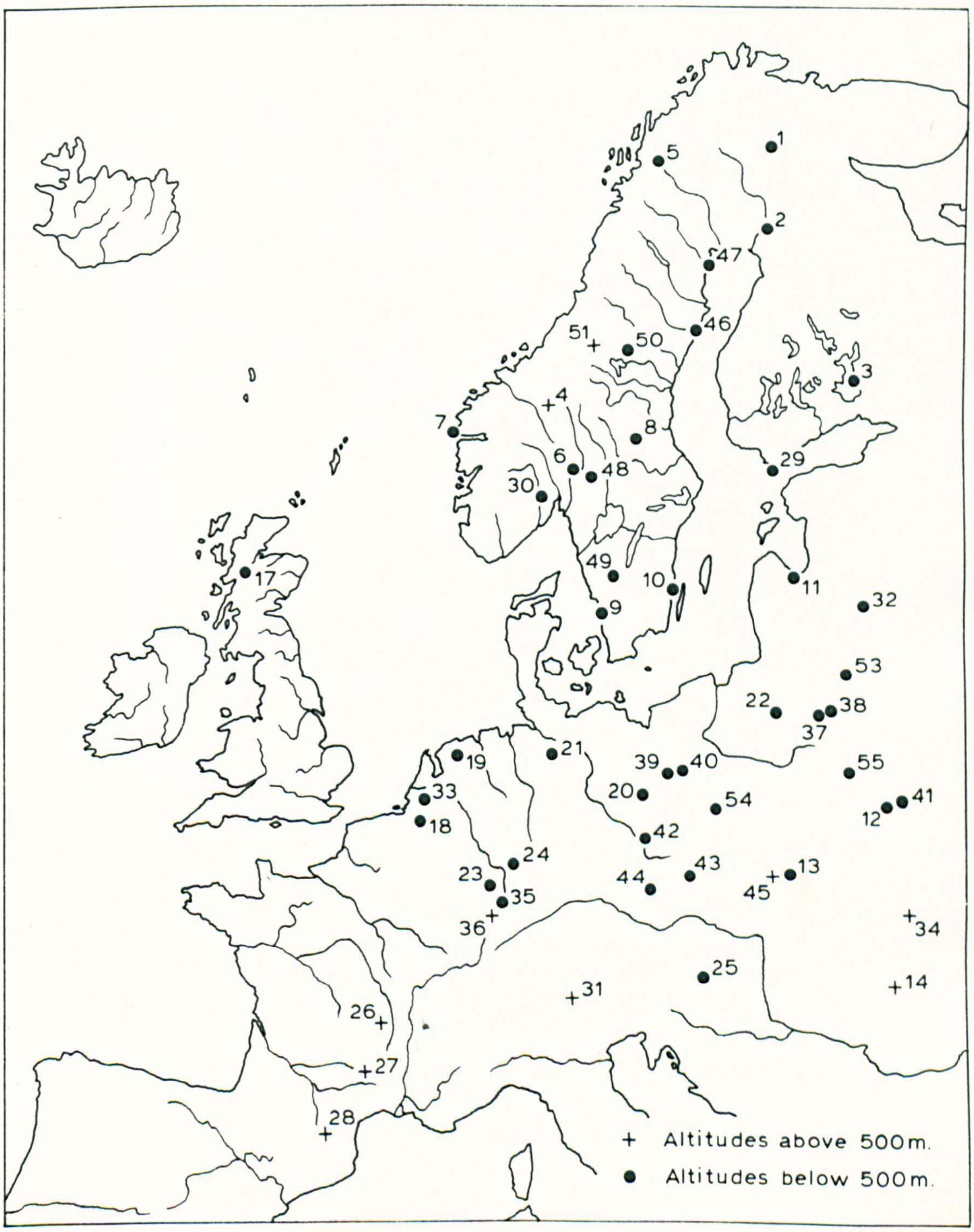
Clinal variation has been demonstrated using many different variables in trees and plants in general. With regard to growth, Callaham (1962) noted that progeny tests are the main tool employed to demonstrate genetic variation, this being identified by bringing different genotypes together under one set of environmental conditions. Replication under a variety of environments will highlight a tree's genetically fixed range of tolerance for influences of its environment, and replication exposes interactions between genotype and environment in growth control. Whenever individuals from many widespread sources are investigated in this way, genetic differences in seeds, germination behaviour, morphology of foliage, stems and roots, periodicity, rate and amount of shoot and root growth and many other characters will be observed (Langlet, 1938; Critchfield, 1957).

Hanover (1963) has studied nineteen races of Pinus ponderosa which were planted in a common garden. They showed continuous variation in the date of leader growth initiation, date of growth cessation, total seasonal elongation, duration of growth, length of dormant apical bud and growth rapidity. Neither beginning date, relative rapidity, duration of growth, nor ending date were related to total height growth, but a strong positive correlation existed between bud length and total elongation. Sources representing geographic regions, in which September-June precipitation was low, began growth later and grew less than sources from areas of high precipitation. The period at which each tree and progeny achieved their maximum rate of growth was related to local temperature.

In studies conducted in Idaho, Oregon and Washington, Squillace & Silen (1962) have confirmed the existence of differences in shoot growth of 22 widely-separated seed sources of Pinus ponderosa. Much of the inherent growth variation was associated with variations in characteristically continuous and specific climatic factors. A strong east-to-west cline in growth differences was identified. This gradient was clearly related to seasonal distribution of moisture. Trees from areas with large amounts of autumn, winter and spring rainfall, or from areas which received much of their total rainfall during those seasons, had inherently rapid growth rates. A moderate latitudinal cline was found in a pattern related to temperature. A moderate altitudinal gradient in growth was also identified. Trees from high altitudes usually grow more slowly than those from low altitudes. This pattern appeared to be correlated with cool temperatures and unfavourable moisture conditions at high altitudes.

Burley (1966) has reviewed seed source variation in many characters of both Pinus elliottii and Pinus taeda. Variation was more pronounced in Pinus taeda than Pinus elliottii, but in both species within-provenance variability often obscured between-provenance differences. For some characters, provenance variation was random, but for most traits the patterns of variability tended to be clinal, in respect of latitude and longitude, resulting in a trend from northwest to southwest.

To demonstrate the clinal nature of variables in Scots pine, Langlet (1962) examined dry-matter content at the time when the species undergoes changes so that it can better endure the winter climate. The dry-matter content increased progressively the colder and the more northerly was their native habitat (Langlet, 1934; 1936; 1943). The existence of this cline was demonstrated further in the international provenance test of 1938, in which 52 provenances of Scots pine were examined. The provenances selected stretched from the north of Norway and Finland down to Rumania and the Pyrenees, and from Scotland in the west to the then eastern parts of Poland (Fig 3.1). Through adjusted mean monthly temperatures, the part of the year with the mean day and night temperature of at least 6°C was determined. Also, the day-length of the first day of this period was noted.



<u>Fig 3.1.</u> The provenances of Scots pine (<u>Pinus sylvestris</u>), for the I.U.F.F.O. international test, 1938. (after Langlet, 1962).

Although this daylength was of no special significance, it combined in one criterion the two factors of temperature and light. Regardless of the implication of the daylength, the study showed that there was a very close correlation with the dry matter contents of the two- and four-year-old pine plants (Fig 3.2), in which "the correlation coefficient R is no less than 0.98 or, in other words, about 97 per cent of the original variance is removed by eliminating the influence of the daylength during the first 6°C day" (Langlet, 1959a). Also, it followed that the variability was continuous, according to the variation of the determining ecological influences. As latitude always, and temperature mostly, varies continuously, this resulted in an ecological variability within the species; and one that was also continuous geographically.

Callaham (1964) has summarised the five basic steps needed in the study of geographic variation in tree species; he proposed that

(1) a summary of available information on variability within and between populations should be collected; then,

(2) decisions concerning the objectives and procedures can be made in the light of known and expected patterns of variation; then,

(3) an experimental design can be formulated for the collection of samples from many provenances to accomplish the objectives; then

(4) an investigation of provenances along a natural gradient should be carried out to determine patterns of variation; and, finally,

(5) an establishment of seed source tests on representative sites can be set up for a few of the most promising or typical provenances.

He concluded that a combined approach using both natural and seed source studies should be the most efficient way of comparing provenances.

Environmental influences and their relationships to ecological differentiation.

Marked genetic differences in growth and other characters usually are expressed when populations are grown at latitudes or elevations substantially different from those of their native habitat. Limiting

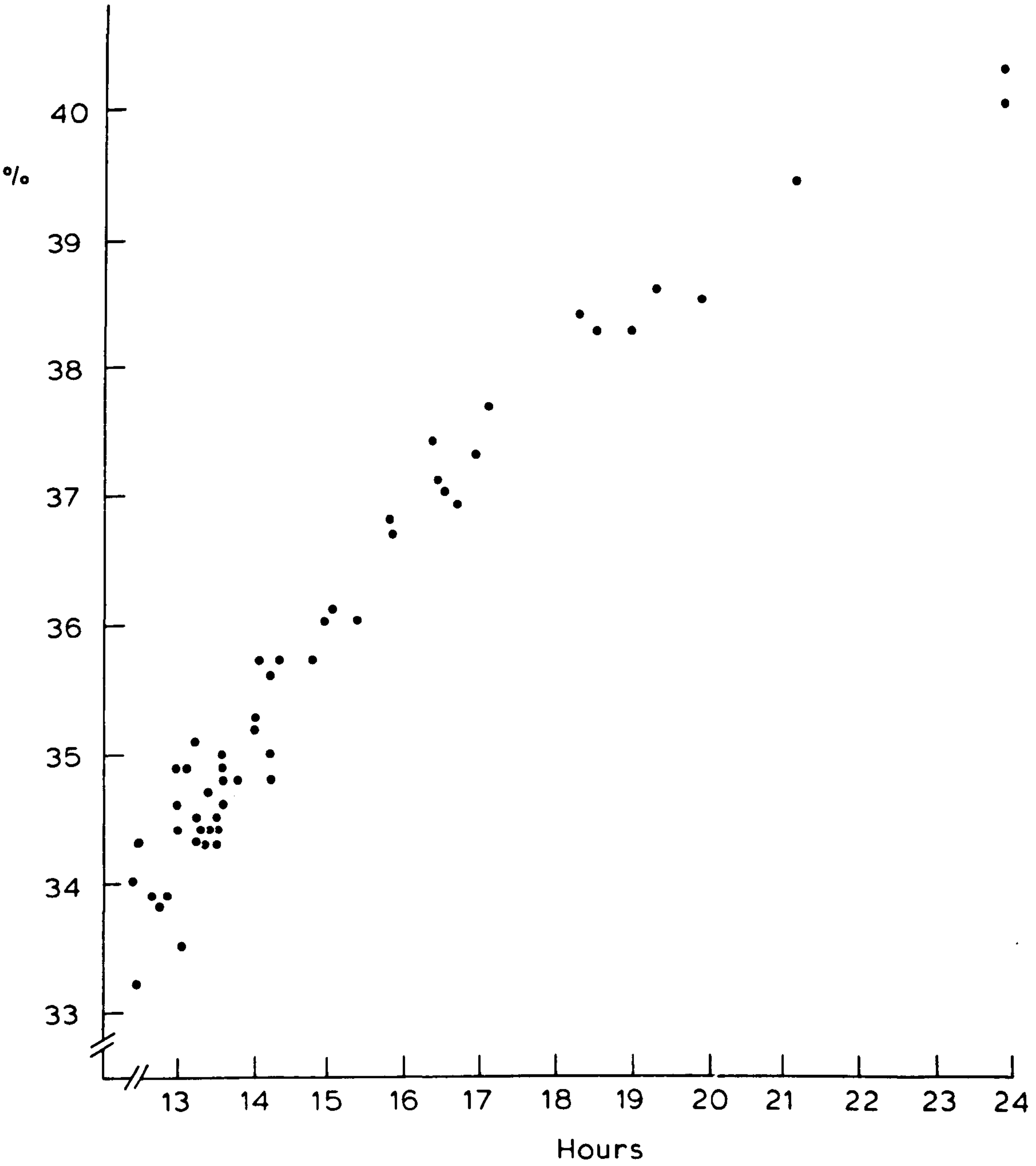


Fig 3.2. The relationship between dry-matter content and the length of day light of the first day of the year with an average normal temperature of +6°C. at the native habitats of the 52 provenances.

(after Langlet, 1962).

environmental influences such as temperature, thermoperiod, photoperiod and the amount and periodicity of rainfall are important factors which act on growth rate and related characters, as they affect the length and nature of the growing season in a tree's native habitat.

Photoperiodism is a response in plants to the timing of light and darkness and is usually expressed as a day-length factor. In almost all genecological tests, populations are grown in day-length regimes different from those that they would experience in their native habitat. In the case of black cottonwood (Populus nigra), for example, individuals of high latitude provenances ceased height growth in June when planted at a low latitude site near Boston, Massachusetts, while southerly populations, which had been moved north to the test site, continued height growth until September and October (Pauley & Perry, 1954), (Fig 3.3), in fact some individuals only ceased growth when their terminal shoots were killed by severe frost. Although a significant, genetically-based, clinal response was shown in relation to latitude, this was not simple or direct, for it may also be shown that there was substantial variation among provenances of black cottonwood growing between latitude 44° to 48°N. It was pointed out that among these provenances there was an elevational range of from sea level to 1525 metres, and thus a marked difference in, the length of growing season, aspect or microsite conditions was displayed. Pauley & Perry (1954) found a clinal, genetic adaptation to the length of growing season within the narrow latitudinal range of 45° to 47°N, (Fig 3.4), and suggested that this probably explained much of the variability not accounted for by latitude. Spurr & Barnes (1973) have noted that the interrelationship between elevation and latitude has rarely been recognised in genecological studies, and that almost without exception correlations of cessation of growth or plant size and latitude of source are confounded by elevational differences. Thus Wiersma (1962) found that, when he modified a formula developed by Langlet (1936) for Swedish conditions to include

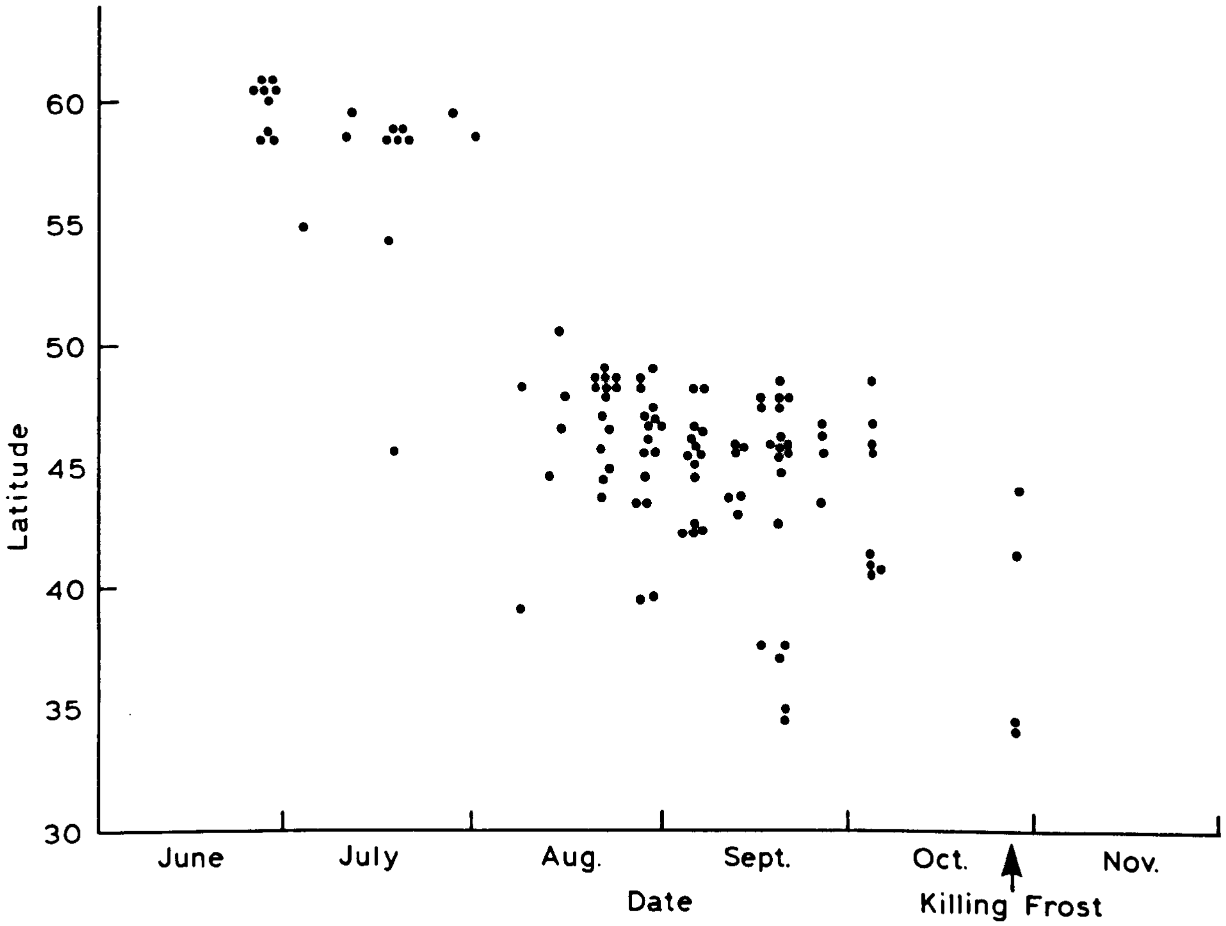


Fig 3.3. The relationship between latitude and time of height growth cessation in black cottonwood.

(after Pauley & Perry, 1954).

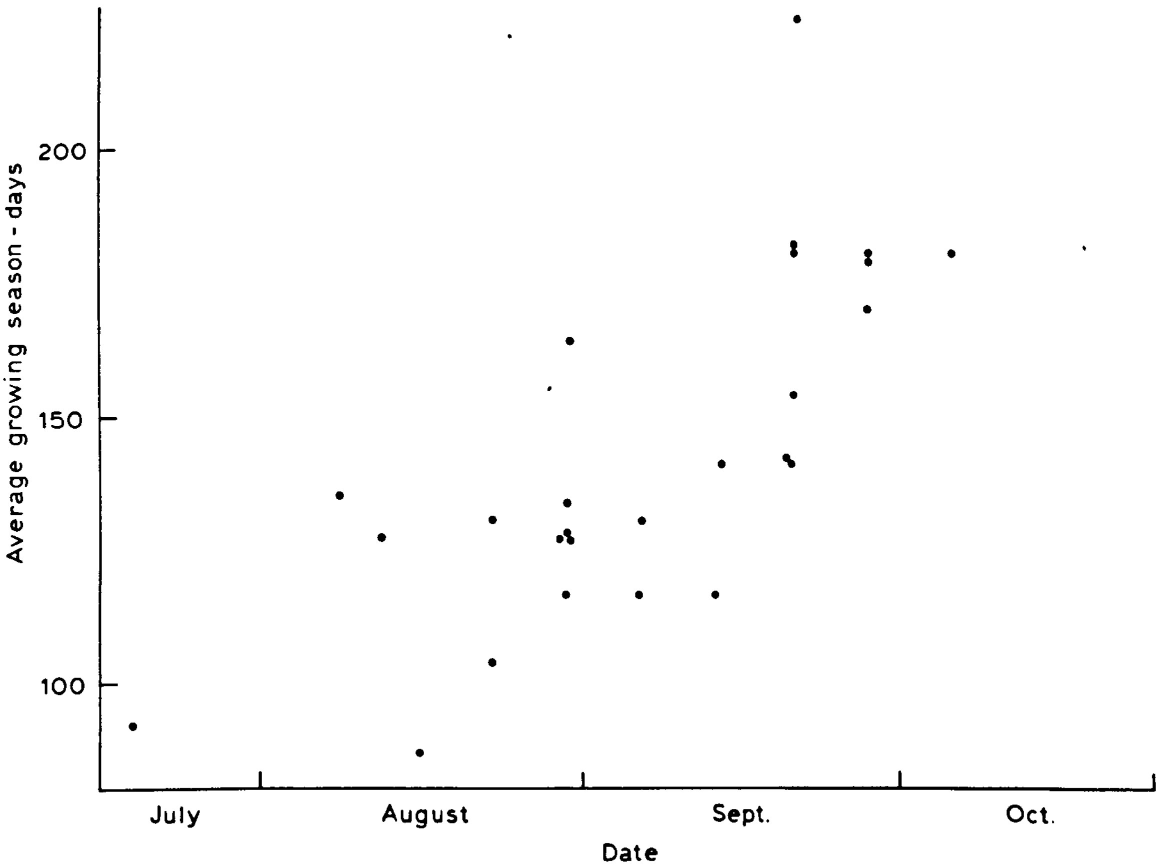


Fig 3.4. The relationship between length of growing season and time of height growth cessation in black cottonwood. (after Pauley & Perry, 1954).

elevation, a displacement of one degree north in latitude was equivalent to a displacement of 100 metres upward in altitude. Using this adjustment Wiersma (1963) recomputed correlations of latitude of source and various characters from published papers and found a greatly improved relationship. Sharik (1970) carried out the same sort of adjustment in the Appalachian Mountains, U.S.A. where he found a relationship of one degree of latitude as being equivalent to a displacement of 189 metres. Using this adjustment, he found that there was a substantial improvement in the correlation of latitude of source and cessation of height growth for yellow birch (*Betula alleghaniensis*) and black birch(*Betula lenta*) populations.

Vaartaja (1954, 1957, 1959, 1960, 1961) tested the hypothesis of photoperiodic ecotypes in forest trees; using the term ecotype "in the widest possible terms", he collected seeds from latitudinally diverse sources. He established the common occurrence of ecotypes in tree species with wide north-to-south ranges in the northern hemisphere. At least 15 out of the 17 species tested in 8 out of 9 genera (*Acer*, *Betula*, *Fraxinus*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga* and *Ulmus*) contained photoperiodic ecotypes. Greenhouse tests showed that the farther north the seed source, the greater was the response to test conditions, and the longer the maximum day length which inhibited growth. Interactions of seed source and photoperiod were shown in the duration of shoot elongation, the amount of terminal shoot elongation, and the development of lateral shoots. Under certain photoperiods, the shoot elongation of northern seedlings ceased early, whereas it continued for a long time in southern seedlings. Heights and shoot weights of northern seedlings were much lower than those in southern ones under some photoperiods, but not under others.

Similarly, Nienstaedt & Olson (1961) collected seeds of *Tsuga canadensis* from 30 locations throughout its latitudinal, longitudinal and altitudinal range. The resulting seedlings were grown under varying photoperiodic regimes. The results showed that for any given photoperiod, seedlings from a region with a long frost-free season tended to form buds and stop shoot elongation later than those from an area with a short frost-free season. The 30 seed sources clearly showed a clinal variation in photoperiodic response.

With the general establishment of the fact that genetic differences in plant size and growth cessation in trees are related to latitude, for example, Kriebel (1957) in the case of sugar maple (Acer saccharum), Wright & Bull (1963) in the case of Scots pine (Pinus sylvestris), Genys (1968) in the case of Norway spruce (Picea abies), Mohn & Pauley (1969) in the case of cottonwood (Populus deltoides), Fowler & Heimburger (1969) in the case of eastern white pine (Pinus strobus), and Clausen (1968) in the case of yellow birch (Betula alleghaniensis), and height above sea level, for example, Callaham & Liddicoet (1961) for ponderosa pine (Pinus ponderosa) and Jeffrey pine (Pinus jeffreyi), Genys (1968) for Norway spruce (Picea abies) and Hermann & Lavender (1968) for Douglas-fir (Pseudotsuga menziesii), one may assume that photoperiod is a timing device of major adaptive significance to this phenomenon. The consistency with which given individuals of many species cease growth from year to year reinforces this conclusion.

Thermoperiodicity is the effect of temperature differences between the day and night periods upon plants, and has been studied in relation to growth in trees. Kramer (1957, 1958), for example, grew Pinus taeda seedlings with various combinations of day and night temperatures. He found that shoot growth was related more to the differences between day and night temperatures than to the actual temperatures applied, and that maximum shoot growth occurred at times of greatest difference between day and night temperatures. Thus shoot growth was least when nights were as warm as days.

Shoot growth adaptation to thermoperiod has also been studied in Pinus ponderosa by Callaham (1962), by means of growing seedlings from different parts of its range in combinations of three day temperatures (30°, 23° and 17°C) and three night temperatures 22°, 14° and 7°C), under constant daylength conditions. He found that there were differences in response from the different geographic sources to the temperature combinations. In general, seedlings from east of the Rocky Mountains grew best with high night temperatures. Seedlings from the southwestern source grew best with cold days and warm nights, and Pacific Coast seedlings showed vigorous growth at lower night temperatures.

Perry (1962) worked along the same lines when studying *Acer rubrum*, and found that the day and night temperature necessary for maximum shoot growth was different for each provenance. In general, it corresponded to the day and night temperature of the site of seed collection, and he concluded that the day temperatures required for optimal growth should be higher than the night temperatures.

The close association of various adaptive responses with different limiting factors of the native environment has been shown for Douglas-fir (*Pseudotsuga menziesii*) seedlings in Oregon, USA, by Irgens-Moller (1968). The late cessation of growth of coastal provenances at the test site was related to the long growing season of their native habitat. In the northern Rocky Mountains, low summer precipitation and a short frost-free season ~~was~~ were suggested to be responsible for the early onset of dormancy of these provenances. Early dormancy was displayed, although soil moisture was kept in ample supply, indicating the lack of a direct effect by moisture stress. Photoperiod was again shown to be important, since only long photoperiods could keep the plants actively growing. Sources from Arizona and New Mexico grew intermittently: they entered a short period of dormancy, after which the majority resumed growth before entering winter dormancy. The distinct intermittent growth in the southwestern provenances, and its absence, in northern Rocky Mountains provenances, was explained by the differences between the seasonal distribution of precipitation in the two areas. "A relatively high summer rainfall is received in Arizona and New Mexico, as compared to Northern Idaho (64% of total annual rainfall, as compared to 29%). The intermittent growth may permit seedlings to go into early dormancy during periods of soil moisture stress, and then resume growth quickly when moisture is abundant" (Irgens-Moller, 1968). Seasonal distribution of precipitation also may be an important factor affecting the adaptation patterns of ponderosa pine (Pinus ponderosa) (Squillace & Silen, 1962) and slash pine (Pinus elliottii), (Squillace, 1966).

Sampling procedures in natural populations.

One other factor of importance to provenance studies needs to be discussed, and that is the question of sampling procedures. Critchfield (1957) has noted that within limits imposed by the scale of a study, the number of samples represents a compromise between the intensity of sampling in the local population and in the individual plant. In an exploratory study, this compromise is usually reached by a series of arbitrary decisions concerning the number of samples, the size of the population sample, and the size of the within-plant sample. The determination of the size of the local population sample (the provenance) is related to the amount of variation within populations, and to the scale of differences between populations. As Woodson (1947) has pointed out, "adequacy of sample size is determined by the unique degree of variability of each organism and can be determined in each case only after special observation". Critchfield (1957) continued by saying that if several characteristics were studied, they were likely to differ in degree of variability; even so, different sample sizes for different characteristics can achieve the same level of accuracy in distinguishing between populations. If the variability of each characteristic based on a different plant part were known in advance, sampling efficiency could be increased by relating the sample size of each part to the variability of the character within and between local populations. Since this information is seldom available, the expedient usually followed is a relatively arbitrary determination of sample size.

The problem of determining sample size also is closely related to the problem of delimiting the size of group to be sampled, i.e. the local population. Anderson (1941) has indicated a solution to this problem: "Lacking the precise information on what an actual interbreeding population may be, one can only use his biological judgement in selecting for each case an area which presents uniform conditions for that species and make his collection from that area". Also, within the census population, made up of those individuals possessing the organs to be sampled, random-sampling techniques are a prerequisite of the statistical estimation of population parameters.

With regard to sampling tree individuals within populations, Critchfield (1957) noted that the large size of the plants, and the delayed production of reproductive structures, may greatly limit the population that can be sampled readily and effectively, particularly if reproductive structures are included. Thus sampling may necessarily be confined to isolated or semi-isolated individuals with accessible organs. This restriction introduces a possible bias into the estimation of population characteristics and the evaluation of differences between populations. However, this bias is more likely to be of importance in the estimation of population parameters than in the comparison of population samples, if sampling is confined to approximately the same fraction of each sample. Although the problem of estimating the characteristics of the individual phenotype exists in all traits in which a single individual exhibits repeated expression of a trait (for example, egg size in chickens); it is most prevalent in plants, as a consequence of the large number of like parts produced by the open system of growth. Thus any leaf characteristic has as many expressions as there are leaves on a plant. The phenotypic expression of a leaf characteristic in an individual plant must therefore be estimated by some kind of sampling of the population of leaves. Most quantitative plant characteristics fall into this category, although a few, such as those describing the dimensions of height of the entire organism, clearly have a single expression in each organism.

Geographic variation between natural populations (provenances).

As has been pointed out above, a study of intraspecific variation of a species for a character or characters should include an investigation of variation along a natural gradient, and seed source tests (Callaham, 1964). In this way, genecological differentiation and the plasticity of characters can be studied, first by identifying variation, and then by looking at the same characters in a uniform or controlled environment. This point is emphasised here, as in a natural gradient survey of populations the intention is to identify patterns of variation.

Within the literature, as might be expected, the study of intraspecific variation based on biometric measurements in natural populations involves similar, simple techniques, as, for example, the use of a ruler for measuring the lengths of shoots, eye-counting for the number of leaves on a shoot, and lower power microscopes or bioscopes for various measurements that cannot be achieved by the naked eye, such as the width of needles. The differences that can be seen in completed studies lie in the methods of analysis. For example Critchfield (1957), determined the significance of the difference between two sample means graphically by aligning a straight edge vertically at the end of a bar representing four standard errors of that sample. If the corresponding bar of another sample did not touch the straight edge, the differences were said to be significant, and if two bars overlapped the difference was said to be insignificant. Squillace (1966) employed the analysis of variance when studying variables singly, and the Mahalanobis' generalised distance function for the examination of groups of traits simultaneously; and Jeffers & Black (1964) used three forms of multivariate analysis on their data, namely the Q technique, discriminant analysis, and princip~~le~~al component analysis (PCA). While there are indeed many ways of dealing with data of this kind; it is not the intention in this presentation to survey comprehensively the various techniques employed. It will however be of interest to mention some of the conclusions drawn from examples of this type of work.

In 1964, Jeffers & Black measured nineteen biometric variables on each of nine provenances of <u>Pinus contorta</u> in North America. Their objectives were (a) to test the discrimination between the broad groups of inland and coastal provenances of the tree; (b) to test discrimination between provenances within the inland and coastal groups; and (c) to construct a classification of the nine provenances, and to relate this classification to meaningful physical or botanical properties. It was found that there was a marked division of the nine provenances into the coastal and inland groups, and that there was a closer degree of similarity between the two Canadian provenances than the two Washington coastal provenances, and two of the inland provenances. These conclusions were drawn from two multivariate techniques, namely the Q technique and discriminant analysis; however, the main conclusions on the classification of the nine provenances were drawn from another multivariate technique, i.e. principal component analysis (PCA). From this it was found that the nineteen variables in the analysis were not independent, and that two broadly correlated groups were evident. The first ~~was~~ comprises of leaf breadth, leaf thickness, thickness of the hypodermis, cone length, seed and seed wing dimensions, and the second of leaf length, number of resin canals, and cone breadth. Other variables, such as ring width, width of autumn wood, and the percentage of autumn wood were shown to link these two groups, i.e. ring width was correlated with cone breadth, width of autumn wood with leaf breadth, cone breadth with leaf length, and percentage of autumn wood with the thickness of the abaxial hypodermis.

It was also found that when these correlations were expressed as linear combinations of the original variables in the analysis, three components were enough to account for almost 80% of the variability contained by all nineteen variables. The first component did not correspond to the division of the provenances into coastal and inland origins, and therefore the authors suggested that a more important dimension than the one above could be used to classify the provenances. The second component corresponded most closely to the classification of the provenances into coastal and inland provenances, while the third component cut across this classification. It was concluded, therefore, that while the two preliminary analyses confirmed that there was some validity in the classification of provenances into coastal and inland origins, a more realistic classification existed as shown by the PCA analysis in the sense that it accounted for a greater proportion of the botanical variation. Finally, it was noted that from this study strong intercorrelations have been found between the variables, and therefore many fewer than nineteen variables needed to be measured to apply this classification further.

In studying the cone sizes and weights and seed weights of Douglas-fir (Pseudotsuga menziesii) from nine provenances in the USA Sorensen & Miles (1978) found that they were split into three regions, namely (a) coastal ranges, (b) Cascade ranges, and (c) central Oregon. Three locations were used from each of these regions. They found that differences among regions for the cone traits, and regression coefficients for change in cone and seed weights with distance from the ocean, were significant. Cone size and weight decreased, seed weight increased, and the regression coefficient of seed weight on cone weight, based on trees within regions, increased with distance from the ocean. This geographic variation in cone and seed weight was compared with the variation in phenology of the cone and seed development. This indicated that where relatively large seeds were important to regeneration success and the growing season was short, Douglas-fir showed at least three changes in the timing of development as compared with milder sites; first, the cone growth period was reduced more than the seed growth period; secondly, the overlap in time of the developmental cycles of the cone and seed was increased; and thirdly, the cones and seeds grew during a greater portion of the growing season.

Barnes (1975) studied the phenotypic variation of leaf, bud and twig characters of the trembling aspen (Populus tremuloides) in North America. He found that there was considerable variation among the 29 populations measured. For example, in the case of leaves, he noted that the size, shape and number of teeth showed important differences, indicating that along a south-north gradient, leaf size, and primarily blade width, decreased markedly. This south-north trend was reversed farther to the west where small leaves were characteristic of central and southern Oregon populations, with large leaves typical of populations from western Washington and Vancouver Island. He also noted that the largest leaves were found among these latter populations, which were at the highest latitudes and the lowest elevations in the study, in areas characterised by a mild, moist climate and a long growing, season. He concluded that the favourable growing conditions may explain the marked size difference between these populations, and those in the more arid climates east of the Cascade Mountains in Oregon, and in southern Idaho. Large leaves are also prominent in southern and central Utah, and may be due in part to the high elevation there, with its increased rainfall and cooler climate. Using this and a multivariate analysis of the variables, he showed that there was a clinal south-north gradient in leaf shape, size and tooth number.

Schoenike (1976) studied the geographical variations in jack pine (Pinus banksiana) in North America, for a number of morphological traits of crown, bark, wood, foliage, and cones. This was a large study, in which material from 1970 trees in 90 sampling localities was collected across the range of jack pine, measuring 33 traits from each tree. He found that all the traits showed significant differences associated with the geographic sources of the material, noting that the amount of variation attributed to locality was particularly high for bark thickness, needle length and width, number of stomata per leaf surface, and cone seritony, while between-locality variation was relatively weak in needle curvature, needle cross-sectional thickness, and the number of resin ducts. Individually, traits showed mainly a mixture of continuous and irregular patterns of variation. The continuous clinal patterns were especially noted in an area from the Lake States to the northwest, while often in another area of its range there were two or three places where high and low trait magnitudes existed. When an attempt was made to correlate individual traits with environmental factors, only low to moderate degrees of association were found for most traits. However, "relatively high correlations" were noted for precipitation and bark thickness, precipitation and needle length, and latitude and needle volume and stomatal counts. It was also found that a multivariate test reinforced the evidence shown by the individual trait variation. Gradients were found to be steepest in the area connecting the lower Great Lakes region to those in western Canada.

Simak (1967) studied the seed weight of larch (Larix decidua) from different provenances in Europe. Samples were taken from 66 autochthonous and 42 introduced provenances of larch, and the seeds were selected from each source in respect to filled, empty and insect-attacked, with the help of x-ray radiography. Provenances were divided into seven geographical regions; Polish, Sudetian, Slovakian, Rumanian, Eastern Alpine, Central Alpine, and Western Alpine. A thousand-grain weight

(TGW) was then determined for each of the above seed types from each provenance. He found that the TGW values for the filled seed lay between 3.73 and 10.81 grammes, and that there was a direct relationship between the TGW and the average altitude of a region. The differences among the regions are gradual, i.e. the greater the difference between the average altitudes of two geographical regions, the farther apart lie the TGW values. In the case of the empty seeds, he found that there was a tendency that with increasing altitude of the provenances, the relative weight of the empty seeds also increased, with the TGW of the empty seeds being about 70% of that of filled ones. The TGW value of the insect-attacked seeds was about 74.4% of that of the filled ones, with this type of seed occurring chiefly in the provenances from low elevations. Finally, he noted that the TGW values do not change even after the provenances had been introduced into other localities; thus, he suggested that TGW is strongly-fixed genetically and only slightly modified by external factors. He concluded that the TGW variation among regions is clinal in character.

Squillace (1966) has studied the geographic variation of slash pine (Pinus elliottii) in the USA, noting that the main purpose of this study was the determination of patterns of geographic variation for a number of morphological and physiological traits of cones, seeds, foliage and seedlings, and the determination of the causes of such variation where it exists. He found that most of the traits studied showed significant differences associated with the geographic source of the material. In the parental data, the stand-to-stand variation was 'relatively strong' for cone dimensions, seed yield per cone, seed weight, needles per fascicle, needle length, fascicle sheath length, and hypoderm thickness. In the progeny data, stand variation was found to be strong for total height, stem diameter, needles per fascicle, needle length, germinability, speed of germination, and cotyledon number. He noted that most of the traits studied showed some type of clinal variation, containing one or more trend reversals or fluctuations, suggesting that the clinal patterns result from adaptation to gradients in environmental factors. The trend reversals, he suggested, were probably due to the existence and interaction of two or more factors affecting each trait. The random variation found in a few instances was possibly due to genetic drift. The general north-south pattern of many traits probably resulted from the latitudinal gradient in winter temperatures (or similar factors) and in the seasonal distribution of rainfall; an interaction of these could cause the reversals. It was also found that longitudinal variation existed in some of the traits in the north, but this was not as pronounced as the latitudinal variation.

Ruby (1967) has studied the variation of parental characters of Scotch pine (Pinus sylvestris) in Europe. He noted that variation patterns of the cone, seed, and leaves in the parent populations were most definitive in seed length, cone length, the ratio between cone length and length of the largest apophysis, weed width, closed cone width, leaf length, width of the largest apophysis and the open cone width. It was noted that the variation pattern based on these eight characters indicated that Scots pine populations could be separated into eleven regions, based upon the significant differences existing between the regional means. These regions were; (1) Northern Scandinavia in the vicinity of the Arctic Circle; (2) Central and Southern Scandinavia, (3) Northeastern Germany and Czechoslovakia; (4) Western Germany, Eastern France, and Belgium; (5) England; (6) Yugoslavia; (7) Northeastern Greece; (8) Scotland; (9) South central mountains of France; (10) Northern and central Spain; and (11) North central Turkey.

Some other works along these lines are those of Carlisle (1955) on Scots pine (Pinus sylvestris),Critchfield (1957) on Pinus contorta, Wettstein (1958) on Scots pine, Thorojornsen (1961) on loblolly pine (Pinus taeda), and Forde (1964) on Pinus radiata. All these authors describe the variation of morphological characteristics of each particular tree studied in similar ways to those described above.

No such work has yet been attempted for Taxus baccata, and it is the intention of the writer in this study to fill this gap, within the areal confines of England. Accordingly, in the next two chapters, a description of the variation of morphological characteristics of this species is given, by means of a biometric investigation of the phenotypic variability of naturally-maintained populations of the yew in this country. It should be finally emphasised that a study of this kind is strictly a study of variation patterns, and in itself cannot measure directly the environmental or genetic components of that variation.

CHAPTER 4.

Variation in morphological characteristics of Taxus baccata L.

1. Materials and methods. Principal Components Analysis.

The main aim of this study was to determine the extent of morphological variation in naturally-maintained local populations (provenances) within and between regions in the north of England, and to compare these with two southern populations. At the outset it should be noted that for the purposes of this dissertation hereinafter the word population will be used as being synonymous with local population (i.e., provenance).

It has previously been determined that the only pure yew woods to be found in England lie in the south, for example at Butser Hill and Kingley Vale (Watt, 1926) with the latter being described as being "the finest yew forest in Europe" (Williamson, 1978). Other populations in England are found in mixtures with other species, as in the other main area of the north-west, or as small groups as in other parts of the tree's range (see Browicz & Gostynska-Jakuszewska, 1969).

The 'probable native distribution' of the yew in Britain already has been described in Chapter 1, after Perring & Walters (1962). Fig 1.3 shows that the yew is present in the south of England, the Welsh border country, the southern tip of the Pennines and the northwest of England, and that towards the northeast of England naturally-maintained populations of yew become increasingly rare. It was from this basic information that the regions for study were identified, as follows.

As there was no previous information about the tree's intraspecific variability, which might have indicated general rules that could be followed, the experimental design in this study was based on intuitive thinking from preliminary, personal observations. The methods used are based on the comments made by Critchfield (1957); within the limits imposed by the scale of study, the number of samples represents a compromise with the intensity of sampling in the population and the individual plant. In any exploratory study, as detailed in the previous chapter, this compromise is usually reached by a series of arbitrary decisions concerning the number of populations, size of population sample, and size of the within-plant sample.

(A) Materials and methods.

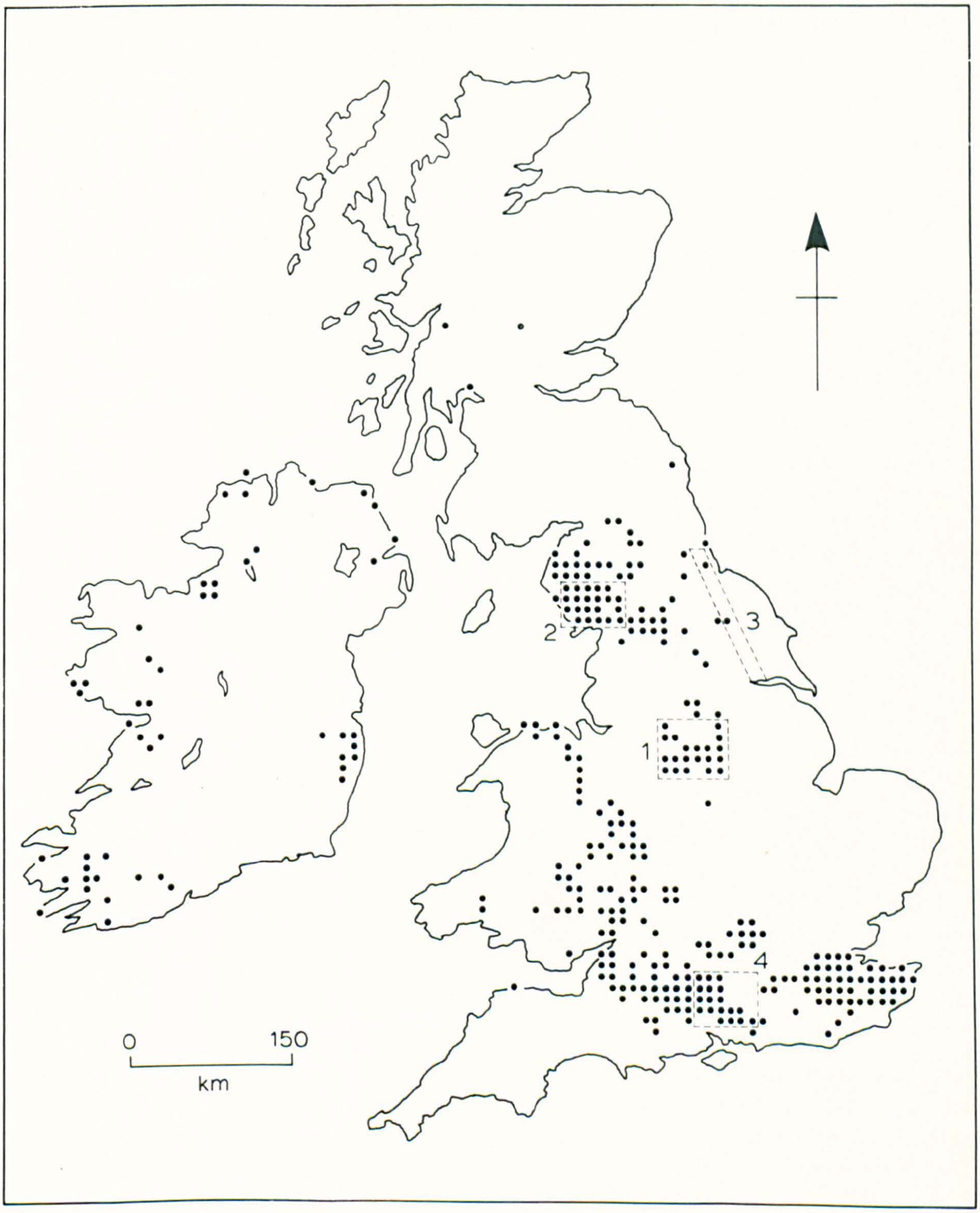
(B) Selection of regions.

From Fig 1.3., which shows the 'probable native distribution' of the yew (Perring & Walters, 1962), four distributional regions were ~~identified~~ selected, three from the north and one from the south (i.e. region 1, Derbyshire; region 2, northwest England; region 3, northeast England; and region 4, southern England; Fig 4.1). Despite the evidence provided by this computerised map, the field location of yew tree populations proved to be difficult to achieve. However, they were identified and recorded within the three northern regions (Table 4.1), a stand being considered to be a population if it contained 25 trees or more. In regions 1 and 3, i.e. in Derbyshire and the northeast respectively, this was achieved by personal field exploration, as it was found that local knowledge could not in itself furnish the exact positions of populations. In region 2, i.e. Cumbria, there are many yew tree populations, and the sites chosen had been previously identified as being particularly important by the Nature Conservancy Council (pers. comm. R. Bunce).

(B) Selection of populations.

It was decided that two populations per region would be used in this study, so as to be able to examine within region as well as between region differences. Accordingly, within each northern region, all identified populations were assigned numbers and by the use of random number tables those chosen for detailed study were subsequently selected. These were as follows: region 1, Ravensdale (Ra:NGR SK 172732) and Overton Hall (Ov:NGR SK 344622); region 2, Scout Scar (Ss:NGR SD 485921) and Yew Barrow (Yb:NGR SD 348873); and region 3, Brantingham (Br:NGR SE 943299) and Guisborough (Gu:NGR NZ 601135) (Fig 4.2). It was also decided that two populations from

Fig 4.1. The four regions used in the study.



Legend: 1 = Derbyshire
2 = Northwest England
3 = Northeast England
4 = Southern England

Table 4.1. Table of recorded stands of yew tree populations in the north of England.

Region	Site Name	Grid reference
1	Milldale	SK 148550
	Tissington Spires	SK 147521
	Ravensdale	SK 172732
	Overton Hall	SK 344622
	Matlock Bath	SK 293583
	Great Shacklow Wood	SK 175698
2	Scout Scar	SD 485921
	Yew Barrow	SD 348873
	Nr. Backbarrow	SD 352844
	Whitbarrow Scar	SD 441864
3	Brantingham	SE 943299
	Guisborough	NZ 601135
	Warter	SE 848499

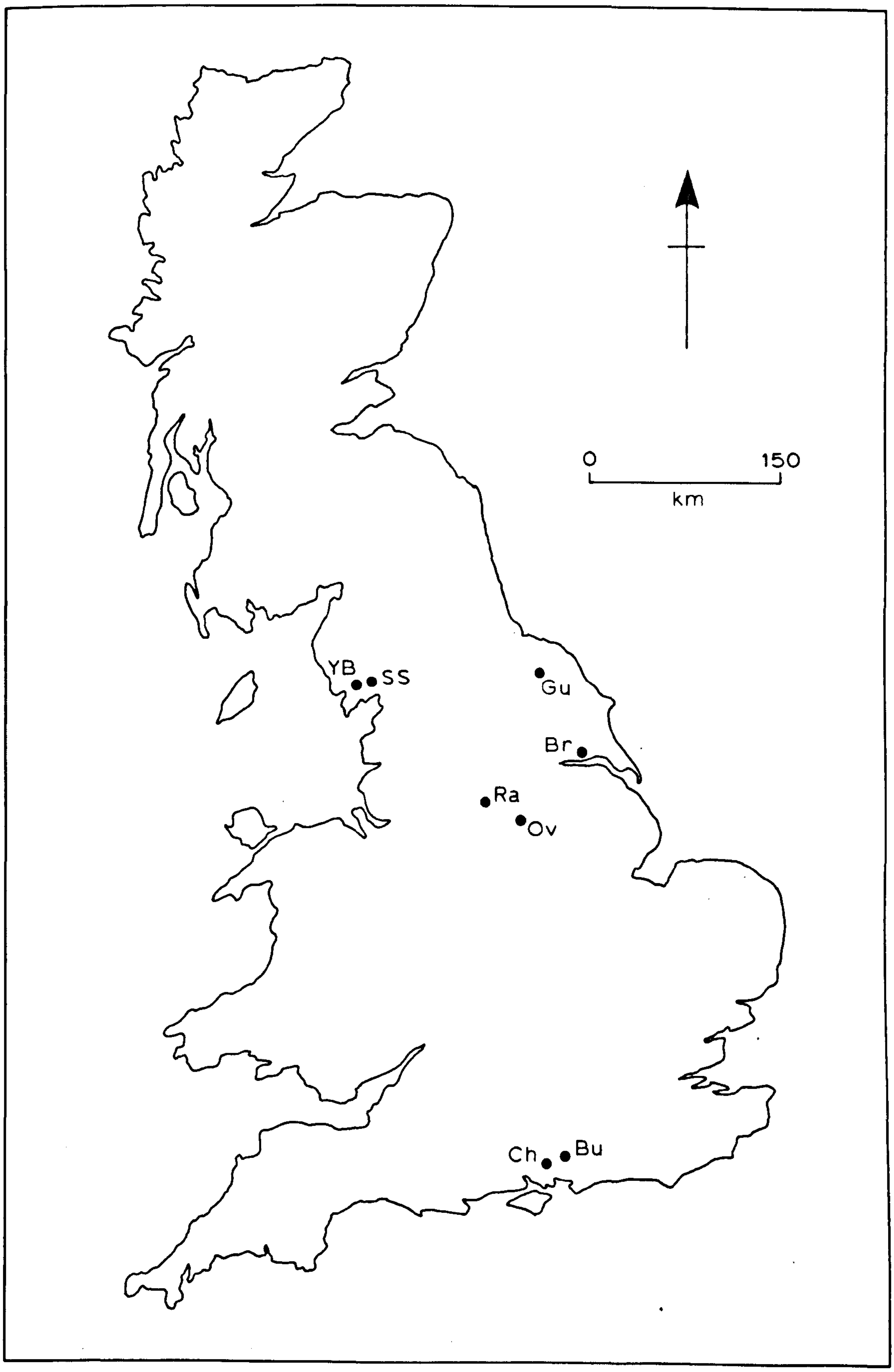


Fig 4.2. Location of populations used in the study.

the south of England should be included for the sake of comparison with northern yew populations. One of these was Butser Hill (Bu: GR 718199), which was one of the populations sampled by Watt (1926), and the other was on the road from Chichester (Ch: GR 807163).

Although a major phytogeographic survey was thought beyond the scope of this work it was noted that all the sites chosen for the study, with the exception of Yew Barrow, were calcareous, and the major site characteristics are shown in Table 4.2.

(B) Within-site sampling.

(C) Selection of trees. At least twenty five trees were sampled from each population. In the sites where there ~~were~~ was a small number of trees, i.e. Ravensdale (Ra) and Overton Hall (Ov) in region 1, and Brantingham (Br) and Guisborough (Gu) in region 3, the individuals measured made up 100% or close to 100% of the total numbers of trees that occurred on the site. In the other four populations, i.e. Scout Scar (Ss) and Yew Barrow (Yb) in region 2, and Butser Hill (Bu) and Chichester Road (Ch) in region 4, the number of trees on each site was much greater than the number of individuals sampled. In these cases, the sampled trees were selected by using random number tables for direction and distance from a chosen point. The initial point was found by arbitrarily throwing a stone within a population. From that point, the first three numbers (from five-figure random number tables) gave the direction in degrees and the next two gave the number of paces in that direction. Once arrived at this point, the nearest yew tree was the individual to be selected. From each of these trees the process was repeated until thirty trees had been selected from each of these sites.

Table 4.2. *General phytosociological details: Major species (pers. obs).*

Population	Altitude (m)	Geological Formation	Canopy	Understorey	Ground
Ravensdale	289	Carboniferous limestone	Taxus baccata Ulmus sp. Pinus sylvestris Acer pseudoplatanus	----	Gramineae sp.
Overton Hall	200	Carboniferous limestone	Taxus baccata Acer pseudoplatanus Sambucus nigra	----	Gramineae sp.
Stout Scar	158	Carboniferous limestone	Taxus baccata Fraxinus excelsior Betula pendula Alnus glutinosa Sambucus nigra Corylus avellana Crataegus monogyna Acer pseudoplatanus	Taxus baccata Corylus avellana Sambucus nigra Ilex aquifolium Rubus sp.	Taxus baccata Gramineae sp. Musci sp.
Yew Barrow	76	Silurian slate	Taxus baccata Quercus petraea Fagus sylvatica Corylus avellana Betula pendula Ilex aquifolium	----	Taxus baccata Fagus sylvatica Quercus petraea Lonicera periclymenum Oxalis acetosella Musci sp.
Brantingham	100	Chalk	Taxus baccata Acer pseudoplatanus Alnus glutinosa Ilex aquifolium	Taxus baccata Sambucus nigra Acer pseudoplatanus	Sambucus nigra Rubus sp.
Guisborough	120	Lower lias	Taxus baccata Acer pseudoplatanus Alnus glutinosa Ilex aquifolium	Sambucus nigra Buxus sempervirens Tsuga heterophylla	Anemone nemorosa Allium vineale Endymion non-scriptus
Buster Hill	137	Chalk	Taxus baccata Fraxinus excelsior Sorbus aria	----	----
Chichester Road	137	Chalk	Taxus baccata Fagus sylvatica Fraxinus excelsior	Sorbus aria	Taxus baccata Sambucus nigra Fraxinus excelsior

(C) Selection of variables.

Since the intention of the study was to obtain an overall impression of variation between populations and regions, it was decided to examine a large number of directly-measurable morphological characteristics (biometric measures). The thirteen variables to be measured related to the size of various parts of the tree, namely the length of the most recent shoot growth (LYG), the length (LL), breadth (LB), and breadth of a transverse section (DL) of the leaf from the most recent shoot growth, the length (BL) and breadth (BB) of the apical resting bud, and overall dimensions of the tree, i.e. its height (HT) and circumference (DT). Other variables studied were the number of leaves on the most recent shoot (NLY), the number of buds on that particular shoot (NBY), the number of boles in each tree (NB), the angle of the leaf (AL), and the length of the petiole of the leaf (LP). Where there was a multiple expression of a variable, four replicates per variable per tree were taken, and single measures where this was not the case; therefore in this study replicates were measured for all the variables except HT, DT and NB.

The shoots were selected from north-facing, south-facing, east-facing, and west-facing positions on the tree at eye level. From each shoot the fourth leaf up from the last bud scar on the right hand side was used for all the leaf measurements. Each shoot was placed in an individual plastic bag for transit to the laboratory, where the measurements were taken. These were made one day after collection so as to ensure freshness of the material. The data ~~was~~ were collected from all the sampled populations between the months of March and May, 1977. Details of the measurement techniques employed are shown in Table 4.3.

The complete data set resulting from the measurements of these variables is shown in Appendix I, and the mean values of the replicates are presented in Table 4.4. This latter is the data set which has been used in the following analysis.

Table 4.3.

Key to names of measured variables.

Variable	Description of variable	Measurement technique	Details
NLY	Number of leaves on last season's shoot	Count	From bud scar to apex
LYG	Length of the same shoot	Ruler (cm)	From bud scar to top of resting bud
AL	Angle of individual leaf	Protractor (degrees)	From tip of leaf to petiole/stem junction
LL	Length of same leaf	Ruler (cm)	From tip of leaf to leaf/petiole junction
LB	Breadth of same leaf	Ruler (cm)	At widest point
LP	Length of petiole of same leaf	Bioscope*(cm)	From base of leaf to where petiole widens
DL	Breadth of transverse section of same leaf	Bioscope*(cm)	From leading edge to leading edge, cut from widest point
NBY	Number of buds on same shoot	Count	All accounted except from terminal bud
BL	Length of resting bud	Bioscope*(cm)	From top to base
BB	Breadth of resting bud	Bioscope*(cm)	At widest point
HT	Height of tree	Clinometer (metres)	Direct measure
DT	Circumference of tree bole	Tape (metres)	Measured at waist height
NB	Number of trunks per tree	Count	Where trunk splits at waist height or lower

* Conversion tables used for real measure

N.B. All leaf variables were taken from the fourth leaf on the right hand side of the shoot.

Table 4.4. The mean value of individual trees in each population for each measured variable.

Population: Butser Hill.

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
1	33.75	3.53	63.25	1.70	0.21	1.35	2.35	1.75	2.60	1.85	10.0	3.33	2
2	39.00	3.80	58.50	1.33	0.21	1.35	2.23	3.75	3.02	2.22	9.4	2.15	3
3	43.00	4.88	59.00	1.93	0.21	1.45	2.45	2.50	3.00	2.30	4.9	1.36	2
4	61.75	10.18	35.75	1.80	0.20	1.35	2.25	11.50	4.10	2.60	6.6	3.12	3
5	39.50	5.53	58.50	2.15	0.21	1.50	2.50	3.00	2.90	2.17	6.0	3.07	3
6	31.25	4.03	47.00	2.15	0.21	1.20	2.44	3.25	2.65	1.75	11.2	1.95	3
7	37.50	5.73	44.25	1.90	0.24	1.60	2.50	2.75	3.60	2.05	7.6	3.58	3
8	46.75	4.23	49.50	1.93	0.20	1.25	2.35	3.75	2.80	2.20	4.3	1.60	1
9	55.75	5.88	43.25	1.40	0.20	1.45	2.15	5.25	3.20	2.25	6.0	3.20	6
10	28.75	3.23	41.75	1.80	0.20	1.50	2.20	0.75	2.70	1.85	5.5	2.68	9
11	45.75	5.55	31.00	1.90	0.21	1.55	2.55	3.75	3.60	2.20	4.9	2.23	3
12	40.00	5.03	43.50	2.05	0.20	1.60	2.40	4.50	3.05	2.40	7.6	2.77	2
13	36.50	4.13	50.75	1.78	0.20	1.15	2.25	1.50	2.35	1.75	7.4	2.75	1

Population: Butser Hill (Cont.)

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
14	39.75	4.45	56.00	1.48	0.19	1.35	2.05	3.50	2.75	1.85	6.2	3.60	2
15	25.50	3.15	40.75	1.85	0.21	1.35	2.35	1.25	2.80	2.00	6.3	3.22	4
16	20.25	2.30	58.50	1.58	0.24	1.25	2.65	1.25	1.85	1.45	10.0	2.02	1
17	23.25	2.38	56.25	1.65	0.20	1.50	2.30	2.75	2.20	1.70	8.5	3.86	6
18	38.75	6.05	44.00	1.90	0.24	1.40	2.50	2.75	3.00	1.90	9.8	2.99	2
19	42.33	5.73	44.67	2.20	0.27	1.75	2.60	3.33	2.90	2.00	11.5	3.31	5
20	31.25	2.63	43.00	1.10	0.20	1.15	2.10	2.00	2.30	1.60	6.4	0.64	1
21	34.25	4.00	52.00	1.88	0.24	1.35	2.60	1.00	2.90	2.10	5.2	0.69	1
22	37.00	4.95	50.00	1.63	0.21	1.10	2.30	2.25	2.55	1.85	4.8	0.97	3
23	44.25	5.45	51.25	1.60	0.21	1.10	2.45	2.50	2.35	1.70	6.8	2.71	5
24	38.50	4.63	44.25	1.73	0.21	1.05	2.40	1.00	2.80	1.70	6.4	0.59	1
25	38.75	4.43	41.00	1.90	0.20	1.50	2.25	2.50	3.05	1.95	10.5	3.05	3
26	39.00	4.15	46.75	1.50	0.20	1.05	2.05	1.25	2.70	1.95	7.5	2.15	10
27	31.00	4.50	57.00	1.83	0.21	1.15	2.30	0.50	2.75	1.80	7.5	3.35	12
28	35.75	4.48	51.75	1.70	0.21	1.00	2.05	1.75	2.45	1.90	7.5	3.35	14
29	34.50	4.65	51.75	1.65	0.20	1.20	2.10	1.00	2.65	1.80	4.7	0.65	3
30	45.75	7.60	48.00	1.80	0.23	1.30	2.35	3.75	2.95	1.80	6.0	0.81	2

Population: Chichester Road.

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
1	27.25	3.58	58.50	1.90	0.24	1.05	2.65	1.25	2.35	1.95	14.8	1.61	1
2	29.25	4.43	56.75	1.85	0.26	0.95	2.75	0.25	2.20	1.60	14.2	1.89	1
3	41.25	6.10	45.50	2.58	0.29	1.45	3.10	0.75	2.35	1.80	20.0	3.35	1
4	17.50	2.20	68.25	1.75	0.26	0.95	2.55	0.00	1.65	1.20	15.4	1.87	1
5	24.50	3.73	62.25	2.08	0.24	1.05	2.85	0.50	2.25	1.30	10.2	2.23	1
6	20.00	2.48	36.75	2.45	0.23	1.30	2.50	0.75	1.60	1.15	19.0	1.93	1
7	27.75	4.43	70.25	1.90	0.29	1.15	2.90	1.00	2.35	1.90	13.6	2.10	1
8	29.25	4.95	44.50	2.33	0.23	1.25	2.55	1.50	2.35	1.70	10.4	1.57	1
9	23.25	3.58	47.00	1.68	0.23	1.10	2.65	1.00	2.45	1.65	10.8	1.44	1
10	23.50	2.95	50.25	1.65	0.23	1.30	2.45	1.25	1.90	1.40	16.0	2.27	1
11	20.25	2.18	40.75	1.40	0.20	1.15	2.20	0.00	2.40	1.65	15.2	3.27	1
12	22.13	2.68	54.50	1.90	0.21	1.00	2.35	0.50	1.90	1.20	14.4	2.09	1
13	22.00	3.33	67.75	2.08	0.23	1.00	2.40	0.00	1.50	1.05	13.6	1.87	1
14	16.50	2.40	55.50	2.25	0.24	0.95	2.70	0.50	2.00	1.15	11.2	2.49	1
15	20.50	3.60	46.75	2.08	0.26	1.00	3.05	0.00	1.45	0.95	12.0	1.83	1

Population: Chichester Road (Cont.)

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
16	20.75	2.48	63.50	1.83	0.21	0.95	2.60	0.25	1.70	1.35	16.8	3.48	1
17	24.00	3.45	56.25	2.45	0.29	1.05	3.10	1.00	2.05	1.45	15.2	3.13	1
18	17.00	2.05	52.50	1.78	0.20	1.05	2.45	0.25	2.10	1.35	15.6	2.45	1
19	28.25	3.70	46.75	1.93	0.23	1.25	2.50	0.75	1.80	1.10	13.4	1.48	1
20	27.75	4.13	63.50	2.30	0.21	1.10	2.40	1.25	2.25	1.55	12.0	2.16	1
21	31.25	4.15	70.50	2.70	0.23	1.20	2.70	0.75	2.95	1.80	14.0	3.66	3
22	19.00	2.33	43.50	1.93	0.26	1.00	3.05	0.50	2.05	1.40	12.4	2.91	1
23	19.25	3.65	57.75	2.35	0.24	1.15	2.75	0.50	2.25	1.20	15.0	1.24	1
24	18.50	3.45	60.00	2.23	0.28	1.20	3.05	0.75	2.95	1.55	16.2	1.40	1
25	16.50	1.83	30.75	1.58	0.19	1.05	2.10	0.75	1.45	1.10	16.0	2.01	1
26	18.75	1.53	33.75	1.38	0.20	0.90	2.40	1.75	1.70	1.35	13.4	3.20	1
27	20.00	2.35	66.25	1.75	0.19	1.05	2.25	1.00	2.60	1.55	14.8	2.32	1
28	37.50	4.95	62.25	2.03	0.26	1.05	2.95	1.00	2.70	1.85	15.0	1.76	1
29	25.00	4.10	50.25	2.30	0.26	1.10	2.80	0.75	2.45	1.65	13.8	2.26	1
30	26.75	3.35	48.50	1.95	0.21	0.90	2.25	1.00	1.80	1.25	17.8	4.25	2

Population: Overton Hall.

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
1	25.25	4.70	43.50	2.15	0.28	1.30	2.95	2.00	2.40	1.50	13.4	0.96	1
2	24.25	4.95	60.25	1.95	0.26	1.30	2.95	0.75	1.95	1.35	7.4	0.88	1
3	29.50	3.95	41.50	1.98	0.24	1.35	2.55	0.75	1.70	1.35	15.0	1.88	1
4	28.00	3.68	39.00	1.73	0.23	1.30	2.50	0.25	2.00	1.45	11.6	1.34	1
5	29.00	4.83	54.50	2.05	0.25	1.60	2.70	1.75	2.05	1.45	9.4	1.35	1
6	32.25	4.08	49.00	1.70	0.23	1.45	2.40	2.50	1.70	1.40	13.4	1.56	1
7	33.00	4.93	42.00	1.90	0.21	1.45	2.30	2.25	2.70	1.80	10.5	1.11	1
8	31.50	3.48	43.75	1.63	0.20	1.50	2.35	2.75	2.05	1.55	9.4	2.74	3
9	21.25	2.48	36.25	2.00	0.21	1.60	2.50	1.00	1.95	1.55	10.8	2.75	2
10	25.75	3.18	39.00	1.85	0.20	1.60	2.20	1.25	2.15	1.55	10.6	1.54	1
11	21.00	3.65	52.50	2.28	0.25	1.70	2.60	0.50	2.55	1.95	10.0	1.93	1
12	25.50	3.40	50.25	2.18	0.24	1.50	2.45	1.75	1.80	1.45	8.2	1.58	1
13	44.75	6.33	49.00	2.10	0.25	1.10	2.25	2.25	2.20	1.50	5.8	1.30	2
14	24.50	4.00	54.75	2.55	0.21	1.65	2.55	1.00	1.95	1.30	5.8	0.73	1
15	19.75	4.05	42.75	2.33	0.25	1.30	2.75	1.25	2.20	1.60	5.0	0.54	1

Population: Overton Hall (Cont).

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
16	34.00	5.13	44.00	2.25	0.21	1.55	2.45	1.50	2.60	1.60	10.8	3.30	1
17	33.00	4.68	46.50	2.75	0.24	1.45	2.60	0.50	1.45	1.45	8.0	0.68	1
18	24.00	3.00	35.25	1.68	0.21	1.40	2.35	1.50	1.60	1.25	8.6	0.81	1
19	29.25	4.18	49.00	2.00	0.26	1.70	2.70	3.50	1.85	1.60	14.6	1.16	1
20	22.75	3.03	52.75	2.10	0.20	1.30	2.35	0.75	1.50	1.30	11.8	1.22	1
21	30.25	4.73	47.50	2.40	0.25	1.60	2.70	2.25	2.45	1.65	9.6	1.52	1
22	30.00	5.70	47.25	2.55	0.25	1.35	2.65	1.75	1.95	1.45	14.2	2.01	1
23	26.00	4.55	55.75	2.33	0.25	1.30	2.90	0.75	1.70	1.25	5.0	0.80	1
24	29.75	5.35	49.75	2.65	0.23	1.45	2.45	2.50	2.70	1.65	11.6	1.26	1
25	28.00	4.33	57.00	2.50	0.25	1.40	2.80	1.50	2.15	1.75	6.2	0.57	2
26	34.25	5.15	64.50	1.53	0.25	1.05	2.65	1.50	2.50	1.80	9.8	1.60	2
27	36.50	5.58	64.25	2.10	0.26	1.15	2.80	2.00	2.30	1.65	11.6	1.41	1
28	31.75	3.98	49.00	2.13	0.21	1.35	2.50	1.75	1.90	1.50	9.4	2.64	4
29	28.25	2.63	50.50	1.85	0.21	1.55	2.25	0.50	1.90	1.50	11.6	2.33	1
30	37.25	4.58	49.00	1.40	0.20	1.25	2.15	3.00	2.35	1.75	14.4	2.24	1

Population: Ravensdale.

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
1	20.50	2.65	59.25	1.93	0.21	1.30	2.40	1.75	1.65	1.10	11.0	1.45	1
2	19.50	2.40	53.50	2.08	0.21	1.20	2.40	0.50	1.40	1.00	9.3	1.50	1
3	26.75	3.28	64.75	1.95	0.28	1.25	2.55	2.00	1.60	1.20	10.5	2.35	2
4	43.50	6.13	46.50	2.05	0.24	1.60	2.50	2.00	2.10	1.50	5.6	0.76	1
5	30.50	4.25	46.50	2.30	0.26	1.65	2.50	2.25	2.20	1.70	9.3	2.01	2
6	37.00	6.33	59.00	2.45	0.25	1.85	2.75	4.50	2.10	1.60	12.6	1.52	2
7	24.00	3.73	63.00	1.80	0.26	1.55	2.70	2.00	1.70	1.10	11.2	0.85	1
8	35.75	5.00	60.50	2.43	0.29	1.75	2.80	2.50	2.30	1.75	11.0	1.05	1
9	26.00	4.68	50.50	2.68	0.29	1.85	2.65	2.50	2.15	1.60	8.2	1.11	2
10	19.75	3.50	51.25	2.58	0.29	1.45	2.90	1.00	2.20	1.30	10.2	1.06	2
11	26.75	4.38	45.50	2.25	0.25	1.65	2.65	0.50	2.40	1.40	9.1	2.40	2
12	21.25	2.55	64.25	1.40	0.21	1.35	2.25	1.50	1.50	1.20	8.6	1.47	2
13	26.75	4.23	57.50	2.05	0.24	1.50	2.50	3.00	1.75	1.15	10.5	1.70	2
14	31.00	4.18	56.75	1.45	0.20	1.35	2.25	2.00	1.70	1.35	14.4	3.75	4
15	28.25	3.45	54.25	1.80	0.24	1.20	2.40	0.50	1.60	1.15	14.1	1.77	2

Population: Ravensdale (Cont).

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
16	19.50	2.80	63.75	1.73	0.26	1.10	2.60	0.25	1.70	1.25	13.0	3.32	3
17	12.50	3.20	60.25	1.78	0.25	1.20	2.70	0.50	1.50	1.05	9.5	1.06	2
18	21.50	3.00	61.00	2.03	0.26	1.30	2.60	0.75	1.30	1.05	9.0	1.01	1
19	22.25	3.80	43.75	2.88	0.30	1.85	2.90	1.00	1.35	1.20	10.8	2.91	3
20	25.75	4.33	58.25	1.90	0.29	1.55	2.90	1.25	2.10	1.45	13.5	1.79	2
21	16.00	2.45	54.75	2.30	0.25	1.45	2.60	1.25	1.25	1.00	9.9	1.76	2
22	23.75	4.45	67.50	1.85	0.25	1.15	2.70	0.50	1.95	1.20	10.3	1.86	2
23	25.75	4.83	59.50	2.08	0.30	1.75	3.00	1.00	2.25	1.55	10.4	1.60	2
24	23.50	3.88	66.00	1.75	0.28	1.40	2.70	0.75	2.05	1.40	10.0	2.12	2
25	17.25	2.73	65.00	1.60	0.30	0.95	3.10	0.25	1.65	1.15	10.1	0.87	1

Population: Yew Barrow.

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
1	24.50	3.93	50.75	2.73	0.23	1.50	2.50	2.00	2.10	1.45	15.2	2.33	4
2	20.75	2.45	50.50	1.85	0.26	1.10	2.65	1.25	+1.00	0.90	11.8	1.90	2
3	28.00	4.60	49.75	2.45	0.24	1.50	2.70	1.50	+++1.65	1.30	13.6	2.04	1
4	22.00	3.65	66.25	2.70	0.30	1.25	2.90	1.50	1.70	1.35	14.0	2.44	3
5	21.25	3.20	53.25	1.90	0.21	1.35	2.45	0.75	+1.85	1.30	14.0	1.75	2
6	22.75	3.98	64.75	2.50	0.25	1.40	2.60	0.75	1.80	1.30	9.0	1.28	1
7	23.00	3.88	58.50	2.23	0.26	1.30	2.80	1.00	2.05	1.40	12.8	2.29	2
8	32.50	4.60	44.75	1.90	0.20	1.25	2.10	1.25	++1.90	1.45	10.8	1.93	2
9	30.00	3.93	48.75	2.10	0.26	1.25	2.65	2.00	++2.00	1.45	9.1	1.18	1
10	16.75	2.58	70.25	2.03	0.20	1.10	2.30	0.50	++1.85	1.30	12.2	1.31	1
11	19.50	3.05	40.75	2.13	0.19	1.05	2.05	0.75	++1.35	1.15	11.4	1.85	2
12	23.00	4.48	50.75	2.43	0.25	1.15	2.65	2.50	2.00	1.40	11.8	1.94	1
13	29.50	3.53	47.00	2.08	0.21	1.15	2.30	1.75	+1.90	1.35	17.2	0.94	1
14	25.25	3.03	46.50	1.75	0.25	1.45	2.55	1.50	2.45	1.75	10.2	1.74	2
15	19.00	3.68	43.25	2.45	0.24	1.20	2.55	1.50	+2.65	1.65	5.2	2.08	2

Population: Yew Barrow (Cont).

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
16	23.50	3.70	62.25	2.55	0.24	1.35	2.40	1.50	$^{+}$1.90	1.40	14.2	1.41	1
17	26.00	3.73	41.25	1.80	0.23	1.45	2.40	1.25	$^{++}$1.65	1.15	15.4	1.63	2
18	27.50	4.93	40.50	2.63	0.25	1.50	2.55	2.00	$^{+++}$2.05	1.35	13.6	2.33	2
19	21.75	3.63	36.25	3.00	0.23	1.40	2.45	2.00	$^{+}$2.70	1.65	13.4	3.09	2
20	18.00	2.00	52.00	1.75	0.20	1.10	2.05	0.75	$^{+++}$1.30	1.10	13.6	1.07	1
21	24.25	4.78	69.75	2.10	0.23	1.25	2.50	2.75	$^{+++}$2.20	1.35	13.0	1.48	2
22	17.00	2.98	48.25	2.15	0.23	1.20	2.25	0.75	$^{+}$1.25	1.35	7.1	1.88	2
23	23.75	4.55	50.75	2.63	0.21	1.35	2.25	1.75	2.00	1.40	10.4	2.08	5
24	27.50	5.65	55.00	2.40	0.25	1.35	3.00	1.75	$^{+}$2.30	1.50	9.6	1.70	2
25	26.75	4.03	48.25	2.60	0.28	1.10	2.85	1.50	$^{+}$1.25	0.90	12.4	1.66	1
26	21.25	3.98	50.75	2.70	0.23	1.25	2.55	0.75	$^{++}$1.85	1.20	16.4	2.52	2
27	23.00	4.73	39.75	2.73	0.20	1.20	2.25	3.00	2.30	1.50	14.5	3.60	9
28	24.00	4.80	52.75	2.63	0.29	1.05	2.90	1.00	$^{+}$2.75	2.25	9.5	2.25	4
29	23.25	3.53	66.25	1.90	0.25	1.15	2.65	2.75	$^{+}$1.10	0.90	10.2	1.51	1
30	15.00	2.58	39.00	2.18	0.26	1.20	2.70	1.00	$^{+++}$1.50	0.95	10.6	1.97	2

Population: Scout Scar.

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
1	32.50	4.30	45.25	1.98	0.20	1.25	2.40	2.00	2.35	1.75	10.4	2.45	1
2	23.25	3.73	50.50	2.20	0.25	1.45	2.75	1.25	2.75	1.85	10.6	3.30	4
3	10.75	1.50	52.75	1.60	0.21	1.20	2.45	0.00	1.20	1.10	9.2	1.40	1
4	25.25	3.63	43.75	1.60	0.24	1.40	2.45	0.75	++2.95	1.85	8.8	2.06	5
5	17.00	1.40	63.33	1.53	0.20	1.15	2.05	0.00	2.45	1.80	6.2	0.97	2
6	32.50	4.45	35.25	2.25	0.21	1.25	2.35	1.75	1.95	1.40	8.8	1.26	1
7	28.25	3.13	53.75	1.50	0.20	1.60	2.15	3.25	2.60	1.75	7.7	1.34	3
8	21.00	2.13	41.25	1.60	0.20	1.15	2.15	1.00	2.25	1.65	8.6	1.11	1
9	20.00	2.33	40.50	1.73	0.23	1.30	2.60	0.75	2.10	1.50	8.3	1.15	1
10	18.75	2.38	47.50	1.50	0.21	1.20	2.40	1.25	++2.80	1.65	12.8	1.46	1
11	24.25	4.80	43.50	2.08	0.26	1.35	2.75	2.00	+++2.25	1.40	13.0	1.45	1
12	19.00	2.83	64.00	2.20	0.25	1.25	2.70	0.00	1.55	1.20	17.5	2.37	1
13	17.25	3.15	61.00	2.50	0.21	1.45	2.45	0.25	+1.75	1.35	11.4	2.19	1
14	21.75	2.55	52.25	1.93	0.24	1.15	2.65	1.25	+3.50	2.30	11.4	1.69	1
15	40.50	5.73	43.75	2.18	0.24	1.40	2.60	0.75	2.90	2.00	12.2	2.22	1

Population: Scout Scar (Cont).

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
16	21.25	2.78	51.50	1.43	0.23	1.40	2.40	0.25	$^{++}$3.50	2.55	9.5	1.24	1
17	25.75	3.98	40.25	1.68	0.26	1.25	2.75	0.50	2.10	1.50	7.5	0.80	1
18	18.50	2.68	47.25	1.93	0.20	1.20	2.30	1.00	$^{+}$1.25	0.95	9.4	1.51	1
19	39.50	4.05	38.75	1.78	0.21	1.25	2.40	1.25	$^{+}$1.30	1.00	14.6	2.36	1
20	30.25	4.28	38.50	1.63	0.20	1.55	1.90	3.00	2.20	1.60	7.8	1.84	3
21	24.75	4.35	48.75	2.53	0.23	1.35	2.60	0.75	2.00	1.40	11.4	1.89	1
22	18.50	2.68	56.75	2.05	0.20	1.30	2.25	0.25	$^{++}$1.45	0.80	10.6	2.11	1
23	28.75	5.13	39.75	2.15	0.23	1.25	2.75	1.25	2.20	1.50	13.0	1.97	1
24	21.75	2.58	34.00	2.40	0.21	1.30	2.30	1.00	$^{+++}$1.75	1.30	11.4	1.92	1
25	24.00	3.43	48.25	1.88	0.25	1.25	2.65	1.75	$^{++}$1.15	0.95	10.6	1.61	1
26	28.75	4.30	37.00	2.13	0.28	1.40	2.80	3.25	3.05	2.05	16.2	2.93	2
27	39.25	7.83	48.75	1.78	0.24	1.45	2.60	2.50	$^{++}$3.10	2.50	12.0	2.05	1
28	38.50	5.03	50.00	1.75	0.24	1.30	2.60	2.25	2.25	1.60	11.4	0.51	1
29	22.50	3.20	50.50	1.63	0.23	1.25	2.50	2.25	$^{+}$2.20	1.50	11.6	1.75	1
30	34.25	5.15	52.00	1.63	0.23	1.15	2.45	3.50	3.30	2.20	9.0	2.33	2

Population: Brantingham.

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
1	32.50	5.00	15.25	2.39	0.21	1.55	2.30	2.50	1.85	1.40	6.1	0.62	1
2	23.00	4.63	11.73	3.04	0.25	1.80	2.55	1.75	1.40	1.25	5.5	0.46	2
3	23.50	4.10	18.88	2.10	0.21	1.20	2.31	1.50	1.80	1.10	3.0	0.75	1
4	27.50	5.53	50.17	3.13	0.26	1.70	2.73	2.00	2.00	1.15	10.1	0.84	1
5	33.25	6.35	43.75	3.15	0.28	1.50	2.80	2.25	1.65	1.30	8.0	0.85	1
6	34.25	5.73	57.75	1.71	0.20	1.70	2.20	2.75	2.10	1.30	5.1	0.87	3
7	43.25	7.85	44.13	2.35	0.23	1.70	2.50	4.00	3.00	1.55	7.3	0.49	1
8	42.00	9.18	42.00	1.83	0.23	1.60	2.34	4.00	2.15	1.55	4.3	0.35	1
9	27.00	5.43	40.00	2.06	0.25	1.65	2.56	2.00	1.75	1.35	6.1	0.45	1
10	23.50	4.29	54.50	2.15	0.28	1.70	2.64	1.50	1.80	1.15	5.9	0.37	1
11	31.25	5.60	60.13	1.63	0.23	1.35	2.59	2.25	2.70	1.15	6.1	0.56	1
12	37.00	6.93	43.00	2.60	0.25	1.80	2.63	3.25	3.00	1.90	10.8	0.75	1
13	20.75	2.85	62.25	1.93	0.25	1.80	2.60	1.25	2.15	1.45	11.3	1.05	1
14	28.50	5.13	65.00	2.03	0.26	2.05	2.67	2.25	1.90	1.30	8.3	0.89	1
15	24.75	4.78	49.25	2.34	0.29	1.55	2.80	1.50	1.55	1.30	7.9	0.62	1
16	40.25	7.55	49.75	2.20	0.28	1.90	2.80	3.50	2.25	1.65	7.5	0.70	1
17	29.00	4.25	58.00	2.38	0.26	1.65	2.70	1.75	2.15	1.65	10.6	0.64	1

Population: Brantingham (Cont).

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
18	25.00	4.58	71.00	2.56	0.28	1.60	2.80	1.00	1.60	1.15	7.2	1.11	4
19	23.25	3.63	55.25	2.28	0.25	1.65	2.59	1.25	1.95	1.35	4.8	0.35	1
20	23.75	3.30	53.75	1.93	0.34	1.55	3.10	1.00	1.60	1.35	6.5	0.75	2
21	29.75	5.50	55.50	2.30	0.29	1.70	2.67	2.25	2.10	1.55	5.9	0.49	1
22	28.50	4.23	57.50	1.86	0.28	1.40	2.75	1.75	2.00	1.30	8.8	0.89	1
23	35.75	4.93	67.25	1.88	0.28	1.50	2.80	2.25	1.70	1.20	6.1	0.54	1
24	39.25	5.05	53.75	2.48	0.25	1.70	2.61	3.00	2.45	1.55	5.3	0.64	2
25	21.50	4.36	43.63	2.55	0.28	1.75	2.77	1.50	2.00	1.55	7.5	0.52	1
26	22.50	3.30	52.00	2.05	0.26	1.80	2.63	1.25	1.80	1.55	7.0	0.56	1
27	26.75	4.65	58.75	1.85	0.26	1.60	2.65	1.75	2.00	1.45	9.6	0.91	1
28	34.33	5.73	42.33	1.90	0.23	2.00	2.38	3.00	1.90	1.35	7.3	0.73	2
29	25.00	4.10	60.25	2.10	0.28	1.60	2.78	1.50	1.85	1.30	5.1	0.59	1
30	21.50	4.23	56.25	2.63	0.28	1.35	2.85	1.00	2.35	1.55	7.5	0.78	1
31	29.25	4.30	47.25	2.23	0.25	2.00	2.54	2.25	1.90	1.60	8.5	0.54	1
32	21.25	4.80	41.25	3.50	0.30	1.60	3.00	1.00	2.20	1.55	13.8	2.04	3
33	30.75	10.50	48.50	2.33	0.20	2.10	2.20	3.25	1.65	1.55	10.5	1.54	3

Population: Guisborough.

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
1	59.25	10.05	42.00	2.03	0.21	1.35	2.40	5.50	2.05	1.70	6.1	0.68	1
2	62.00	9.55	50.00	2.10	0.24	1.90	2.60	4.80	2.15	1.75	6.8	0.71	3
3	41.25	7.85	59.75	2.03	0.23	1.70	2.70	4.00	1.70	1.35	7.4	2.01	3
4	46.75	9.08	46.00	2.50	0.30	1.80	2.70	4.75	2.25	1.50	9.6	2.44	4
5	39.00	8.07	45.75	2.25	0.29	1.60	2.75	3.00	1.90	1.45	8.7	1.70	2
6	25.75	3.10	50.00	1.85	0.20	1.30	2.25	0.75	1.60	1.20	8.5	1.56	2
7	19.50	2.30	54.50	1.63	0.28	1.25	2.80	1.00	1.35	1.05	9.5	0.95	1
8	27.25	4.05	43.00	1.75	0.28	1.75	2.60	2.50	2.10	1.25	10.0	2.40	2
9	35.50	5.70	48.00	1.80	0.28	1.30	2.70	3.00	2.60	1.70	8.7	1.26	1
10	22.50	4.00	43.25	2.58	0.28	1.40	2.75	0.00	2.15	1.40	11.5	3.62	4
11	43.50	7.33	42.75	2.18	0.25	1.55	2.55	4.75	2.55	1.65	6.8	0.72	2
12	39.50	7.63	55.25	2.95	0.31	1.45	3.10	4.50	2.65	2.05	9.0	2.22	2
13	25.00	4.65	46.00	2.13	0.29	1.45	2.90	1.00	2.10	1.60	9.7	1.05	1
14	16.50	2.28	48.00	1.55	0.21	1.90	2.50	0.00	1.80	1.25	13.8	1.45	1
15	20.00	2.55	47.00	1.98	0.21	1.40	2.35	0.75	1.90	1.50	10.2	1.72	1

Population: Guisborough (Cont).

Individual No.	NLY	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
16	32.25	5.23	63.50	2.00	0.24	1.55	2.45	2.75	2.05	1.45	6.5	0.95	2
17	20.00	3.20	53.75	2.40	0.29	1.50	2.90	0.00	1.35	1.05	8.3	0.91	1
18	32.50	5.60	58.75	1.85	0.25	1.35	2.55	2.25	2.35	1.45	8.1	1.15	1
19	25.00	3.83	52.75	2.11	0.28	1.45	2.65	0.00	1.30	1.00	10.2	1.89	2
20	18.00	4.60	42.25	2.70	0.25	1.15	2.55	0.75	1.95	1.30	6.6	1.26	1
21	20.25	2.40	71.00	1.38	0.23	0.95	2.30	0.00	1.50	1.10	9.0	2.90	2
22	25.25	3.35	53.25	1.98	0.26	1.20	2.65	1.75	1.70	1.20	7.0	1.03	1
23	21.75	4.93	50.00	3.48	0.26	1.35	2.60	1.00	2.50	1.55	9.0	1.23	1
24	19.00	3.70	41.25	2.50	0.30	1.45	2.75	2.00	1.95	1.25	12.0	2.58	2
25	17.00	2.45	61.25	1.80	0.23	1.15	2.25	0.25	1.55	1.05	11.0	1.34	1

(A) The data set (Table 4.4).

When studying the mean values of the thirteen variables as shown in Table 4.4, it should be noted that in the case of the Scout Scar and Yew Barrow data for bud length and breadth, some of the samples are marked with one or more crosses signifying that the mean was taken from either one bud, i.e. shown by one cross; two buds, shown by two crosses; or three buds shown by three crosses. This was necessary as some of the buds had burst and therefore could not be measured as resting buds. In Scout Scar, the samples in question were; means taken from one bud, samples 13, 14, 18, 19 and 29; means taken from two buds, samples 4, 10, 16, 22, 25 and 27; and means taken from three buds, samples 11 and 24. In Yew Barrow, the samples in question were; means taken from one bud, samples 2, 5, 13, 15, 16, 19, 22, 24, 25, 28 and 29; means taken from two buds, samples 8, 9, 10, 11, 17 and 26; and means taken from three buds, samples 3, 18, 20, 21 and 30. In fact in this population only two sample means were taken from four resting buds, namely samples 1 and 4. In Scout Scar, therefore, 13 samples out of 30 measured did not have a full quota of resting buds, i.e. 43%. In Yew Barrow, 22 samples out of 30 did not have the full quota of resting buds, i.e. 73%. So in the case of Scout Scar, five samples out of thirty measured were based on one bud, six out of thirty were based on two buds and two out of thirty on three buds. In Yew Barrow, eleven out of the thirty buds measured were based on one bud, six out of thirty were based on two buds and five out of thirty on three buds. Although this is so, when studying the data from the various individuals it will be noticed that there seems to be reasonable agreement of bud size although the replicates from each individual are different, with no extraordinarily high or low outliers. In this event, these measurements were taken as being sufficiently viable to use in the subsequent analysis.

(A) Statistical analysis.

The intention of the study was to get an overall impression of variation between populations and regions of the yew. It was decided that the best way to carry out this comparison was not to study the variables measured individually, but to subject them to a multivariate analysis. This kind of analysis has the effect of compressing the original variables into a form that gives a greater overall impression of differences between trees and, it was hoped, populations and regions. The multivariate technique used for this purpose was Principal Component Analysis (PCA).

The choice of PCA was derived from the nature of the study. It has been pointed out in the first chapter that no investigation has been undertaken thus far that looks at the variation of yew tree populations in terms of morphology, so in this essentially exploratory study of variation between populations in England it was decided that no *a priori* reasons for arbitrarily separating the populations could be assumed. As Jeffers (1965) has pointed out, the main means of investigation into the taxonomy of a particular group under such conditions is usually obtained by Principal Component Analysis.

After the identification of the individual trees along the major components has been achieved from PCA, one is left with a scatter diagram of individuals. This can of course be described in itself, but in order to get increased clarity as to how the individuals are grouped, a cluster analysis was used, subsequently, which compared the eight populations used in the study to eight clusters, in which the most similar individuals in the scatter diagram group into one or other of the eight clusters. Ward's method of clustering was found to be efficient for clustering in this case.

Both the PCA and Ward's method of cluster analysis were carried out on the computor ICL 1904S at Hull University, the program package names being Stats. package XDS3 and Clustan respectively. More information about these methods is given at appropriate places in the text.

(B) The mechanics of P.C.A.

First, the basic data matrix is constructed. This matrix will have as many rows as there are individuals and as many columns as there are variables. Then the coefficients of correlations between every pair of variables is calculated, according to the formula;

$$r_{st} = \frac{\Sigma X_s X_t - (\Sigma X_s)(\Sigma X_t)/M}{\sqrt{\left[\Sigma X_s^2 - (\Sigma X_s)^2/M\right]\left[\Sigma X_t - (\Sigma X_t)^2/M\right]}}$$

where r_{st} is the coefficient of correlation between the s_{th} and t_{th} variables, X_s and X_t are the individual values of s_{th} and t_{th} variables, and M is the number of individuals observed. It is of value to examine the correlation coefficients themselves so as to discover what correlations may exist between the basic variables. These correlations can be set out in a linkage diagram which might or might not show clusters of variables. Indeed, as Jeffers (1964) has pointed out, it is usually difficult to decide, from an examination of the correlation matrix alone, what constitutes a cluster and what does not. Nevertheless, it is usually of interest to know what correlations there are of the basic variables, when these can be identified, and to know whether these are positive or negative. Jeffers (1964) mentioned that large numbers of significant correlations suggest that a relatively small number of useful components may be extracted from the matrix, while few correlations suggest that the selection of the basic variables has been such as to avoid the inclusion of closely-correlated measures.

The next stage of the analysis is the calculation of the eigenvalues and eigenvectors, the object being to economise in the number of dimensions used to describe the individuals by seeking linear transformations. If the data can be expressed in terms of fewer than n of these transformations, a genuine reduction in the dimensions of the problem will have been achieved. However, in general, this will not be possible and an approximate reduction is attempted in the following way;

(1) coefficients are chosen so that the first of the new transformations has as large a variance as possible;

(2) a second set of coefficients are then chosen so that the new transformation is uncorrelated with the first, and has as large a variance as possible; and

(3) this is continued until all transformations are uncorrelated with each other, and until each accounts for as much of the remaining variation as possible.

Mathematically, the calculation of the transformations (components) is equivalent to finding the eigenvalues, i.e. the amount of variation accounted for in each component, and the eigenvectors, i.e. values proportional to the weighting of the original variables required in their combination to form the new component. So, for each of the components extracted, there will be an eigenvalue. This is expressed as a percentage of the number of basic variables included, giving the percentage of the total variability described by the variables which is accounted for by the component.

There is a general rule of thumb used when examining the eigenvalues, and that is to ignore any component which has an eigenvalue with a value of less than one. The reasoning behind this is that, if the basic variables had been completely uncorrelated, all the eigenvalues would be close to one and so a component with an eigenvalue of less than one would represent a component which is accounting for a smaller proportion of variability than would be represented by each of the basic variables separately.

Once the eigenvalue cutoff point has been decided, and the number of components that are to be used in the next stage of the analysis has been determined, an examination of the eigenvectors is made. It is usual for these eigenvectors to be scaled so that the maximum weighting is 1, and the weighting of the other variables are then scaled accordingly. The weightings of variables on each component are examined to discover which are relatively highly positive or negative. These are said to constitute an index of the combined action, or the contrast, of the basic variables. Once these variables have been identified, it might be possible to assign a new variable name to the component, which could then be used in the rest of the analysis.

The next step is to calculate the value of the individuals and/or populations along the selected components. To do this for the individual, the eigenvector for each component is divided by the square root of the sum of squares of the elements. For each individual, the standardised variates are calculated, i.e. the difference between the mean overall individual divided by the standard deviation of the individual values. The products of the weighted eigenvectors and the standardised variables for the individual gives the transformed coordinates of the original data set. It should be noted that all the stages from the calculation of the correlation matrix up to this point will be automatically performed by a standardised P.C.A. computer package. The transformed coordinates of individuals can now be plotted, by hand or computer.

If an overall indication of between-population differences along these components is required, the calculation proceeds in the following manner (after Jeffers & Black, 1964).

First the means of the individual variables in each provenance are standardised,

$$\text{i.e.} \quad \frac{M - M'}{\sigma'} = X$$

where M = the mean of the individual variable in each provenance,

M' = the gross mean of the sample,

σ' = the gross standard deviation of the sample,

X = the standardised figure.

Then X is multiplied by the component weighting for that variable, and the addition of all the variables for each component gives a transformed, weighted, component coordinate for each provenance for each component. These can then be plotted graphically, as in the case of the individual coordinates.

(A) Results.

(B) The correlation matrix.

As has been pointed out in the previous section, the starting point of P.C.A. is the correlation matrix, in which the correlation coefficient, r, is calculated for each pair of variables. The number of correlations in the matrix can be calculated according to the equation $n(n-1)/2$ (Jeffers, 1964), where n equals the number of variables measured. In this case n=13; therefore the number of correlation coefficients is 78. The results can be seen in Table 4.5. The level of significance used to extract some meaning from this matrix was one per cent, $p=0.01$, which gives the correlation coefficient cutoff point of $r=0.17$. The significant correlation coefficients have been identified on Table 4.5 by crosses. It should be mentioned that a large number of observations increases the chance of there being a significant correlation between two variables, and in this case the number of observations was high, i.e. 233. This being the case, it is not surprising that there are a large number of significant correlation coefficients in the matrix. Within these correlations there are some that are more powerful than others, i.e. their relationship is stronger, e.g. $r=0.673$ for NLY and LYG, whereas $r=0.174$ for BL and NB. To get some indication of these varying strengths of relationship, a subjective system of asterisks was used to separate the large number of significant correlations, i.e. $r \geq 0.6$ was given xxxxx, $r \geq 0.5$ was given xxxx, $r \geq 0.4$ was given xxx, $r \geq 0.3$ was given xx, and the rest down to $r = 0.17$ was given x (see Table 4.5). This was done as it had been

Table 4.5. **Coefficients of correlation (r) between pairs of the thirteen original variables.**

	LYG	AL	LL	LB	LP	DL	NBY	BL	BB	HT	DT	NB
NLY	xxxxx 0.796	-0.150	-0.082	-0.099	x 0.274	-0.124	xxxxx 0.752	xxxx 0.519	xxxx 0.568	xx -0.344	0.013	x 0.211
LYG		-0.140	x 0.266	x 0.172	xxx 0.439	0.132	xxxxx 0.709	xx 0.366	xx 0.373	xx -0.304	-0.141	0.112
AL			-0.116	x 0.207	-0.159	x 0.225	x -0.206	-0.113	-0.130	0.103	-0.021	-0.040
LL				xxx 0.435	x 0.295	xxx 0.439	-0.007	-0.094	-0.115	0.079	-0.078	-0.062
LB					x 0.246	xxxxx 0.858	-0.078	-0.139	-0.145	0.035	x -0.225	x -0.172
LP						0.120	xx 0.374	0.059	0.114	xx -0.302	x -0.275	-0.007
DL							-0.138	-0.075	-0.107	0.147	-0.148	x -0.268
NBY								xxx 0.432	xxx 0.451	xx -0.307	0.000	0.153
BL									xxxxx 0.890	x -0.178	x 0.224	x 0.245
BB										x -0.209	x 0.222	x 0.270
HT											xxx 0.420	-0.154
DT												xxx 0.443
NB												

KEY: r ≥ 0.6 xxxxx
r ≥ 0.5 xxxx
r ≥ 0.4 xxx
r ≥ 0.3 xx
r ≥ 0.17 x

suggested by Jeffers (1964) that when there are a large number of significant correlations, the number of useful components will be small, and therefore a consideration of the correlation matrix in this manner might indicate major clusters of variables which could help in the overall analysis. A linkage diagram was then constructed showing the significant correlations between the variables diagramatically (Fig 4.3). It can be seen from this diagram that the picture is complex, making interpretation difficult. However some evidence of clustering of variables emerges if everything above $r \geq 0.4$ is considered; this isolates variables, NLY, LYG, NBY, BL and BB into one cluster; LL, DL and LB into another; and HT, DT and NB into a third. All the other correlations cross between these three groups. However, as these groups are subjective and not statistically-proven, comments about them have to be interpreted with caution.

From the correlation matrix, the first five principal components were computed, as shown in Table 4.5. The first component explains a low amount of variability indicating a weak structure in the data.

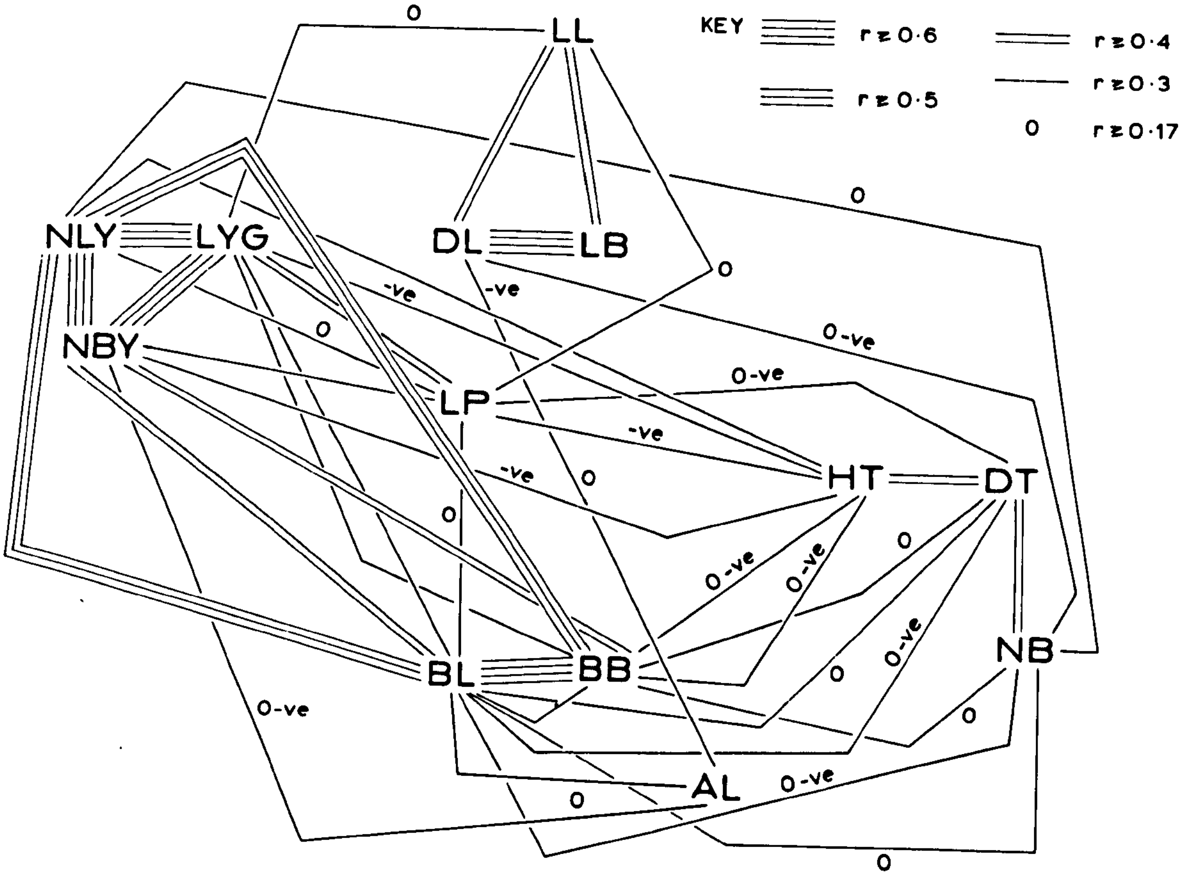


Fig 4.3. Linkage diagram showing the significant correlations between the thirteen original variables.

Table 4.6. The eigenvalue and cumulative percentages for the first five principal components.

Component	Eigenvalue	Cumulative Percentage of Total Variance
I	3.81	29.29
II	2.66	49.77
III	1.61	62.19
IV	1.16	71.09
V	0.94	78.33

These five components accounted for close to 78% of the total variability. It can also be seen that the eigenvalue drops below one in the fifth component, and thus it is only the first four components that are considered meaningful for the reasons mentioned above. The next stage is to examine the eigenvectors for the first four components as presented in Table 4.7.

If, from among these positive or negative weightings, note is made of those which are greater than 0.35, i.e. the variables with relatively high values with respect to all the variables in each component, it is possible to identify these basic variables that constitute an index of combined or contrasting action from the four components. They are as follows:

Component I; the number of leaves on the shoot (NLY), length of the shoot (LYG), number of buds on the shoot (NBY), bud length (BL) and breadth (BB). These five variables all have positive weightings along this component.

Component II; the length of the leaf (LL), breadth of the transverse section of the leaf (DL), and the breadth of the leaf (LB). These three variables have positive weightings along this component.

Component III; the height (HT) and circumference (DT) of the tree and the breadth of the transverse section of the leaf (DL). These three variables have negative weightings along this component.

Component IV; the angle of the leaf (AL) and the length of the leaf (LL). These two variables have a positive and negative weighting respectively along this component.

It will be noted that the first two components correspond closely with two of the variable groupings suggested from the linkage diagram of Fig 4.3; Component III corresponds to the third group, apart from the combination with the breadth of the transverse section of the leaf; and the fourth component suggests that the smaller the leaf, the

Table 4.7. Proportional weightings of the original variables for components.

Variable	I	II	III	IV
NLY	0.45	0.05	0.01	0.09
LYG	0.39	0.27	0.00	-0.06
AL	-0.15	0.05	-0.19	0.64
LL	-0.02	0.38	-0.19	-0.48
LB	-0.09	0.50	-0.27	0.12
LP	0.20	0.33	0.20	-0.24
DL	-0.11	0.47	-0.36	0.16
NBY	0.42	0.08	0.07	-0.05
BL	0.37	-0.11	-0.30	0.22
BB	0.39	-0.11	-0.27	0.21
HT	-0.24	-0.09	-0.43	-0.21
DT	0.03	-0.32	-0.53	-0.28
NB	0.18	-0.22	-0.23	-0.22

higher the angle between it and the shoot stem.

The analysis is now at the stage when the components may be given names to identify them in more general terms with the variables chosen in the study. Component I will be called shoot vigour, component II leaf dimensions, component III tree dimensions, and component IV leaf angle. .

(B) Calculation of population coordinates.

So as to see where the populations might lie along these four components, their coordinates then were calculated, using the standardised variable means from each population, (see mechanics of PCA for method). For the analysis, the means of the individual variables for each population, shown in Table 4.8, and the overall mean and standard deviation of the sample are required (Table 4.9). Within this latter table, note has also been made of the maximum and minimum values for each variable for the total sample. For NLY the mean of the total sample was found to be 28.04; however, there is a large variation in the amount of leaves on the shoot, as the minimum recorded value is 10.75, and the maximum 62.00, with the standard deviation for this variable being 8.54. For LYG, the mean was found to be 4.24, the minimum value being 1.40, and the maximum 10.50, with the standard deviation being 1.55. For AL the mean was 50.75, the minimum 11.73, the maximum 71.00 and the standard deviation 9.59. For LL the mean was 2.07, the minimum was 1.10, the maximum 3.50 and the standard deviation 0.40. For LB the mean was 0.24, the minimum 0.19, the maximum 0.34 and the standard deviation 0.03. For LP the mean was 1.37, the minimum 0.90, the maximum 2.10 and the standard deviation 0.24. For DL the mean was 2.55, the minimum was 1.90, the maximum 3.10, and the standard deviation 0.24. For NBY the mean was 1.69, the minimum 0.00, the maximum 11.50 and the standard deviation 1.30. For BL the mean was 2.13, the minimum 1.00, the maximum 4.10 and the standard deviation 0.53. For BB the mean was 1.50, the minumum 0.80, the maximum 2.60 and the standard deviation 0.33. For HT the mean was 10.17, the minimum 3.00, the maximum 20.00 and the standard deviation was 3.26. For DT the mean was 1.74, the minimum 0.35, the maximum 4.25 and the standard deviation 0.86. Finally for NB the mean was 1.86, the minimum was 1.00, the maximum was 14.00 and the standard deviation was 1.69.

Although no such detailed analysis has been attempted elsewhere

Table 4.8. The mean values of the thirteen variables in each population.

	Butser Hill	Chichester Road	Overton Hall	Ravensdale	Scout Scar	Yew Barrow	Brantingham	Guisborough
Variables	Mean	Mean	Mean	Mean	Mean	Mean	Mean	Mean
NLY	37.96	23.83	29.00	25.44	25.27	23.34	29.07	30.17
LYG	4.70	3.33	4.26	3.85	3.64	3.80	5.22	5.09
AL	48.76	53.70	48.66	57.31	47.34	51.28	49.38	50.76
LL	1.76	2.01	2.08	2.04	1.89	2.29	2.28	2.14
LB	0.21	0.24	0.23	0.25	0.23	0.24	0.26	0.25
LP	1.32	1.08	1.41	1.44	1.30	1.26	1.66	1.44
DL	2.33	2.63	2.53	2.64	2.47	2.51	2.63	2.61
NBY	2.74	0.71	1.57	1.44	1.36	1.53	2.09	2.04
BL	2.81	2.11	2.07	1.81	2.27	1.88	2.00	1.96
BB	1.95	1.43	1.53	1.27	1.60	1.35	1.40	1.39
HT	7.23	14.40	10.11	10.48	10.76	12.07	7.43	8.96
DT	2.39	2.31	1.52	1.72	1.77	1.90	0.73	1.58
NB	3.86	1.10	1.30	1.88	1.46	2.16	1.39	1.76

Table 4.9. The mean, minimum and maximum value, and standard deviation of the thirteen variables.

Variable	Mean	Minimum value	Maximum value	Standard deviation
NLY	28.04	10.75	62.00	8.54
LYG	4.24	1.40	10.50	1.55
AL	50.75	11.73	71.00	9.59
LL	2.07	1.10	3.50	0.40
LB	0.24	0.19	0.34	0.03
LP	1.37	0.90	2.10	0.24
DL	2.55	1.90	3.10	0.24
NBY	1.69	0.00	11.50	1.30
BL	2.13	1.00	4.10	0.53
BB	1.50	0.80	2.60	0.33
HT	10.17	3.00	20.00	3.26
DT	1.74	0.35	4.25	0.86
NB	1.86	1.00	14.00	1.69

before, from general information relating to the tree, a partial comparison of some of these variables can be achieved. The Dendroflora of the Caucasus (1959) has noted that yew trees can grow to 25 metres in height, although some (the Closewalk Yews, see Chapter 1) have achieved an extraordinary height of about 28 metres (Hummel & Lewis, 1955). However, Bugala (1975) has intimated that the yew generally attains a height of eight to twelve metres, and is seldom taller, although some specimens can grow to 20 metres. Comparing these comments with my results, it can be seen that they agree with the analysis of Bugala (1975), as the tallest tree in the sample was 20.00 metres and the mean was 10.17 metres.

It has been noted by Mitchel (1974) that the length of the leaf of the yew is from 2 to 4 cm, and its width about 3 mm. Bugala (1975) suggests that the length is 3 cm and the width is 2.0 to 2.5 mm. Comparing this with the results above, it can be seen that the maximum leaf-length attained in my study was 3.50 cm, with a mean length of 2.07 cm, suggesting that for this sample at least,Mitchel's 4.00 cm is an exaggeration. Bugala (1975) again comes closest to the above results in that the maximum attained is one of 3.50 cm, although my average is low in comparison to his, at 2.07 cm. Finally, comparing these authors' figures of leaf width with the results above shows that my mean agrees with Bugala's (2.4 mm, as compared to a width of 2.0 to 2.5 mm), and my maximum agrees with Mitchel's (i.e. 3.4 mm, as compared with 3 mm).

For the rest of the data, no comparative information can be found, but there are some general points that can be made. For example, it can be seen that for the NB variable, i.e. the number of boles per tree, the minimum is one, which is understandable, and the mean is 1.86; however, the maximum number of boles was 14.00.

The large variation in the number of leaves on the shoot, NLY, should be stressed; while the mean was about 28 leaves per shoot, the maximum found was 62 leaves on a shoot, and this might be correlated with the length of the shoot, i.e. the longer the shoot the more leaves will be found. The mean for AL, i.e. the angle of the leaf, is about 50 degrees. Further comparisons between these data, and the others noted in Table 4.9, will have to wait until future work is completed.

For the present, the means and standard deviation shown in Table 4.9, along with the means shown in Table 4.8 have been used to calculate the standardised variable means for each population, the results being shown in Table 4.10. This set of figures was then multiplied by the component weighting for that variable in the four components, results of which are shown in Tables 4.11a to d. The addition of all the variables within each component gives a transformed, component coordinate for each population for each component which is summarised in Table 4.12. These new coordinates have been plotted graphically (Figs 4.4 to 4.9) to see whether any further patterns of variation could be seen between populations.

(B) Description of Figures.

In Fig 4.4, the shoot vigour and leaf dimension coordinates for the eight populations have been plotted. As in all the graphs, the name of the population is shortened as in Fig 4.2. Bu is Butser Hill, Sussex, and Ch is Chichester Road, Sussex, the two populations included from the south of England. Ss is Scout Scar and Yb is Yew Barrow from the northwest, Cumbria, Ov is Overton Hall and Ra, Ravensdale from Derbyshire and Br is Brantingham and Gu is Guisborough from the northeast. Along component I, the shoot vigour axis, Butser Hill shows a notably higher score than all the other populations, with a group of four, i.e. Scout Scar, Overton Hall, Guisborough and Brantingham, having similar scores. Lower still, Yew Barrow and Ravensdale make up another group, with Chichester Road having the lowest score of all. Along component II, the leaf dimension axis,

Table 4.10. The standardised means for each measured variable for each population.

	Population							
Variable	Bu	Ch	Ov	Ra	Ss	Yb	Br	Gu
NLY	1.162	-0.493	0.112	-0.304	-0.324	-0.550	0.121	0.249
LYG	0.297	-0.587	0.013	-0.252	-0.387	-0.284	0.632	0.548
AL	-0.208	0.308	-0.218	0.684	-0.356	0.055	-0.143	0.001
LL	-0.775	-0.150	0.025	-0.075	-0.450	0.550	0.525	0.175
LB	-1.000	0.000	-0.333	0.333	-0.333	0.000	0.666	0.333
LP	-0.208	-1.208	0.167	0.292	-0.292	-0.458	1.208	0.292
DL	-0.920	0.330	-0.080	0.370	-0.330	-0.170	0.330	0.250
NBY	0.800	-0.754	-0.100	-0.200	-0.254	-0.123	0.308	0.269
BL	1.283	-0.038	-0.113	-0.604	0.264	-0.472	-0.245	-0.321
BB	1.364	-0.212	0.091	-0.636	0.303	-0.454	-0.303	-0.333
HT	-0.902	1.298	-0.018	0.095	0.181	0.583	-0.841	-0.371
DT	0.755	0.663	-0.256	-0.023	0.035	0.186	-1.174	-0.186
NB	1.183	-0.450	-0.331	0.012	-0.234	0.178	-0.278	-0.059

Table 4.11a. The result of the multiplication of the component I weightings (Table 4.7) and the standardised means (Table 4.10) for each measured variable and for each population.

Variable	Population							
	Bu	Ch	Ov	Ra	Ss	Yb	Br	Gu
NLY	0.523	-0.222	0.050	-0.137	-0.146	-0.248	0.055	0.112
LYG	0.116	-0.230	0.005	-0.099	-0.152	-0.111	0.248	0.215
AL	0.031	-0.046	0.033	-0.100	0.053	-0.008	0.021	0.000
LL	0.016	0.003	-0.001	0.002	0.009	-0.011	-0.011	-0.004
LB	0.090	0.000	0.030	-0.030	0.030	0.000	-0.060	-0.030
LP	-0.042	-0.242	0.033	0.058	-0.058	-0.092	0.242	0.058
DL	0.101	-0.036	0.009	-0.041	0.036	0.019	-0.036	-0.028
NBY	0.336	-0.316	-0.042	-0.084	-0.110	-0.052	0.129	0.110
BL	0.475	-0.014	-0.042	-0.224	0.098	-0.175	-0.091	-0.119
BB	0.053	-0.083	0.036	-0.248	0.118	-0.177	-0.118	-0.130
HT	0.217	-0.312	0.004	-0.023	-0.043	-0.140	0.202	0.090
DT	0.022	0.020	-0.007	-0.001	0.001	0.005	-0.035	-0.006
NB	0.213	-0.081	-0.059	0.002	-0.043	0.032	-0.050	-0.011
Σ	2.151	-1.559	0.049	-0.925	-0.206	-0.958	0.496	0.257

Table 4.11b. The result of the multiplication of the component II weightings (Table 4.7) and the standardised means (Table 4.10) for each measured variable and for each population.

Variable	Bu	Ch	Ov	Ra	Ss	Yb	Br	Gu
NLY	0.058	-0.025	0.006	-0.015	-0.016	-0.028	0.006	0.013
LYG	0.080	-0.158	-0.004	-0.068	-0.104	-0.077	0.171	0.148
AL	-0.010	0.015	-0.011	0.034	-0.018	0.003	-0.007	0.000
LL	-0.295	-0.057	0.009	-0.029	-0.171	0.209	0.200	0.066
LB	-0.500	0.000	-0.167	0.167	-0.167	0.000	0.333	0.167
LP	-0.069	-0.400	0.055	0.096	-0.096	-0.151	0.400	0.096
DL	-0.432	0.155	-0.038	0.174	-0.155	-0.080	0.155	0.118
NBY	0.064	-0.061	-0.008	-0.016	-0.020	-0.010	0.025	0.021
BL	-0.141	0.004	0.012	0.066	-0.029	0.052	0.027	0.035
BB	-0.150	0.023	-0.010	0.070	-0.033	0.050	0.033	0.037
HT	0.081	-0.117	0.002	-0.009	-0.016	-0.052	0.076	0.033
DT	-0.242	-0.212	0.081	0.007	-0.011	-0.059	0.376	0.059
NB	-0.260	0.099	0.073	-0.003	0.052	-0.039	0.061	0.013
Σ	-1.816	-0.734	0.000	0.474	-0.784	-0.182	1.856	0.806

(Column heading above Bu–Gu: Population)

Table 4.11c. **The result of the multiplication of the component III weightings (Table 4.7.) and the standardised means (Table 4.10.) for each measured variable and for each population**

Population.

Variable	Bu	Ch	Ov	Ra	Ss	Yb	Br	Gu
NLY	0.012	-0.005	0.001	-0.003	-0.003	-0.005	0.001	0.002
LYG	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
AL	0.039	-0.058	0.041	-0.130	0.068	-0.010	0.027	0.000
LL	0.150	0.029	-0.005	0.014	0.086	-0.105	-0.100	-0.033
LB	0.270	0.000	0.090	-0.090	0.090	0.000	-0.180	-0.090
LP	-0.042	-0.242	0.033	0.058	-0.058	-0.092	0.242	0.058
DL	0.331	-0.119	0.029	-0.133	0.119	0.061	-0.119	-0.009
NBY	0.056	-0.053	-0.007	-0.014	-0.018	-0.009	0.022	0.018
BL	-0.385	0.011	0.034	0.181	-0.079	0.142	0.074	0.096
BB	-0.368	0.057	-0.025	0.172	-0.082	0.123	0.082	0.090
HT	0.388	-0.558	0.008	-0.041	-0.078	-0.251	0.362	0.160
DT	-0.400	-0.351	0.136	0.012	-0.019	-0.099	0.622	0.099
NB	-0.272	0.103	0.076	-0.003	0.054	-0.041	0.064	0.014
Σ	-0.221	-1.186	0.411	0.023	0.080	-0.286	1.097	0.405

Table 4.11d. The result of the multiplication of the component IV weightings (Table 4.7.) and the standardised means (Table 4.10) for each measured variable and for each population

	Population							
Variable	Bu	Ch	Ov	Ra	Ss	Yb	Br	Gu
NLY	0.105	-0.044	0.010	-0.027	-0.029	-0.049	0.011	0.022
LYG	-0.018	0.035	0.001	0.015	0.023	0.017	-0.038	-0.033
AL	-0.133	0.197	-0.140	0.440	-0.230	0.035	-0.092	0.001
LL	0.372	0.072	-0.012	0.036	0.216	-0.264	-0.252	-0.084
LB	-0.120	0.000	-0.040	0.040	-0.040	0.000	0.080	0.040
LP	0.050	0.290	-0.040	-0.070	0.070	0.110	-0.290	-0.070
DL	-0.147	0.053	-0.011	0.059	-0.053	0.027	0.053	0.004
NBY	-0.040	0.038	0.005	0.010	0.013	0.006	-0.015	-0.013
BL	0.282	-0.008	-0.025	-0.133	0.058	-0.104	-0.054	-0.071
BB	0.286	-0.044	0.019	-0.134	0.064	-0.095	-0.064	-0.070
HT	0.189	-0.273	0.004	-0.020	-0.038	-0.122	0.177	0.078
DT	-0.211	-0.186	0.072	0.006	-0.010	-0.052	0.329	0.052
NB	-0.260	0.099	0.073	-0.003	0.052	-0.039	0.061	0.013
Σ	0.355	0.229	-0.084	0.219	0.096	-0.584	-0.094	-0.131

Table 4.12. Coordinate values for individual populations for the first four components.

Population	I	II	III	IV
Bu	2.151	-1.816	-0.221	0.355
Ch	-1.559	-0.734	-1.186	0.229
Ss	-0.206	-0.784	0.080	0.096
Yb	-0.958	-0.182	-0.286	-0.584
Ov	0.049	0.000	0.411	-0.084
Ra	-0.925	0.474	0.023	0.219
Gu	0.257	0.806	0.405	-0.131
Br	0.495	1.856	1.097	-0.094

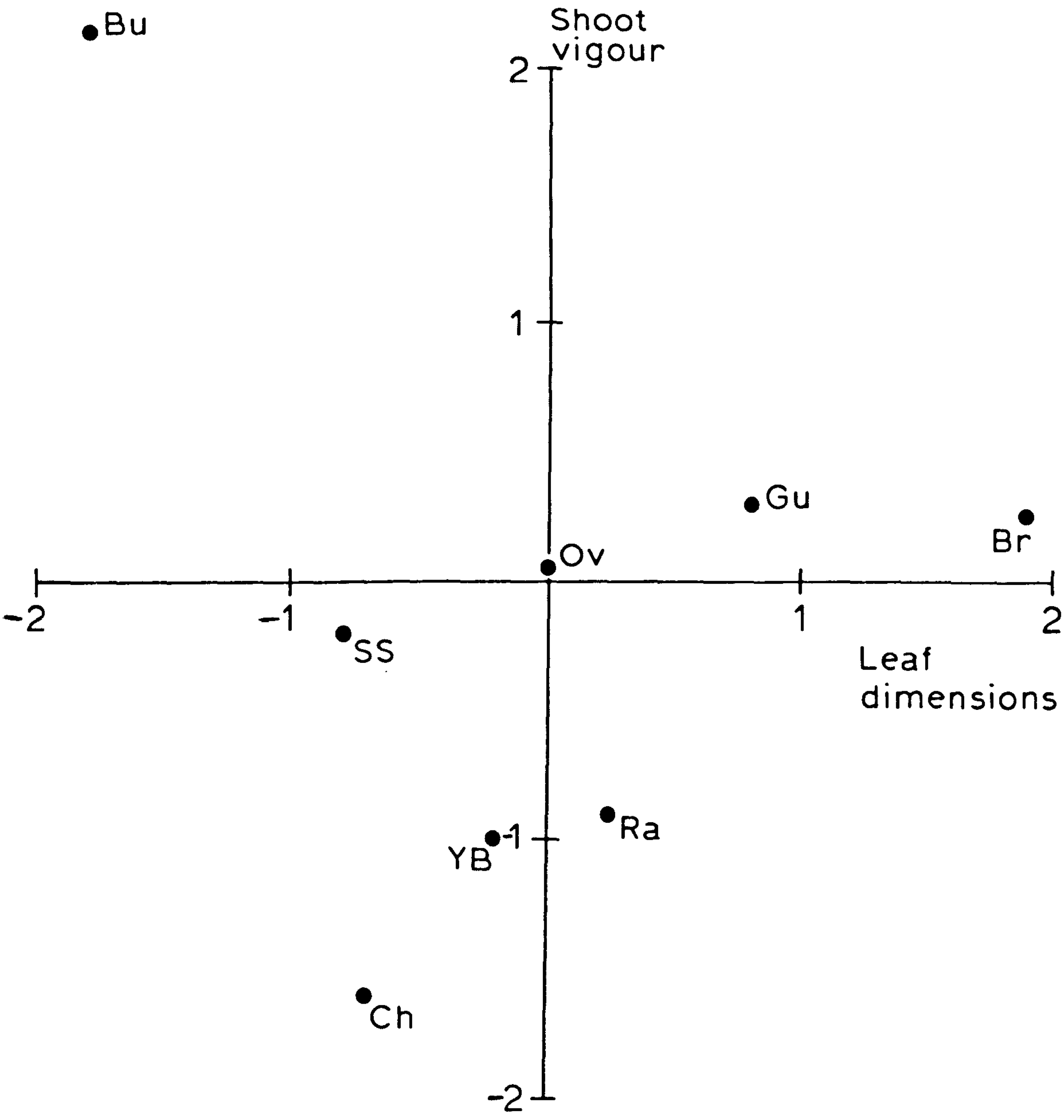


Fig 4.4. The mean population coordinates along the shoot vigour and leaf dimension axes.

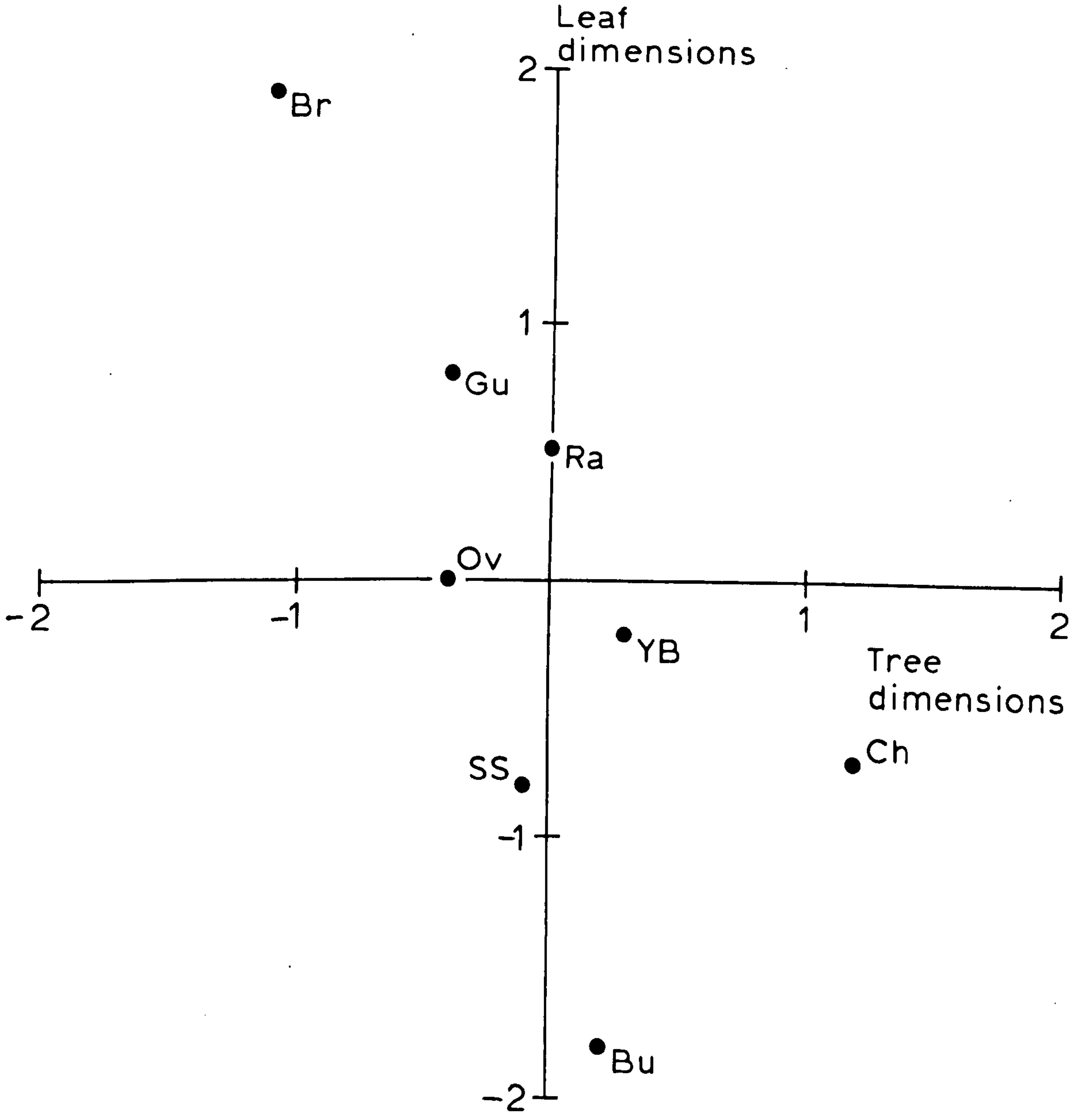


Fig 4.5. The mean population coordinates along the leaf dimension and tree dimension axes.

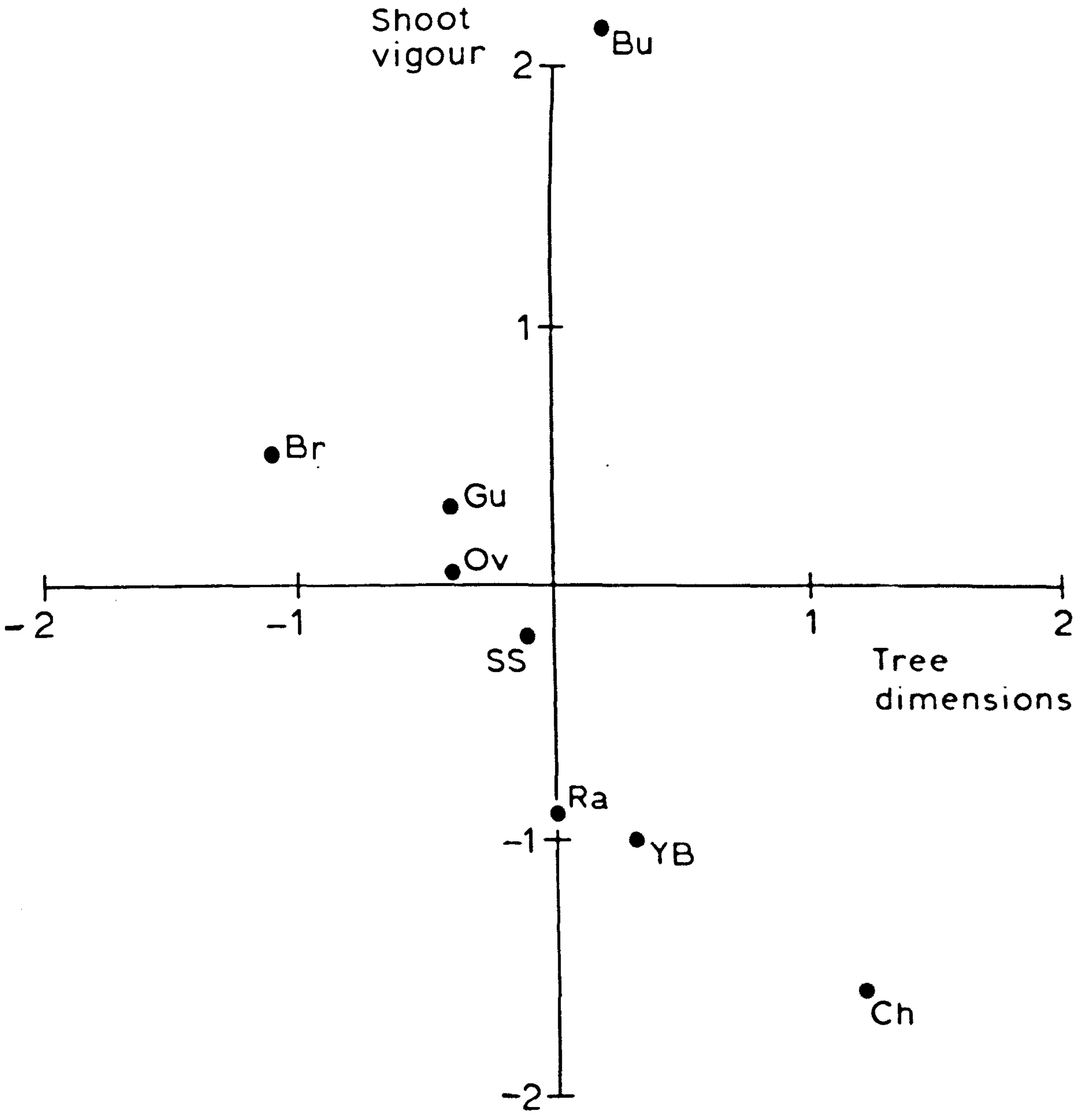


Fig 4.6. The mean population coordinates along the shoot vigour and tree dimension axes.

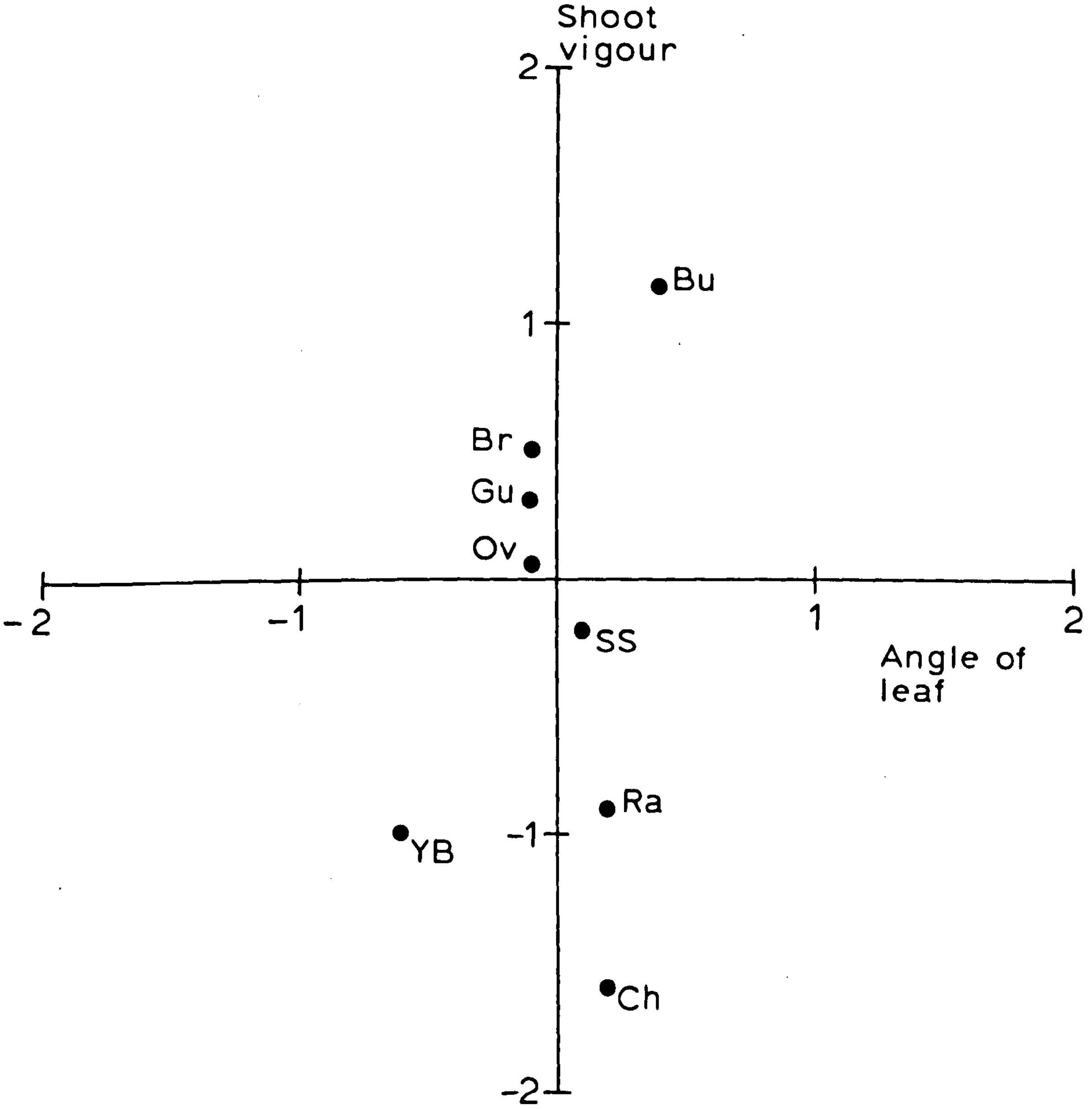


Fig 4.7. The mean population coordinates along the shoot vigour and angle of leaf axes.

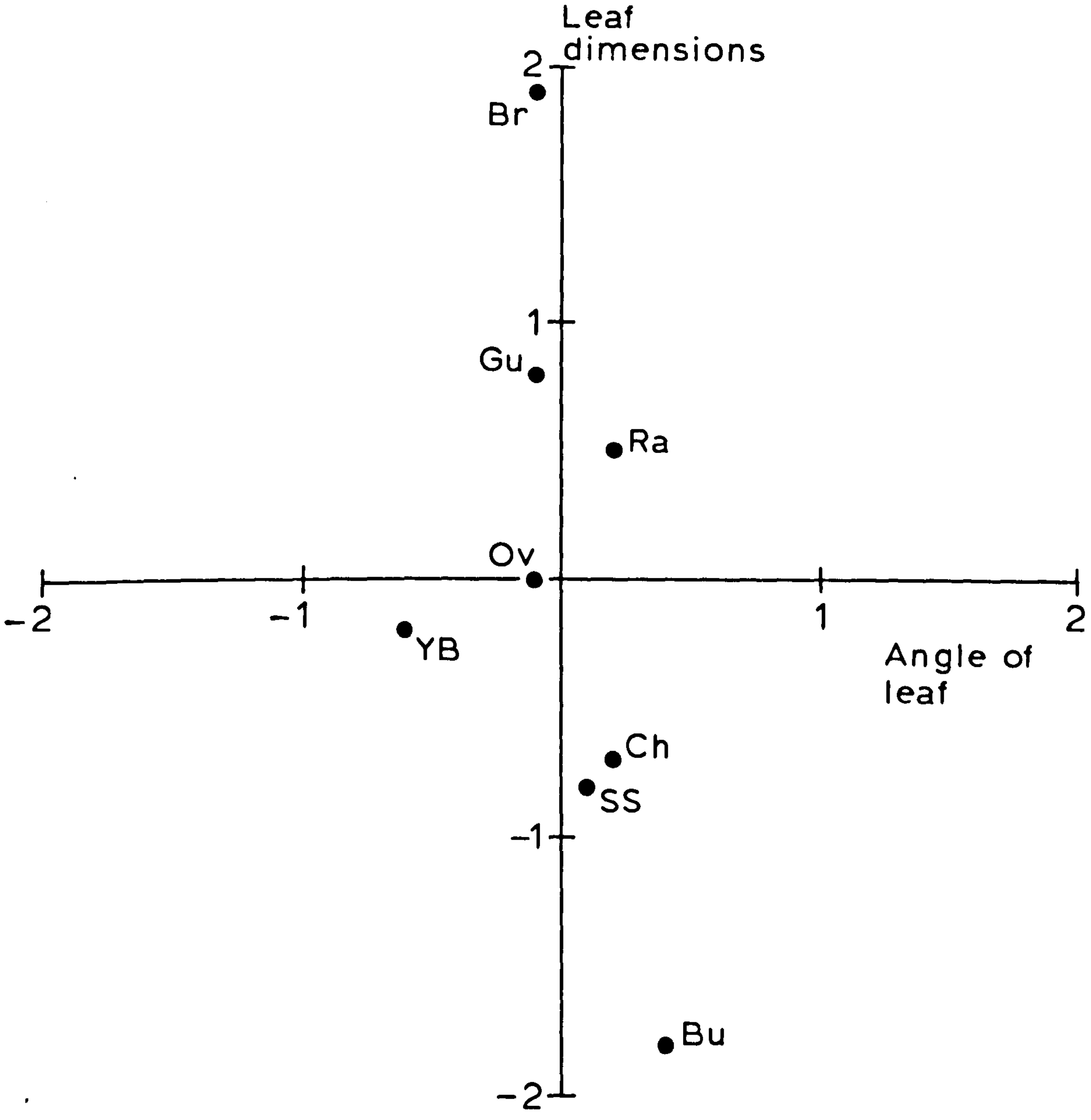


Fig 4.8. The mean population coordinates along the leaf dimension and angle of leaf axes.

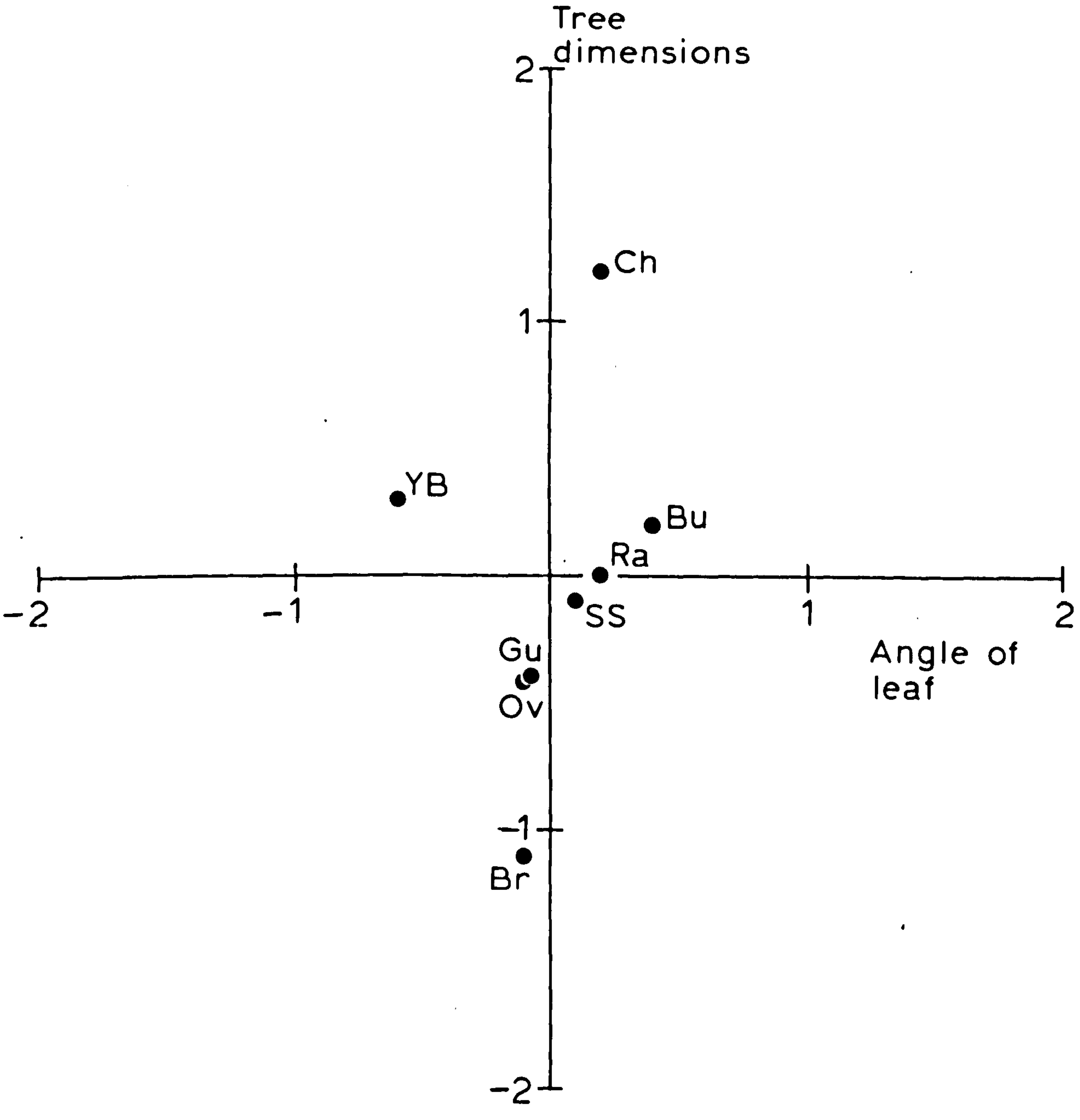


Fig 4.9. The mean population coordinates along the tree dimension and angle of leaf axes.

there are no distinct groupings of populations. There is however, a gradual increase of leaf dimensions from Butser Hill to Scout Scar, Chichester Road, Yew Barrow, Overton Hall, Ravensdale and Guisborough to Brantingham. This trend can also be seen in Fig 4.5, which is a plot of component II and component III, the leaf and tree dimension axes respectively. Along component III, a group of six populations can be seen, namely Butser Hill, Scout Scar, Yew Barrow, Overton Hall, Ravensdale and Guisborough. Chichester Road has the highest score along this axis, and Brantingham the lowest. This grouping can also be seen in the component III plot of Fig 4.6. Figs 4.7 to 4.9 represent component IV, that is leaf angle against shoot vigour, leaf dimensions and tree dimensions. The groupings of populations in Fig 4.7 show the same groupings as in graph 4.4 along the shoot vigour axis; however, the separation of the populations along the angle of leaf axis is very small, with six out of the eight populations showing similar values, namely Brantingham, Guisborough, Overton Hall, Scout Scar, Ravensdale, and Chichester Road. Butser Hill shows the highest leaf angle value, and Yew Barrow the lowest. This pattern is repeated in Figs 4.8 and 4.9, with the patterns along the leaf dimension (Fig 4.8) and tree dimensions (Fig 4.9) being the same as those found in the preceding graphs (Fig 4.5 and 4.6) and along the leaf angle axis there being little difference between the populations.

(A) Discussion of results.

At this point a reiteration of the aims of this study should be noted. The main purpose was to assess variation of yew tree populations in the north of England. A second aim was a comparison of northern populations with populations from the south of the country. When examining the linkage diagram of significant correlations from the matrix, three groups of variables were suggested. Group I consisted of the number of leaves on the shoot, the length of the shoot, the number of buds on the shoot, and the bud's length and breadth.

Group II consisted of the leaves' length and breadth and the transverse section of the leaf. Group III consisted of the height and circumference of the tree. Although these were subjective groupings, they were the most highly correlated variables from the correlation matrix, and indeed these three groupings of variables corresponded closely to the first three components in the analysis. The examination of the eigenvalues indicated that only the first four components should be considered, which confirms the comment that large numbers of significant correlations suggest that a relatively small number of useful components will be extracted from the matrix. Component names were given to combined groups of the original variables extracted from the eigenvectors within each component, namely shoot vigour for component I, leaf dimensions for component II, tree dimensions for component III and leaf angle for component IV.

By plotting the population scores for the four components graphically, an indication of variation between populations has been achieved. It has been mentioned that Butser Hill is a pure yew wood in the south of England. When looking at its position along component I (Fig 4.4), it can be seen to exhibit a very high shoot vigour as compared to other populations. This fact suggests in a negative and contrasting way that the yew tree is beyond its optimal environmental growth conditions in the north of England. With reference to the groupings of yew tree populations along this component, indicated in the description of figures section, it will be noted that there are two groups, one of four populations, i.e. Ss, Ov, Gu and Br; and one of two, i.e. Yb and Ra. This shows that there are no regional differences between the northern populations, and if anything the within-region differences are greater; with Ss forming a group with Ov, Gu and Br, representing three different regions, i.e. Cumbria, Derbyshire and the northeast, and Yb and Ra forming the other group representing Cumbria and Derbyshire respectively. It should also be pointed out that the two populations from the northeastern side of England, i.e. Gu and Br, have a shoot vigour equivalent to any of the other northern populations sampled. This is surprising, as a priori reasoning might suggest that they should show the lowest growth potential as this is the region in which populations of yews are rare.

At this point, an explanation for the lowly position of the Chichester Road population along this component also should be made. If the suggestion above is correct, that the yew is beyond its optimal environmental conditions in the north of England, this suggests that the yews in the south should be nearer the optimal conditions for growth in the British Isles. That being the case, why does Ch show such a low shoot vigour? It must be remembered that the southern populations were selected for comparison with those of the northern regions.

The stand at Chichester Road contained tall yews, with the healthy branches skyward; these branches were too high for the shoot samples to be collected. The shoots were therefore collected from the lower dying branches. For this reason it is not surprising that the shoots showed a low vigour. The population was included in the analysis, as they were taken from the tallest yews sampled in the south, and therefore presented an important comparison with those taken from northern yews.

In examining Fig 4.4, along the second component, the leaf dimension axis, the populations show a continuous trend of increasing leaf dimensions with the southern population, Bu having the lowest. Looking at the northern populations, leaf dimensions increase in the following way; Ss and Yb show the lowest leaf dimensions in the north, then Ov and Ra with Gu and Br showing the largest leaf dimensions of all. The increase in leaf dimensions in the north in comparison with the southern population is quite a typical pattern; as southern shoots are longer, they will need less leaf area for the photosynthetic process, and thus an increase in leaf dimensions in the north would be expected. Within the north there is a gradual increase in leaf dimensions towards the northeast region, i.e. from Cumbria to Derbyshire to the northeast, a trend that can be clearly seen in Fig 4.5. This clinal trend amongst the northern regions is difficult to explain without added experimental data, but from this analysis it is clear that this trend exists.

The tree dimension axis, component III (Fig 4.5) shows little variation between the northern yew populations and the yews of the pure wood at Butser Hill. The two extremes are shown to be the Chichester Road population and the Brantingham population: the yews in Brantingham show very poor height and circumference growth relative to other populations; and those in Chichester Road suggest that trees can assume large proportions with respect to those of other regions. In Fig 4.6, the clustering of the six populations is seen clearly. Fig 4.7 shows shoot vigour plotted against component IV, i.e. leaf angle. As might be expected the groupings of populations are the same as in Fig 4.4, along the shoot vigour axis; however, there is very little difference between the populations along the leaf angle axis, with Brantingham, Guisborough, Overton, Scout Scar, Ravensdale and Chichester clustering around the central axis. The two extremes are Butser Hill, showing the highest leaf angle and therefore the lowest leaf length, and Yew Barrow, showing the lowest leaf angle and therefore the highest leaf length. In these three graphs (Fig 4.7 to 4.9) there is very little separation of the populations along the leaf angle axis, and the general trends along the first three components are seen to be similar to those of the first three figures.

A graphical representation of population coordinates indicates the general trends of populations, but what of the within-site variability? In order to get some understanding of this the coordinates of the individual trees were plotted for the first three components. These coordinates were calculated by the P.C.A. package, and the results are shown in Table 4.13.

Table 4.13. Coordinates for individual trees for the first three components.

Individual	Component		
No.	I	II	III
1	0.96	-2.08	-1.05
2	2.85	-2.15	-0.50
3	3.23	-0.58	0.19
4	10.05	-1.11	-0.75
5	3.23	-0.81	-1.06
6	1.38	-1.21	-0.53
7	3.60	-0.84	-1.69
8	3.41	-1.14	0.79
9	5.98	-2.78	-0.41
10	1.95	-3.07	-0.30
11	4.86	-0.77	-0.14
12	4.17	-1.12	-0.49
13	1.04	-2.09	0.28
14	2.78	-2.96	0.17
15	1.39	-2.41	-0.66
16	-1.61	-0.70	-0.06
17	0.81	-2.97	-0.88
18	2.69	-0.58	-1.18
19	3.37	0.29	-2.27
20	0.55	-2.47	2.58
21	1.47	0.15	0.42
22	2.04	-1.46	1.17
23	2.35	-1.93	-0.40
24	1.28	-1.03	1.26
25	2.71	-2.10	-0.66
26	2.59	-4.01	-0.51
27	1.89	-3.55	-2.22
28	2.73	-4.53	-1.90
29	1.61	-1.87	1.71
30	3.78	0.07	1.03

Table 4.13. (Cont.)

Individual	Component			Individual	Component		
No.	I	II	III	No.	I	II	III
31	-0.52	-0.65	-1.43	46	-2.75	-2.12	-1.86
32	-1.14	-0.17	-1.55	47	-1.93	1.15	-3.18
33	0.34	1.90	-3.91	48	-2.38	-2.31	-0.66
34	-3.44	-0.84	-0.98	49	-1.45	-0.39	0.51
35	-1.51	0.03	-1.12	50	-0.53	-1.02	-0.63
36	-2.51	-0.44	-0.45	51	0.17	-0.66	-3.58
37	-0.67	0.85	-2.51	52	-2.21	-0.15	-1.87
38	0.46	0.09	-0.13	53	-2.13	0.43	-0.88
39	-0.55	-0.81	-0.16	54	-1.55	1.25	-2.55
40	-1.44	-1.29	-0.42	55	-2.57	-3.10	1.29
41	-1.23	-3.51	-0.66	56	-1.82	-3.22	0.00
42	-2.17	-1.87	-0.11	57	-1.34	-2.80	-0.75
43	-2.88	-0.88	-0.15	58	0.15	0.58	-2.42
44	-2.60	-0.56	-0.97	59	-0.84	0.29	-1.92
45	-2.99	0.89	-0.61	60	-1.62	-3.03	-1.80

Table 4.13. (Cont.)

Individual	Component		
No.	I	II	III
61	-0.35	1.72	-0.88
62	-1.12	1.51	0.19
63	-1.09	-0.18	-0.09
64	-0.78	-0.65	0.70
65	0.08	1.20	0.34
66	-0.10	-0.45	0.75
67	1.64	-0.76	0.87
68	0.99	-1.86	0.50
69	-0.57	-1.18	0.13
70	0.06	-1.35	1.49
71	0.03	0.53	-0.71
72	-0.42	0.26	0.89
73	1.86	0.00	0.98
74	-0.28	0.42	2.13
75	-0.30	1.23	0.95
76	1.22	-0.72	-0.68
77	-0.46	1.61	1.15
78	-0.81	-0.84	2.44
79	0.29	1.33	-0.01
80	-1.69	-0.92	1.20
81	0.88	1.31	-0.18
82	-0.14	1.01	-0.86
83	-1.03	1.80	0.85
84	1.12	0.66	-0.15
85	0.29	1.59	0.21
86	0.63	-0.46	-0.87
87	0.41	1.04	-1.09
88	0.41	-1.12	-0.29
89	-0.73	-1.47	0.58
90	1.32	-2.36	0.20

Table 4.13. (Cont.)

Individual No.	Component I	II	III
91	-1.78	-0.84	1.08
92	-2.48	-0.87	1.38
93	-1.35	0.26	-0.57
94	1.85	1.23	1.71
95	0.93	0.70	-0.16
96	1.96	2.17	-0.46
97	-1.37	1.22	0.71
98	0.98	2.68	-0.70
99	0.70	2.61	0.07
100	-1.33	2.18	-0.70
101	-0.01	0.59	-0.43
102	-1.49	-1.65	1.66
103	-0.31	0.36	0.56
104	-0.07	-2.80	-0.74
105	-1.75	-0.87	0.09
106	-2.39	-1.21	-1.73
107	-2.20	0.26	0.61
108	-2.41	0.79	0.97
109	-1.31	2.57	-1.24
110	-0.81	1.49	-1.36
111	-2.47	0.55	0.55
112	-1.56	0.06	-0.58
113	-0.26	2.47	-1.20
114	-1.15	0.52	-0.88
115	-3.26	1.35	-0.65
116	0.89	-1.43	-0.04
117	0.52	-0.46	-2.36
118	-3.33	-1.43	1.62
119	1.03	-1.59	-0.72
120	-1.00	-2.80	1.34

Table 4.13. (Cont.)

Individual		Component		Individual		Component	
No.	I	II	III	No.	I	II	III
121	0.35	-0.47	1.45	136	-0.85	0.38	-0.24
122	1.62	-1.85	1.36	137	-2.68	-1.37	1.30
123	-0.58	-2.34	1.64	138	-0.12	0.16	-0.60
124	-1.09	-0.57	0.98	139	-1.28	-1.03	0.91
125	-0.65	-2.01	0.07	140	-2.00	0.38	0.92
126	-0.36	0.92	-0.42	141	1.47	0.28	-2.89
127	-3.15	0.00	-1.52	142	3.50	0.08	-1.46
128	-1.91	-0.38	-0.04	143	0.85	0.41	0.63
129	0.58	-1.02	-1.78	144	-0.54	-0.96	0.17
130	1.74	0.05	-1.30	145	2.81	-1.43	-1.12
131	1.09	-1.70	-0.60	146	-0.24	-0.11	-1.31
132	-0.60	0.55	0.80	147	-2.90	-0.12	0.31
133	-2.29	-1.29	1.95	148	-0.85	0.96	-0.39
134	-1.43	-1.23	0.76	149	-1.85	1.67	-2.52
135	1.78	-2.22	1.96	150	-1.54	-1.13	0.14

Table 4.13. (Cont.)

Individual	Component			Individual	Component		
No.	I	II	III	No.	I	II	III
151	-1.41	1.13	0.19	166	-0.39	-0.11	0.45
152	-1.27	0.55	-1.48	167	-1.71	-0.98	1.23
153	0.58	-1.79	1.10	168	0.16	-0.99	-0.10
154	-0.24	0.76	0.32	169	0.18	1.59	-1.05
155	-2.38	-1.50	0.46	170	-2.24	1.79	-0.40
156	-1.84	-2.32	1.49	171	-1.80	-0.16	-1.31
157	-0.64	0.54	-0.64	172	1.15	-2.52	-2.15
158	-0.98	-1.07	0.45	173	0.69	0.84	-3.06
159	0.13	-0.45	-0.22	174	-2.11	0.51	0.70
160	0.20	-0.20	-0.20	175	-2.53	0.24	0.15
161	-1.27	0.30	-0.29	176	1.40	0.34	2.95
162	-1.18	-0.68	0.57	177	0.21	2.35	2.55
163	0.00	0.71	-0.71	178	-0.11	-0.49	3.25
164	0.29	-0.37	-1.62	179	-0.15	2.99	0.36
165	-2.71	-2.21	1.79	180	0.37	3.43	0.40

Table 4.13. (Cont.)

Individual	Component			Individual	Component		
No.	I	II	III	No.	I	II	III
181	1.70	-0.44	2.45	196	0.78	2.70	0.87
182	3.61	1.75	1.29	197	-0.59	1.49	0.38
183	3.53	1.38	2.65	198	-0.10	2.28	1.03
184	0.41	1.56	2.12	199	1.98	1.88	0.98
185	-0.72	2.28	1.61	200	-0.18	2.66	0.75
186	0.72	0.48	1.39	201	-0.51	1.53	1.39
187	2.94	2.15	-0.05	202	-0.20	1.22	0.60
188	-0.99	0.82	0.39	203	1.74	1.06	2.40
189	0.27	2.31	1.12	204	-0.64	2.26	1.06
190	-0.82	2.65	0.79	205	-0.68	2.20	-0.37
191	2.60	3.24	0.68	206	0.74	1.81	1.56
192	0.07	1.81	0.12	207	-0.59	3.13	-2.47
193	-1.05	2.30	-0.17	208	2.93	1.10	1.61
194	-0.51	1.57	1.73	209	4.96	1.10	2.09
195	-1.43	3.21	-0.12	210	5.20	2.38	1.27

Table 4.13. (Cont.)

Individual No.	Component I	II	III
211	2.30	1.40	0.51
212	3.73	2.83	-1.04
213	1.88	2.58	-0.10
214	-1.10	-1.49	1.64
215	-2.69	0.89	0.74
216	0.21	0.77	0.04
217	1.56	1.13	-0.21
218	-0.91	0.39	-2.38
219	3.51	1.61	1.03
220	2.99	3.58	-2.63
221	-0.44	2.02	-0.35
222	-1.93	-0.61	1.15
223	-1.15	-1.15	0.87
224	0.95	0.73	1.15
225	-2.57	2.47	0.47
226	0.73	0.64	0.52
227	-2.10	1.09	0.15
228	-1.08	0.89	0.65
229	-2.68	-2.37	0.02
230	-1.18	0.72	0.96
231	-0.25	2.06	-0.67
232	-1.11	1.47	-1.26
233	-2.77	-1.18	1.10

These coordinates were plotted onto graphs, shown in Figs 4.10 to 4.12, which display scatter diagrams of the tree individuals. The different symbols on the figures indicate the eight populations in the survey, and each point represents an individual tree showing its position along the first three components in relation to the others. Representing the eight populations with different symbols will give an indication of differences between them, and therefore supplement the conclusions obtained by reference to the comparison of overall population means in the section above.

It can immediately be seen that in all three graphs (Figs 4.10 to 4.12) individuals from populations intermingle, suggesting that there is no absolute and discrete separation of populations in terms of the measured variables. One way of examining these graphs more closely is to find out how many individuals from each population fall into each quadrant. These are identified by ++, --,+-, and -+, as shown on the graphs. Individuals that lie in the ++ quadrant of the graph show a positive value along both of the components being discussed; individuals in the negative quadrant show a negative value; individuals in the positive-negative quadrant show a positive value along the vertical axis and a negative value along the horizontal axis; and the individuals in the negative-positive quadrant show a negative value along the vertical axis and positive along the horizontal axis. When an individual lies on the line of an axis, it will be considered positive in all cases. Each graph is accompanied by a table summarising the number of individual trees that lie within each quadrant for each population. When examining the number of individuals from a particular population within each quadrant of the graph, it can be said that the segments that have low numbers of individuals from a population would suggest that these individuals are outliers of the general trend in that population. Conversely, when it is found that the spread of individuals is not obviously different between

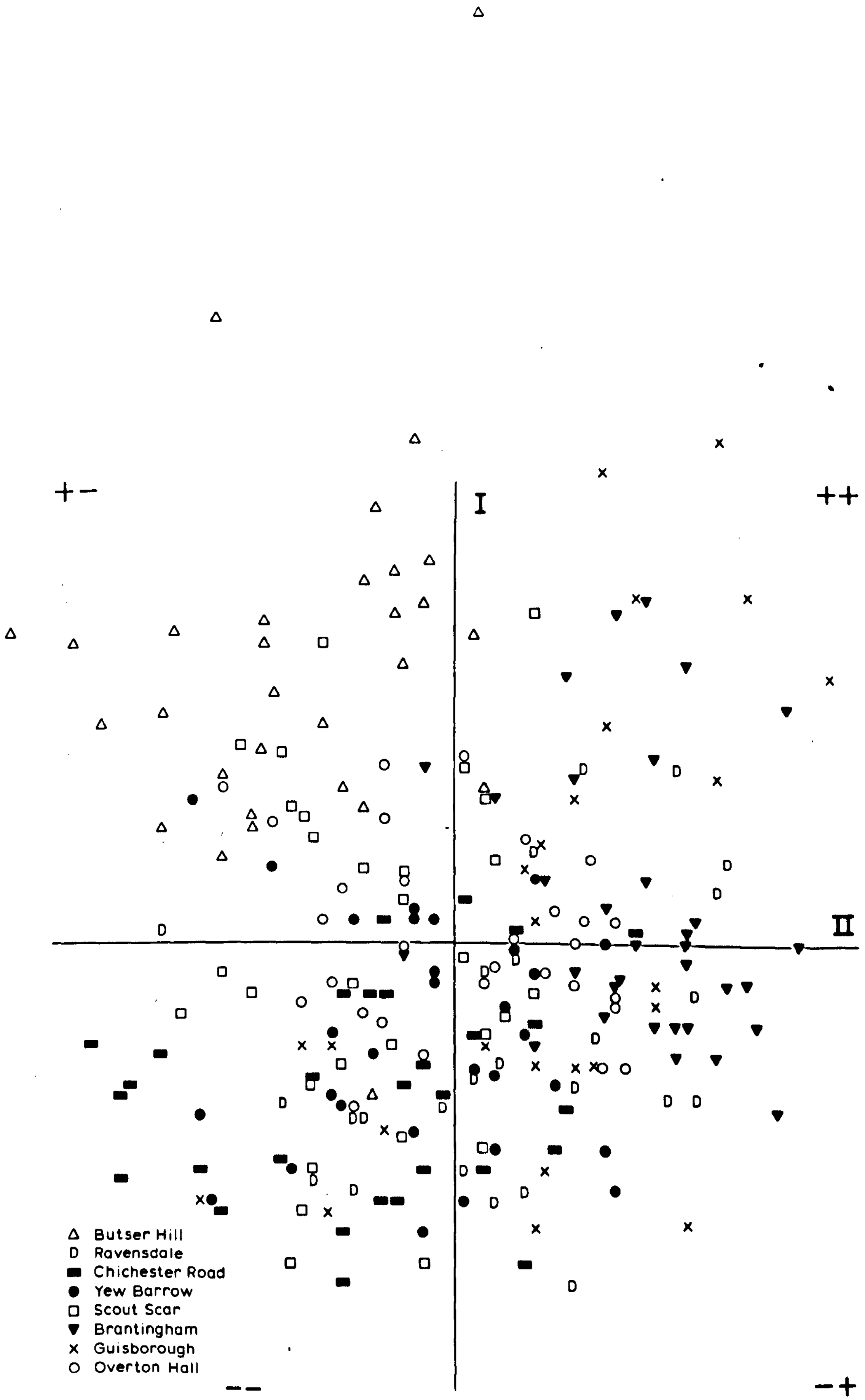


Fig 4.10. Scatter diagram of individual tree coordinates along component I and component II.

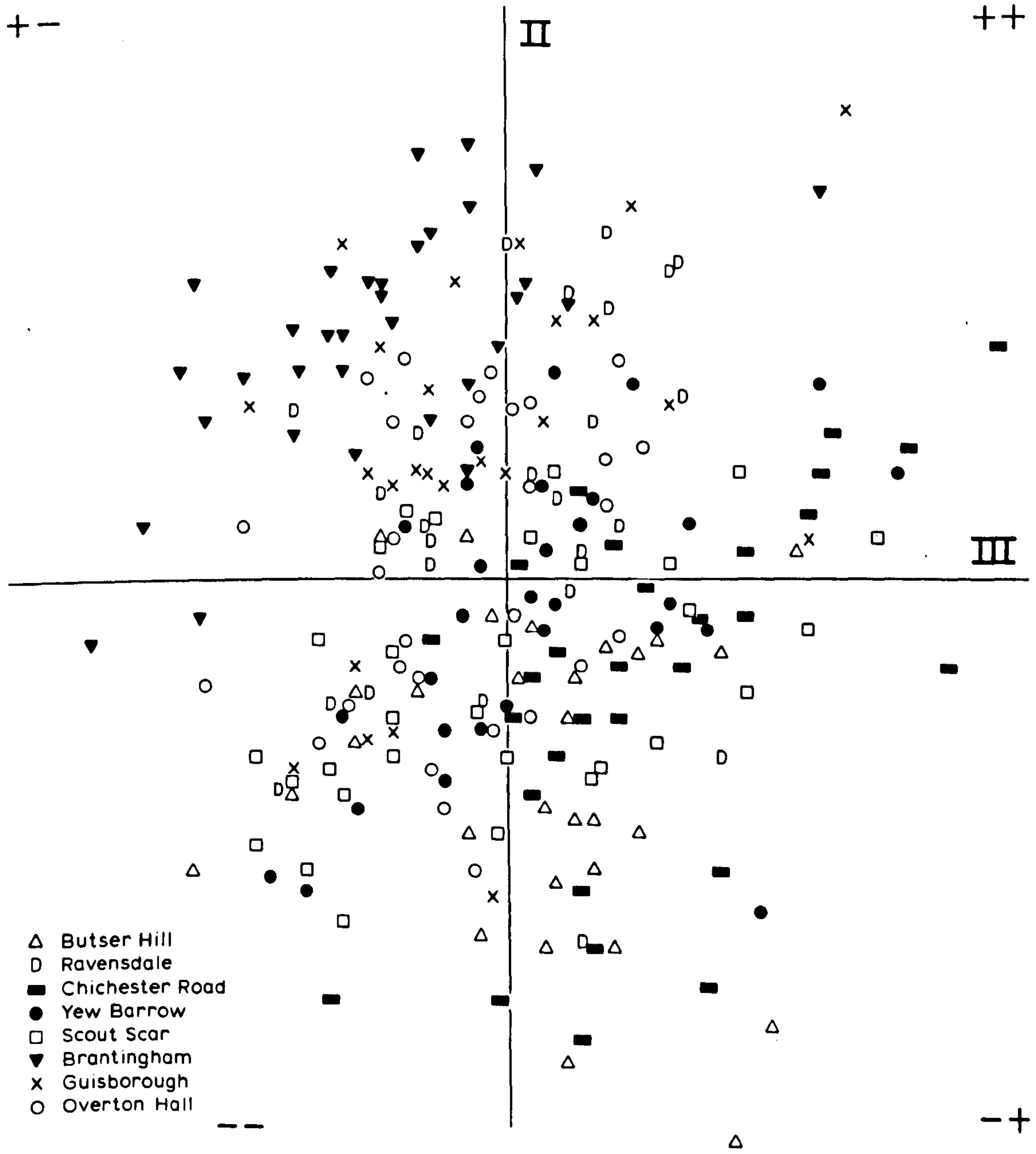


Fig 4.11. Scatter diagram of individual tree coordinates along component II and component III.

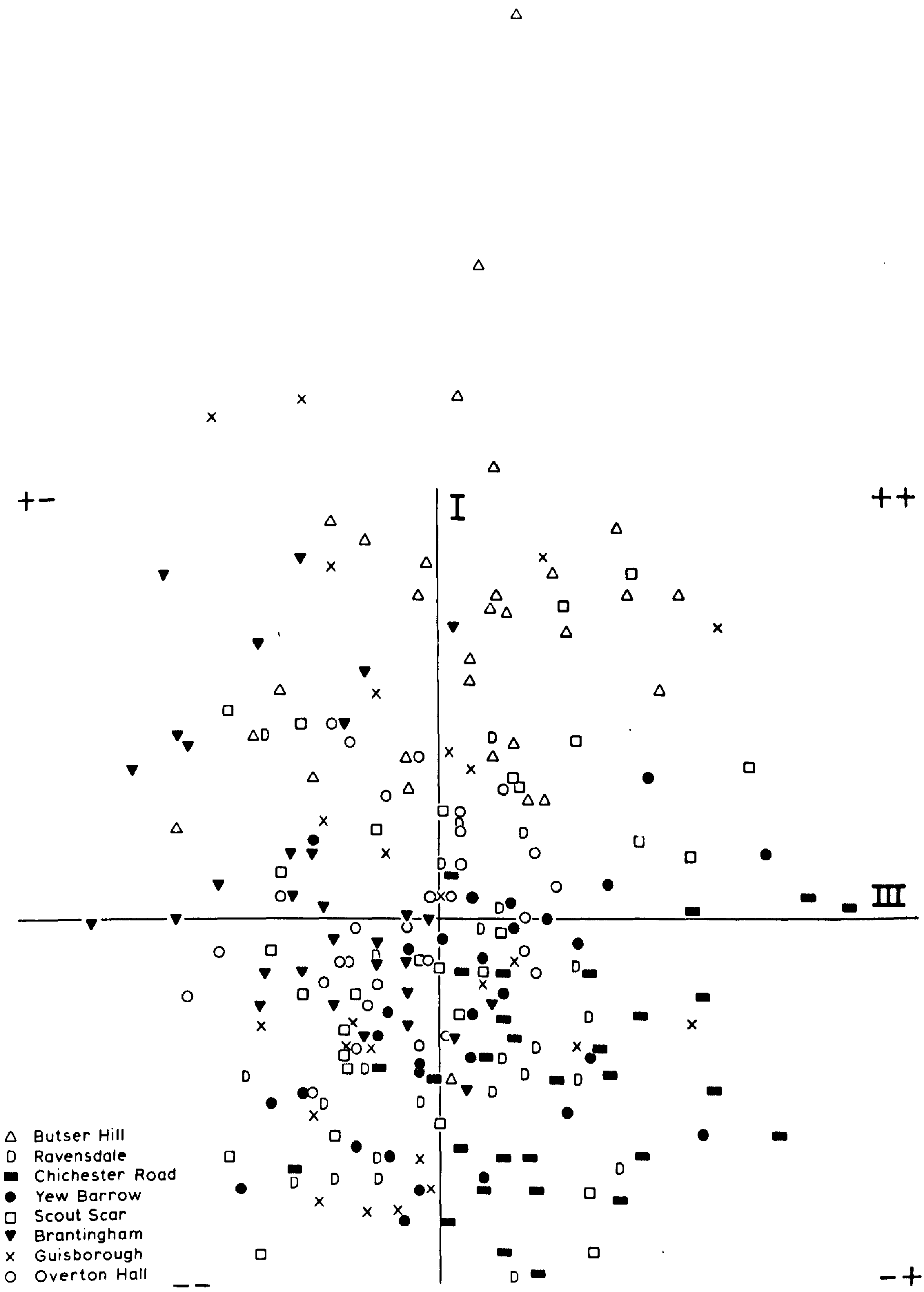


Fig 4.12. Scatter diagram of individual tree coordinates along component I and component III.

the segments no outliers can be noted. Further analysis is given below.

Fig 4.10. This graph is a scatter diagram of the individual tree coordinates along component I and component II, i.e. shoot vigour and leaf dimensions respectively. Therefore, the ++ quadrant shows the individuals that have a positive value for both shoot vigour and leaf dimensions, the +- quadrant shows the individuals that have a positive shoot vigour value and negative leaf dimension value, the quadrant -- shows the individuals that have negative values for shoot vigour and leaf dimension, and finally, the -+ quadrant shows the individuals that have a negative value for the shoot dimension character and a positive value for the leaf dimension character.

Table 4.14 summarises the number of individuals from each population that fall within the quadrants as described above. It can be seen from this table that 26 out of 30 trees sampled in Butser Hill (Bu) fall in the +- quadrant, i.e. with positive shoot vigour and negative leaf dimensions; of the other four individuals, 3 are in the ++ quadrant and 1 in the -- quadrant, and these can be said to be outliers of this population. In the Chichester Road population (Ch), 20 trees lie in the -- quadrant out of the 30 sampled, while 3 of the other 10 are in the ++ quadrant, 1 is in the +- quadrant and 6 are in the -+ quadrant, suggesting that negative shoot vigour and leaf dimensions characterise this population, although this is not as clear cut as in Bu. In Scout Scar (Ss), there is not one quadrant that typifies the population, for 12 trees lie in the -- quadrant and 9 lie in the +- quadrant, i.e. 21 out of 30 trees sampled have a negative leaf dimension in common although these are spread across the shoot dimension characteristic. The 9 remaining trees lie in the other two quadrants, 4 in ++, and 5 in -+. From Yew Barrow (Yb), the majority of trees lie in two quadrants of the graph, i.e. 11 in -- quadrant and 11 in -+ quadrant, indicating that 22 trees out of the 30 sampled show a negative shoot vigour while they are evenly distributed

Table 4.14. Numbers of individuals that fall into each quadrant from each population along components I and II.

Quadrant	Population Bu	Ch	Ss	Yb	Ra	Ov	Gu	Br
++	3	3	4	2	5	8	11	16
--	1	20	12	11	6	7	5	1
+-	26	1	9	6	1	7	0	1
-+	0	6	5	11	13	8	9	15

across the leaf dimension characteristic. The remaining 8 trees lie in the other two quadrants, 2 in ++, and 6 in +-. Out of the 25 trees sampled at Ravensdale (Ra), 13 fell in the -+ quadrant, 5 were in the ++ quadrant and 6 in the -- quadrant, while 1 and therefore an outlier fell in the +- quadrant. The most evenly-spread population through the four quadrants was Overton Hall (Ov) where, out of the 30 trees sampled, 8 fell in the ++ quadrant, 7 in the -- quadrant, 7 in +- quadrant, and 8 in -+ quadrant. In the Guisborough population (Gu), 20 out of the 25 trees sampled fell into two quadrants, 11 in ++, and 9 in -+, with the common characteristic of positive leaf dimensions and a spread across the shoot vigour characteristic. The remaining 5 trees fell into the -- quadrant and therefore for leaf dimensions can be considered to be outliers. A stronger positive leaf dimension characteristic is found in the last of the populations, Brantingham (Br), which showed the same general bias as Guisborough, with 31 of the 33 trees falling into the two quadrants, ++ and -+, i.e. with 16 trees in ++, and 15 in -+. This also shows that there is an approximately even spread of the trees across the shoot vigour axis. Finally, the two outliers in this population fall into the two remaining quadrants, 1 in --, and 1 in +-.

According to these results, the tendency is not towards distinct population differences along these two components, but for an overlap of trees from different populations. However, it is possible to say that the most consistent population, as far as shoot vigour is concerned, is Butser Hill, which shows 29 out of the 30 trees sampled having a positive value for this character. Also, the general trend in this population is to have positive shoot vigour and negative leaf dimensions, and therefore the population mean coordinate graph in the section above is confirmed, with the qualification that the variation within the population shows that there is overlapping with the other populations to some degree. The general trend in the Chichester Road population is also confirmed by the majority of the individuals lying in the -- quadrant. In the case of Scout Scar, although there is a trend showing negative leaf dimensions, shoot vigour seems to be highly variable; however, Yew Barrow, its regional neighbour, is variable in the opposite direction with the trend being one of low shoot vigour and variable leaf dimensions. In the Ravensdale sample, it can be seen that the majority of the trees show positive leaf dimensions, with variable shoot vigour; however, 13 out of the 25 trees measured, i.e. over 50% of the sample, fell into the -+ quadrant, suggesting that this might be considered its general trend. Large variation along the shoot vigour axis can also be seen for Guisborough; in fact, apart from Butser Hill, this population has two individuals that show the highest shoot vigour of all the other populations. However, it is extremely variable for this characteristic. The general trend along the leaf dimension axis is for a positive characteristic. Overton Hall shows itself to be very 'cosmopolitan' with no extremes and with the general collection of individuals lying around the point of origin, and showing no distinct trend. Finally, the Brantingham population shows a large shoot vigour variance, as does its northeastern neighbour, Guisborough; it also displays positive leaf dimensions.

From this scatter diagram, it can be seen that the general trend suggested by the population means is confirmed, but that individuals from all the populations can acquire high positive shoot vigour. But the lack of consistency in this variable in all the northern populations, as compared with Butser Hill, suggests a lack of overall optimum growth for this characteristic. It might be suggested that a surprising outcome of this study indicates that a few individuals from the two northeastern populations, Guisborough and Brantingham, show a high shoot vigour which is comparable to any of the other northern populations, and indeed approximates to that of the southern yew. The general trend of increasing leaf dimensions from the south to the north is confirmed by these results, with the extremes being Guisborough and Brantingham, which are highly positive, and Butser Hill, which is highly negative, with the other populations intermediate. It is of interest to note that of these intermediate populations there seems to be no regional consistency; for example, while the majority of the Scout Scar individuals show a negative leaf dimension characteristic and a variable shoot vigour, Yew Barrow shows a shoot vigour and a variable leaf dimension characteristic. Also, whereas Ravensdale shows a tendency towards negative shoot vigour and positive leaf dimensions, Overton Hall is described as 'cosmopolitan' as it does not fall into any particular quadrant and therefore cannot be said to have any general trend.

Fig 4.11. This is a scatter diagram of the individual tree coordinates along component II and component III, i.e. leaf dimensions and tree dimensions. Therefore, the ++ quadrant shows individuals that have a positive value for both leaf dimensions and tree dimensions, the +- quadrant shows individuals that have a positive leaf dimension and negative leaf and tree dimension, and finally, the -+ quadrant shows individuals that have a negative leaf dimension and a positive tree dimension.

Table 4.15 summarises the number of individuals from each population that fall within the quadrants. It can be seen from this table that 19 out of 30 trees sampled from Butser Hill fell in the -+ quadrant, i.e. with negative leaf dimensions and positive tree dimensions, whereas 8 trees fell in the -- quadrant, leaving three outliers, 1 in ++ and 2 in +-. This suggests that the majority of the trees show a negative leaf dimension characteristic, so agreeing with Fig 4.10 and Table 4.14, and as 20 out of the 30 trees show a positive tree dimension character this can be said to be the general trend. In the Chichester Road population, 18 trees out of the 30 sampled fell in the -+ quadrant, while 9 fell in the ++ quadrant, with 3 outliers in the -- quadrant,

Table 4.15. **Numbers of individuals that fall into each quadrant from each population along components II and III.**

	Population							
Quadrant	Bu	Ch	Ss	Yb	Ra	Ov	Gu	Br
++	1	9	6	9	12	7	9	5
--	8	3	13	9	4	10	5	2
+-	2	0	3	4	6	9	11	26
-+	19	18	8	8	3	4	0	0

suggesting that tree dimensions are strongly positive and, as in Butser Hill, the majority lie in the -+ quadrant; thus this can be considered as the general trend of this population. In Scout Scar, 21 trees out of 30 show negative values for leaf dimension, 13 in the -- quadrant and 8 in the -+ quadrant, with 6 in the ++ quadrant and 3 in the +- quadrant. However, a general trend of tree dimension is difficult to decide as 13 trees fall in the -- quadrant and 8 in the -+ quadrant; no overall trend can be suggested, only that tree dimensions vary in this population. The same problem arises with the Yew Barrow population, where 9 trees lie in the ++ quadrant, 9 in the -- quadrant, and 8 in the -+ quadrant, with 4 outliers in the +- quadrant. Therefore the conclusion should be drawn that there is a variation in both directions that shows no general trend. The Ravensdale population does show a general trend for leaf dimension with 19 out of 25 trees sampled falling into two quadrants, 12 in ++, and 6 in +-. The other 7 trees fall into the other two quadrants, 4 in -- and 3 in -+; these can be considered outliers. Therefore there is a trend towards positive leaf dimensions; however, there is no absolute trend in tree dimensions, and thus this can again be considered variable. Again, with the Overton Hall population, 10 trees fell in the -- quadrant, 9 in the +- quadrant, 7 in the ++ quadrant, with 4 outliers in the -+ quadrant. Therefore no general trend in either leaf dimension or tree dimension could be established for this population. In Guisborough, a trend could be suggested as 11 trees out of 25 could be found in the +- quadrant and 9 in the ++ quadrant, suggesting that there is a general trend of positive leaf dimensions but that tree dimensions are variable. There were 5 outliers in this sample in the -- quadrant. The overwhelming majority of trees from the Brantingham population fell in the +- quadrant, i.e. 26 out of 33 trees, suggesting that the trend for this population was for positive leaf dimensions and negative tree dimensions. Out of the 7 outliers, 5 fell in the ++ quadrant, and 2 in the -- quadrant.

The same point should be made here as was noted for the results in Fig 4.10, and that is that the tendency is not towards distinct population differences but towards an overlap between populations. In this particular scatter, it can be noted that there is agreement with the results in Fig 4.10 and Table 4.14 for leaf dimension, i.e. the general trends are the same for all the populations. In the case of tree dimensions, the overall trend is demarcated by the Chichester Road sample and the Brantingham sample, as these are highly positive and highly negative for this character respectively. It could also be suggested that Butser Hill tends towards positive tree dimensions, as 18 out of the 30 trees sampled showed this characteristic. However, the results from the other populations suggest that they are very variable for this character, with no general pattern being established.

Fig 4.12. So as to complete the picture, a scatter diagram of the individual tree coordinates along component I and component III and tree dimensions were drawn up, i.e. shoot vigour. From the results already presented, it would be expected that a comparison between these two variables would show corresponding results. Indeed, when studying the Butser Hill population, it can be seen that 29 out of the 30 individuals showed positive shoot vigour (Table 4.16), as in Fig 4.10 and Table 4.14. While there is a spread of individuals from positive to negative along the tree dimension axis, however, it could be suggested that the general trend is towards the positive side of the graph, as 19 individuals can be found in the ++ quadrant. For Chichester Road, 23 out of 30 trees fell in the -+ quadrant, suggesting the same general trend as before, i.e. towards positive tree dimensions and negative shoot vigour. In Scout Scar, the variable nature of the shoot growth and tree dimensions is demonstrated, for 10 trees lie in the -- quadrant, 9 in the ++ quadrant, 7 in the -+ quadrant, and 4 in the +- quadrant. The majority of the Yew

Table 4.16. Numbers of individuals that fall into each quadrant from each population along component I and III.

Quadrant	Bu	Ch	Ss	Yb	Ra	Ov	Gu	Br
	Population							
++	19	4	9	6	5	8	5	1
--	0	3	10	12	9	13	10	12
+-	10	0	4	1	1	6	6	16
-+	1	23	7	11	10	3	4	4

Barrow trees fall into two quadrants, 12 in --, and 11 in -+, indicating a general negative shoot vigour characteristic and a variable tree dimension characteristic. Ravensdale also shows this trend, with the majority of the trees lying in the same two quadrants as Yew Barrow, i.e. with a negative shoot characteristic and a variable tree dimension characteristic. The Overton Hall population is also variable for both these characteristics, with 13 trees in the -- quadrant, 8 in the ++ quadrant, 6 in the +- quadrant and 3, which could be considered outliers, in the -+ quadrant. For Guisborough there seems to be more of a definite pattern to the tree dimension character, as 16 trees out of 25 fell into two quadrants, 10 in the -- quadrant and 6 in the +- quadrant, with 4 in the -+ quadrant and 5 in the ++ quadrant. This suggests that the general trend is towards the negative side of the graph for tree dimensions, but that shoot vigour is variable. Brantingham has a very strong trend towards the negative side of the graph with 28 trees out of 30 falling into two quadrants, 16 in +- quadrant and 12 in -- quadrant. Therefore the trend for tree dimensions is highly negative, whereas the shoot vigour characteristic is variable.

(A) Summary conclusions.

From this information, the general population trend can be assigned to one of three categories, either positive (+), negative (-) or variable (V), with respect to the three characteristics shoot vigour, leaf dimensions and tree dimensions, and based on 70% of individuals of a population being found in different areas of the graph. The results are shown in Table 4.17: The positive and negative signs show whether the general trend of a particular population for the particular characteristic is high or low respectively, with respect to the other populations. Variable (V), indicates that there is no overall trend for that particular population for the characteristic concerned, but that the characteristic under discussion can be high and low in relation to

Table 4.17. The positive, negative or variable category assigned to the populations for the three variables.

			Variable	
Regions	Variable Population	Shoot Vigour	Leaf Dimensions	Tree Dimensions
4	Bu	+	-	✓
	Ch	-	-	+
2	Ss	✓	-	✓
	Yb	-	✓	✓
1	Ra	-	+	✓
	Ov	✓	✓	✓
3	Gu	✓	+	✓
	Br	✓	+	-

the other populations. This is important as it suggests that these populations have no general trend for the characteristic and therefore the individual trees can show either high or low values within the same population.

(B) Shoot vigour.

The only consistently positive population for shoot vigour in this analysis is Butser Hill, while Chichester Road, Yew Barrow and Ravensdale are seen to show a negative characteristic. The other four populations, Scout Scar, Overton Hall, Guisborough and Brantingham, are all variable for shoot vigour. Since the original aim of this survey was to see if there were differences between northern regions of the yew and to make a comparison of these with two southern populations, ~~One~~ one may note from these results that the only region that has been assigned the same category for shoot vigour from different populations is region 3, i.e. Guisborough and Brantingham, which are both variable for this characteristic. Although region 4, i.e. the Butser Hill and Chichester Road populations, have been assigned a positive and negative category, for the reasons identified in the population mean coordinates section, Butser Hill has been suggested as showing the typical characteristic for this region. The other two regions show no consistency at all. In region 1, Ravensdale is negative and Overton Hall is variable, and in region 2, Yew Barrow is negative and Scout Scar is variable. Therefore it can be concluded that shoot vigour in the south is consistently high in comparison with that of the northern populations. However, in all the northern regions variation of this characteristic has been shown, and therefore it can be said that some trees in every region show high shoot vigour, while others show low shoot vigour. Accordingly, the overall conclusion is that there are no distinctive regional differences between the northern populations of yew for shoot vigour and that the southern yew can produce a higher shoot vigour more consistently than is found in the north.

(B) Leaf dimensions.

For this character, two regions show consistent but opposite trends. Region 4, i.e. the south, shows negative leaf dimensions, while region 3, the northeast, shows a positive value. In region 2, Scout Scar has a negative value for this character, while Yew Barrow is variable, and in region 1, Ravensdale is positive and Overton Hall is variable. It can therefore be concluded that there is a strong trend towards negative leaf dimensions in the southern region and a strong positive trend in the northeastern region. Although this might suggest a clinal trend of this character, the variable nature of Yew Barrow in region 2 and Overton Hall in region 1 indicates that this can only be described as a weak trend and not, as suggested in the last section on population mean coordinates when it was described as a distinctive east to west cline in the north of England.

(B) Tree dimensions.

The variable nature of this character is seen in all regions; in fact, only two populations show distinctive trends, namely Brantingham, region 3, which shows a negative trend, and Chichester Road, region 4, which shows a positive trend. It can be concluded that while trees in the south can produce larger trees more consistently than in the northern regions, it is a very highly variable character. In regions 1, 2 and 3 it can be seen that five out of the six populations are variable for this character, suggesting that there are no distinctive regional differences between them.

CHAPTER 5.

Variation in morphological characteristics of Taxus baccata L.

II. Cluster Analysis.

So as to get an indication of the similarities between individual trees in comparison to the eight populations per se, a cluster analysis was performed on individuals, based on information in Figs 4.10 to 4.12. Ward's method of clustering was applied to the individual coordinates. As this method has been found not to be commonplace in the literature, it seems appropriate to discuss the details here.

(A) Ward's method of cluster analysis.

The intention of this method of clustering was to group individuals in terms of more than one variable (Ward, 1963). The idea was to form each possible number of groups, n,n-1,...1, in a manner that would minimise the "loss of information" associated with each grouping (see below).

(B) Objective function.

Given a set of ratings for ten individuals, 2,6,5,6,2,2,2,0,0,0, a common practice is to use the mean value to represent all the scores rather than consider individual scores. The "loss of information" that results from treating the ten scores as one group with a mean of 2.5 can be indicated by a "value-reflecting" number, i.e. the error sum of squares (ESS).

The error sum of squares is guven by the functional relation,

$$ESS = \sum_{i=1}^{n} x_i^2 - \frac{1}{n}\left(\sum_{i=1}^{n} x_i\right)^2$$

where x_i is the score of the ith individual. Therefore in this case

$$ESS_{(\text{one group})} = \sum_{i=1}^{10} x^2_i - \frac{1}{10}\left(\sum_{i=1}^{10} x_i\right)^2 = 113-62.5 = 50.5$$

Similarly, if the 10 individuals are classified according to their scores into four sets, i.e. (0,0,0), (2,2,2,2), (5), (6,6), this grouping can be evaluated as the sum of the four error sums of squares,

ESS (four groups)= ESS (group 1) + ESS (group 2) + ESS (group 3) + ESS (group 4).

A functional relation that provides a "value -reflecting" number of this type is referred to as an "objective function". In general, an objective function may be any functional relation that an investigator selects to reflect the relative desirability of groupings. In this example, the objective function is the "loss of information", as reflected by the ESS. The most desirable level of this function is its minimum value, 0.0. The objective function values that were computed indicate the information lost when the ten scores are treated as a single set (50.5), and as four sets (0.0).

(B) Hierarchical groups.

The grouping procedure is based on the premise that the greatest amount of information, as indicated by an objective function, is available when a set of n members is ungrouped. Hence, the grouping process starts with these n members, which are termed groups, or subsets, although they contain only one member. The first step in grouping is to select two of these n subsets which, when united, will reduce by one the number of subsets, while producing the least impairment of the optimal value of the objective function. The n-1 resulting subsets are then examined to determine if a third member should be united with the first pair, or another pairing made, in order to secure the optimal value of the objective function for n-2 groups. This procedure can be continued until all n members of the original array are in one group. Since the number of subsets is systematically reduced (n,n-1,...1), the process is called "hierarchical groupings", and the resulting mutually exclusive groups "hierarchical groups".

(B) Hierarchical grouping cycle.

(C) Optimal union of subsets, S(i,n).

The grouping procedure starts with a universal set (U), $(e_1, e_2 \ldots, n$, consisting of n one-element subsets. To reduce the number of subsets to n-1, one new subset, which minimises the change in the objective function's value, is formed by uniting two of the original n subsets, say,

$$\left[S(1,n)\right] \cup \left[S(2,n)\right] = \left\{e_1, e_2\right\}.$$

This requires an evaluation of the objective function for each of the n (n-1) /2 possible unions of subsets, S(i,n), i=1, 2,...,n, where i refers to the number identifying the set, and the second parameter, n at this stage, refers to the number of sets under consideration. As each union is considered in turn, the value of the corresponding objective function is computed and hypothesised to be equal to or better than that of any preceding union. The identity of the best union is maintained throughout the sequence of comparisons. This facilitates identification of that union which has an objective function value, equal or better than that of any of the n(n-1) /2 possible unions. This union is accepted as an optimal grouping when the number of subsets is reduced from n to n-1. The union resulting in n-1 subsets is

$$S(pn-1, n-1) = \left[S(pn-1, n)\right] \cup \left[S(qn-1, n)\right],$$

where pn-1 = the smaller of the two numbers used to identify the subset in the original subsets. This number is used to identify the new subset. qn-1 = the larger of the two numbers used to identify the subset in the n original subsets. This number is inactive after it is used at this stage for the printout showing which two subsets have been united.

The objective function value is denoted in the same manner to identify it with this union

$$Z\left[pn-1,\ q_{n-1},\ n-1\right].$$

The term at the right, i.e. n-1 in this case, shows the number of subsets remaining after the union; the left hand and centre terms are the original identification numbers of the united subsets.

Selection of an optimal union to reduce the n-1 subsets to n-2 requires evaluation and comparison of the (n-1) (n-2) /2 possible unions in the same way as for the reduction of n subsets to n-1. When this is done, the accepted union and its associated objective function value are

$$S(p_{n-2},n-2) = \left[S(p_{n-2}, n-1)\right] \cup \left[S(q_{n-2}, n-1)\right]$$

and $$Z\left[p_{n-2}, q_{n-2}, n-2\right] \quad (p_{n-2} < q_{n-2}).$$

The identifications are maintained as before, i.e. p_{n-2} is the identification number with the smaller numerical value and q_{n-2} is that with the larger numerical value.

This grouping cycle can be continued, if desired, until all subsets have been united to form a universal set, U. At any phase in which k mutually exclusive subsets are under consideration, the objective function value, and the union with which it is associated would be expressed as;

$$Z\left[i,j,k-1\right] \text{ associated with } \left[S(i,k)\right] \cup \left[S(j,k)\right]$$

where $i=1,2,\ldots,n-1$

$i \neq q_{n-1}, q_{n-2},\ldots,q_k$

$j=i+1, i+2,\ldots,n$

$j \neq q_{n-1}, q_{n-2},\ldots,q_k$

Following selection of an optimal union, this union and its corresponding objective function value would be designated;

$$S(p_{k-1}, k-1) = \left[S(p_{k-1},k)\right] \cup \left[S(q_{k-1},k)\right]$$

and $$Z\left[p_{k-1}, q_{k-1},k-1\right] \quad (p_{k-1} < q_{k-1})$$

Furthermore, the elements of any subset, S(i,k), would be designated

$$S(i,k)= \left\{e_{m_i},\ldots e_{m_a},\ldots,e_{m_t}\right\}$$

where t=number of elements in the subset and m_a identification number of ath element in the subset.

Finally, the mean coordinates and the standard deviations from each mean are calculated for each subset, S(i,k). These calculations were carried out by the ICL 1904S computer at Hull University, the name of the programme being Clustan.

(A) Results.

In this case the number of subsets required was eight, so as to compare the original eight populations with eight clusters of similar individuals, along component I, shoot vigour, and component II, leaf dimensions; along component II and component III, i.e. leaf dimensions with tree dimensions; and along component I with component III, i.e. shoot vigour with tree dimensions. The results of the analysis applied to the individual component coordinates are shown in Table 5.1a to c. For each cluster the total number of individuals ~~are~~ is shown (number of cases), the mean coordinate and standard deviation for each cluster are given, and the individual trees that make up the cluster are identified (case numbers). A summary of the mean coordinates and standard deviations are shown in Tables 5.2, 5.3, 5.4. Once the individual trees that make up a particular cluster have been identified, the number of trees from each original population within each cluster can be found. This information is summarised in Tables 5.5, 5.6, 5.7. The mean coordinates and standard deviations of the clusters were then plotted graphically as shown in Figs 5.1 to 5.3.

(B) Fig 5.1.

This graph shows the mean coordinates of the eight clusters and their standard deviations from the mean along component I and component II. The numbers of individuals from each population for each cluster are shown in Table 5.5. Cluster 1 can be seen to have a positive value for shoot vigour and negative for leaf dimensions and is made up of 17 trees from Butser Hill, 8 from Scout Scar, 2 from Yew Barrow, 4 from Overton Hall, 1 from Ravensdale and 1 from Brantingham. Cluster 2 is found to be in the same quadrant as cluster 1 although the trees found in it have a higher shoot vigour value than is found in cluster 1; only two populations are represented, 11 individuals from Butser Hill and 1 from Scout Scar.

Table 5.1a.

Results of Ward's cluster analysis for shoot vigour and leaf dimensions.

Cluster	Number of cases	Mean coordinate shoot vigour	Standard deviation shoot vigour	Mean coordinate leaf dimensions	Standard deviation leaf dimensions
1	33	1.44	0.89	-2.11	0.88
	Case numbers 1 2 6 10 13 14 15 17 20 22 23 24 25 26 27 28 29 67 68 76 90 104 116 119 122 123 125 131 135 145 153 172 181.				
2	12	4.32	1.92	-0.77	0.77
	Case numbers 3 4 5 7 8 9 11 12 18 19 30 142.				
3	56	-1.76	0.77	-1.22	0.87
	Case numbers 16 31 32 34 35 36 39 40 41 42 43 44 46 48 49 50 55 56 57 60 63 64 69 78 80 89 91 92 102 105 106 112 118 120 124 127 128 133 134 137 139 144 147 150 155 156 158 162 165 167 171 214 222 223 229 233.				
4	20	1.51	0.58	0.89	0.68
	Case numbers 21 73 84 94 95 96 130 141 143 173 176 186 199 203 208 211 213 217 224 226.				
5	31	-0.09	0.65	2.21	0.59
	Case numbers 33 65 79 81 85 87 98 99 100 109 113 169 177 179 180 184 185 189 190 192 193 195 196 198 200 204 205 206 207 221 231.				

Table 5.1a (Cont).

Results of Ward's cluster analysis for shoot vigour and leaf dimensions.

<table>
<tr><th>Cluster</th><th>Number of cases</th><th>Mean coordinate shoot vigour</th><th>Standard deviation shoot vigour</th><th>Mean coordinate leaf dimensions</th><th>Standard deviation leaf dimensions</th></tr>
<tr><td>6</td><td>56</td><td>-0.42</td><td>0.58</td><td>0.48</td><td>0.78</td></tr>
<tr><td></td><td colspan="5">Case numbers
37 38 51 54 58 59 61 62 66 70 71 72 74 75 77 82 83 86
88 93 97 101 103 110 114 117 121 126 129 132 136 138
146 148 151 152 154 157 159 160 161 163 164 166 168
178 188 194 197 201 202 216 218 228 230 232.</td></tr>
<tr><td>7</td><td>16</td><td>-2.36</td><td>0.37</td><td>0.90</td><td>0.66</td></tr>
<tr><td></td><td colspan="5">Case numbers
45 47 52 53 107 108 111 115 140 149 170 174 175 215
225 227.</td></tr>
<tr><td>8</td><td>9</td><td>3.68</td><td>0.83</td><td>2.22</td><td>0.80</td></tr>
<tr><td></td><td colspan="5">Case numbers
182 193 187 191 209 210 212 219 220.</td></tr>
</table>

Table 5.1b.

Results of Ward's cluster analysis for shoot vigour and leaf dimensions.

<table>
<tr><th>Cluster</th><th>Number of cases</th><th>Mean coordinate shoot vigour</th><th>Standard deviation shoot vigour</th><th>Mean coordinate leaf dimensions</th><th>Standard deviation leaf dimensions</th></tr>
<tr><td>1</td><td>27</td><td>-2.62</td><td>0.70</td><td>-0.63</td><td>0.75</td></tr>
<tr><td></td><td colspan="5">Case numbers
1 2 9 10 13 14 15 17 23 25 26 27 28 41 42 46 48 56 57 60
68 90 104 116 125 172 229.</td></tr>
<tr><td>2</td><td>43</td><td>-1.22</td><td>0.75</td><td>1.37</td><td>0.66</td></tr>
<tr><td></td><td colspan="5">Case numbers
3 8 20 22 24 29 49 55 64 66 67 70 74 78 80 89 91 92 102
118 120 121 122 123 124 133 134 135 137 139 153 155 156
162 165 167 176 178 181 214 222 223 233.</td></tr>
<tr><td>3</td><td>35</td><td>-0.87</td><td>0.38</td><td>-0.54</td><td>0.56</td></tr>
<tr><td></td><td colspan="5">Case numbers
4 5 6 7 11 12 16 18 31 34 36 39 40 43 44 50 63 69 76 86
88 105 106 119 128 129 131 144 145 150 158 159 160 166 168.</td></tr>
<tr><td>4</td><td>23</td><td>0.35</td><td>0.65</td><td>-2.18</td><td>0.76</td></tr>
<tr><td></td><td colspan="5">Case numbers
19 32 33 35 37 47 51 52 54 58 59 117 127 130 141 142 146
149 152 164 171 173 218.</td></tr>
<tr><td>5</td><td>25</td><td>0.56</td><td>0.36</td><td>0.72</td><td>0.28</td></tr>
<tr><td></td><td colspan="5">Case numbers
21 30 72 73 75 97 103 107 108 111 132 140 143 147 154 174
175 186 188 202 215 224 226 228 230.</td></tr>
</table>

Table 5.1b (Cont).

Results of Ward's cluster analysis for shoot vigour and leaf dimensions.

<table>
<tr><th>Cluster</th><th>Number of cases</th><th>Mean coordinate shoot vigour</th><th>Standard deviation shoot vigour</th><th>Mean coordinate leaf dimensions</th><th>Standard deviation leaf dimensions</th></tr>
<tr><td>6</td><td>36</td><td>0.95</td><td>0.49</td><td>-0.38</td><td>0.48</td></tr>
<tr><td></td><td colspan="5">Case numbers</td></tr>
<tr><td></td><td colspan="5">38 45 53 61 62 65 71 79 81 82 84 85 87 93 95 101 110 112
114 115 126 136 138 148 151 157 161 163 169 192 197 211
216 217 227 232.</td></tr>
<tr><td>7</td><td>28</td><td>2.08</td><td>0.67</td><td>1.26</td><td>0.67</td></tr>
<tr><td></td><td colspan="5">Case numbers</td></tr>
<tr><td></td><td colspan="5">77 83 94 177 179 180 182 183 184 185 189 190 191 194 195
196 198 199 200 201 203 204 206 208 209 210 219 225.</td></tr>
<tr><td>8</td><td>16</td><td>2.46</td><td>0.44</td><td>-0.78</td><td>0.77</td></tr>
<tr><td></td><td colspan="5">Case numbers</td></tr>
<tr><td></td><td colspan="5">96 98 99 100 109 113 170 187 193 205 207 212 213 220
221 231.</td></tr>
</table>

Table 5.1c.

Results of Ward's cluster analysis for shoot vigour and tree dimensions.

<table>
<tr><th>Cluster</th><th>Number of cases</th><th>Mean coordinate shoot vigour</th><th>Standard deviation shoot vigour</th><th>Mean coordinate tree dimensions</th><th>Standard deviation tree dimensions</th></tr>
<tr><td>1</td><td>54</td><td>0.29</td><td>0.65</td><td>-0.39</td><td>0.50</td></tr>
<tr><td></td><td colspan="5">Case numbers
1 6 13 15 17 21 31 38 39 50 61 65 68 71 76 79 81 82 84 85
86 87 90 95 98 99 101 104 110 113 116 119 126 131 136 138
143 146 148 157 159 160 163 166 168 169 180 192 205 216
221 226 231.</td></tr>
<tr><td>2</td><td>22</td><td>2.74</td><td>0.57</td><td>-0.73</td><td>0.86</td></tr>
<tr><td></td><td colspan="5">Case numbers
2 3 5 7 10 14 18 19 23 25 26 28 96 142 145 187 191 211
212 213 217 220.</td></tr>
<tr><td>3</td><td>12</td><td>4.67</td><td>1.84</td><td>0.83</td><td>1.03</td></tr>
<tr><td></td><td colspan="5">Case numbers
4 8 9 11 12 30 182 183 208 209 210 219.</td></tr>
<tr><td>4</td><td>38</td><td>-1.85</td><td>0.65</td><td>-0.72</td><td>0.61</td></tr>
<tr><td></td><td colspan="5">Case numbers
16 32 34 35 36 40 41 42 44 45 46 48 52 53 56 57 60 63 93
100 105 106 109 112 114 115 127 128 150 151 152 161 170
171 193 195 227 232.</td></tr>
<tr><td>5</td><td>24</td><td>1.08</td><td>0.68</td><td>1.68</td><td>0.68</td></tr>
<tr><td></td><td colspan="5">Case numbers
20 22 24 29 67 70 73 94 121 122 135 153 176 177 178 181
184 186 189 196 199 203 206 224.</td></tr>
</table>

Table 5.1c (Cont).

Results of Ward's cluster analysis for shoot vigour and tree dimensions.

Cluster	Number of cases	Mean coordinate shoot vigour	Standard deviation shoot vigour	Mean coordinate tree dimensions	Standard deviation tree dimensions
6	18	0.04	1.14	-2.49	0.64

Case numbers

27 33 37 47 51 54 58 59 117 129 130 141 149 164 172 173
207 218.

7	25	-2.36	0.44	0.96	0.55

Case numbers

43 55 80 91 92 102 107 108 111 118 133 137 140 147 155
156 165 167 174 175 215 222 225 229 233.

8	40	-0.73	0.39	0.87	0.53

Case numbers

49 62 64 66 69 72 74 75 77 78 83 89 97 103 120 123 124
125 132 134 139 144 154 158 162 179 185 188 190 194 197
198 200 201 202 204 214 223 228 230.

Table 5.2.

The mean coordinates and standard deviations of the shoot vigour and leaf dimension components for the eight clusters.

Cluster	Mean shoot vigour	Standard deviation shoot vigour	Mean leaf dimension	Standard deviation leaf dimension
1	1.44	0.89	-2.11	0.88
2	4.32	1.92	-0.77	0.77
3	-1.76	0.77	-1.22	0.87
4	1.51	0.58	0.89	0.68
5	-0.09	0.66	2.21	0.59
6	-0.42	0.58	0.48	0.78
7	-2.36	0.37	0.90	0.66
8	3.68	0.83	2.22	0.80

Table 5.3.

The mean coordinates and standard deviations of the leaf dimensions and tree dimension components for the eight clusters.

Cluster	Mean leaf dimension	Standard deviation leaf dimension	Mean tree dimension	Standard deviation tree dimension
1	-2.62	0.70	-0.63	0.75
2	-1.22	0.75	1.37	0.66
3	-0.87	0.38	-0.54	0.56
4	0.35	0.65	-2.18	0.76
5	0.56	0.36	0.72	0.28
6	0.95	0.49	-0.38	0.48
7	2.08	0.67	1.26	0.67
8	2.46	0.44	-0.78	0.77

Table 5.4.

The mean coordinates and standard deviations of the shoot vigour and tree dimension components for the eight clusters.

Cluster	Mean shoot vigour	Standard deviation shoot vigour	Mean tree dimension	Standard deviation tree dimension
1	0.29	0.65	-0.39	0.50
2	2.74	0.57	-0.73	0.86
3	4.67	1.84	0.83	1.03
4	-1.85	0.65	-0.72	0.61
5	1.08	0.68	1.68	0.68
6	0.04	1.14	-2.49	0.64
7	-2.36	0.44	0.96	0.55
8	-0.73	0.39	0.87	0.53

Table 5.5. The number of trees from each original population within each cluster along the shoot vigour and leaf dimension axes.

	Population							
Cluster	Bu	Ch	Ss	Yb	Ov	Ra	Gu	Br
C_1	17	0	8	2	4	1	0	1
C_2	11	0	1	0	0	0	0	0
C_3	1	19	10	9	6	6	5	0
C_4	1	0	3	1	2	3	5	5
C_5	0	1	0	1	5	5	2	17
C_6	0	6	7	13	13	6	5	6
C_7	0	4	1	4	0	4	3	0
C_8	0	0	0	0	0	0	5	4

Table 5.6. **The number of trees from each original population within each cluster along the leaf dimension and tree dimension axes.**

	Population							
Cluster	Bu	Ch	Ss	Yb	Ov	Ra	Gu	Br
C_1	13	7	2	1	2	1	1	0
C_2	6	2	11	6	8	3	4	3
C_3	8	8	6	6	5	2	0	0
C_4	1	10	5	6	0	0	1	0
C_5	2	0	3	4	3	5	5	3
C_6	0	3	3	6	10	7	5	2
C_7	0	0	0	0	2	1	4	21
C_8	0	0	0	1	0	6	5	4

Table 5.7. The number of trees from each original population within each cluster along the shoot vigour and tree dimension axes.

Cluster	Population							
	Bu	Ch	Ss	Yb	Ov	Ra	Gu	Br
C_1	6	4	7	9	14	7	4	3
C_2	12	0	2	0	0	1	5	2
C_3	6	0	0	0	0	0	3	3
C_4	1	16	2	6	1	8	2	2
C_5	4	0	3	1	3	1	1	11
C_6	1	7	4	4	0	0	1	1
C_7	0	2	4	7	1	6	5	0
C_8	0	1	8	3	11	2	4	11

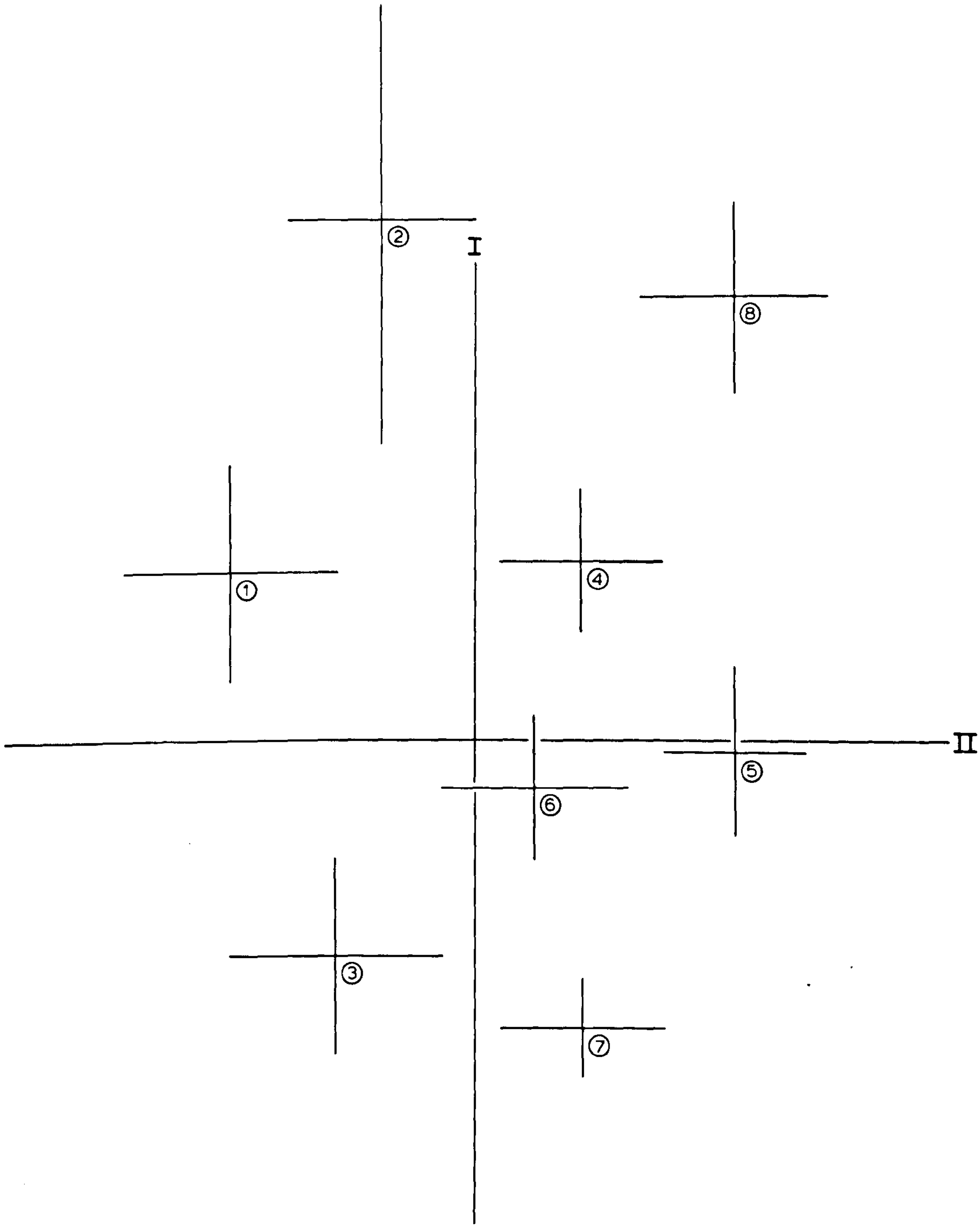


Fig 5.1. Mean coordinates and standard deviations of the eight clusters along components I and II.

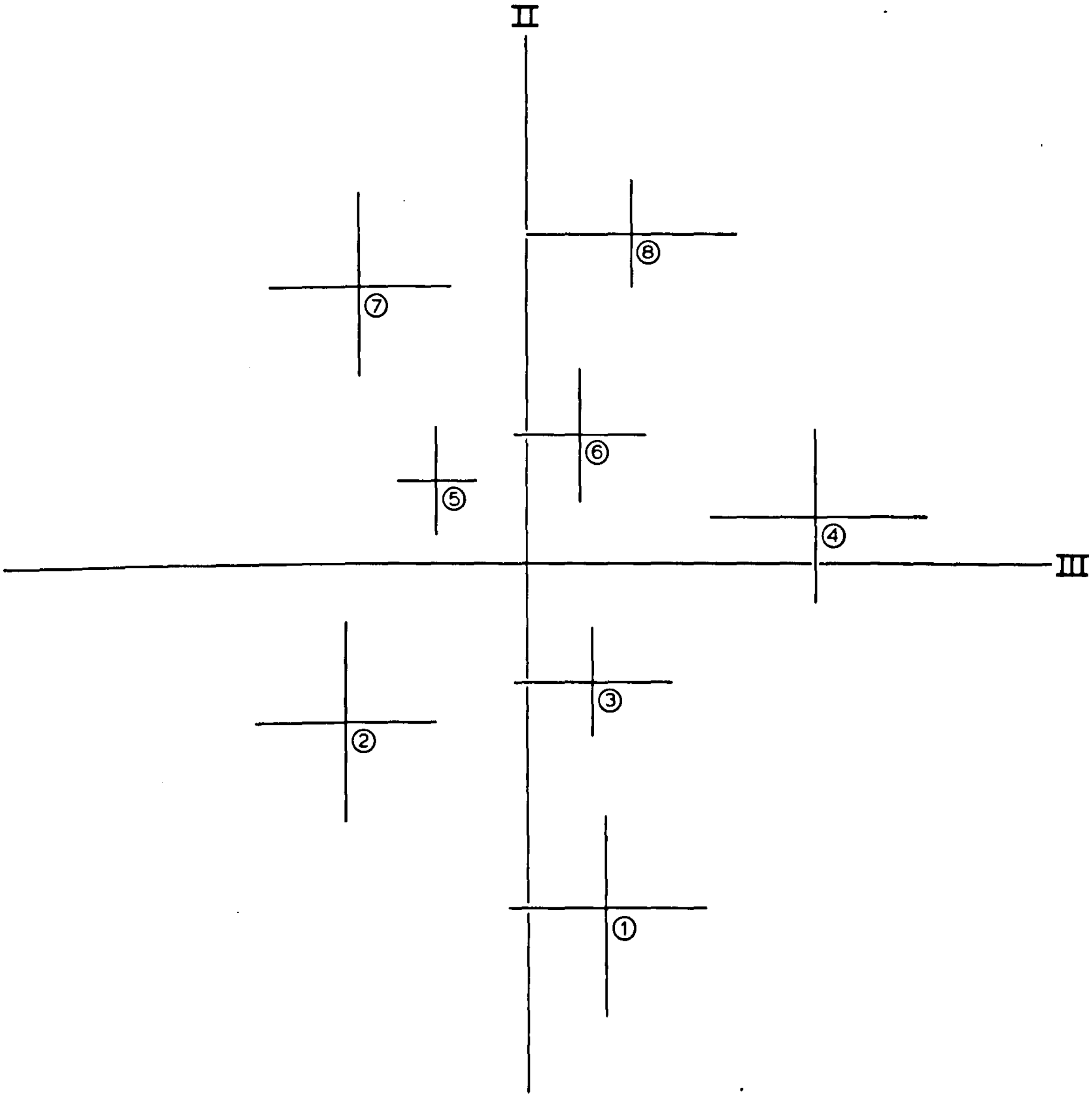


Fig 5.2. Mean coordinates and standard deviations of the eight clusters along components II and III.

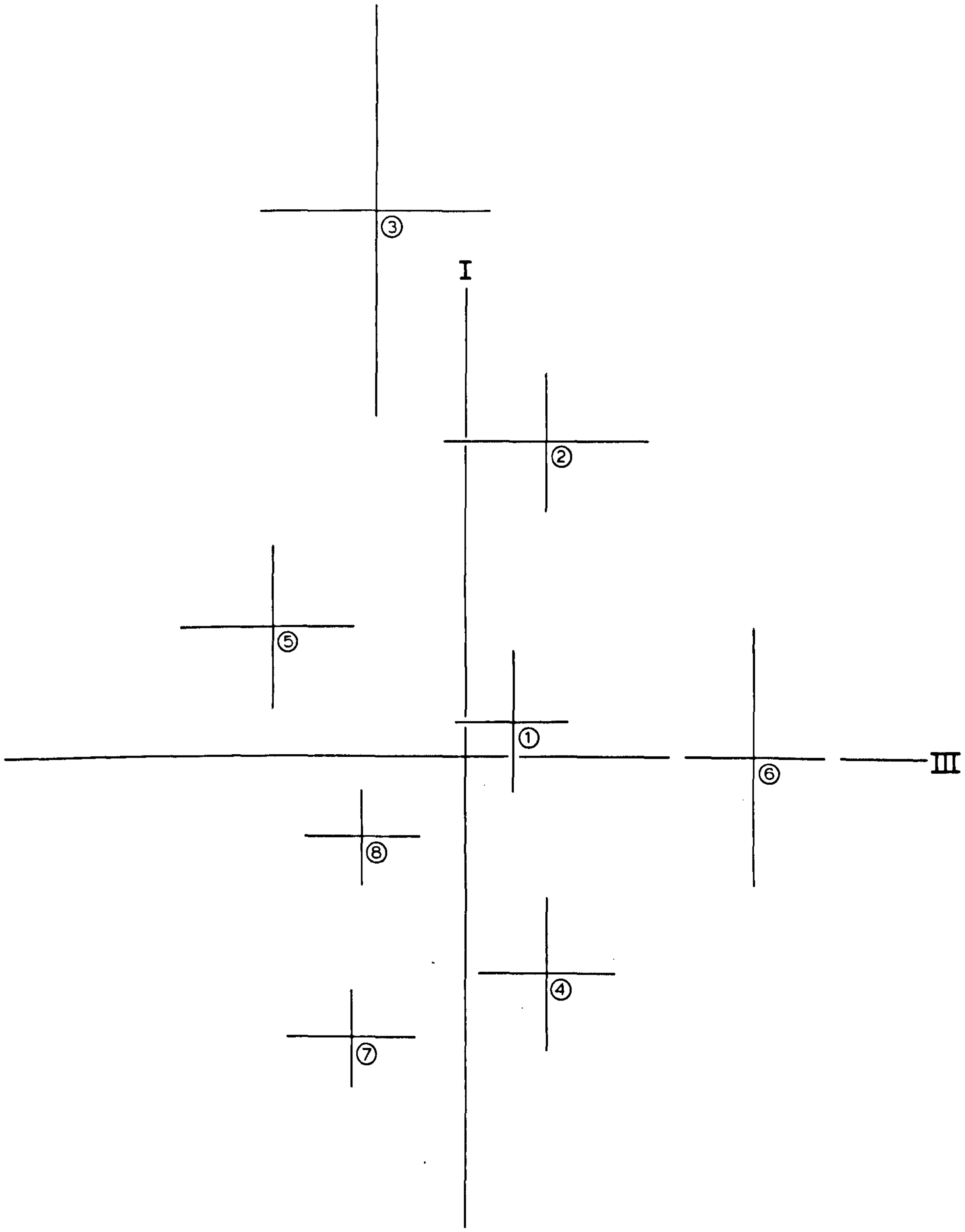


Fig 5.3. Mean coordinates and standard deviations of the eight clusters along components I and III.

Cluster 3 is made up of individuals having a negative value for both shoot vigour and leaf dimensions comprising 1 tree from Butser Hill, 19 from Chichester Road, 10 from Scout Scar, 9 from Yew Barrow, 6 from Overton Hall, 6 from Ravensdale, and 5 from Guisborough. This cluster (and therefore these trees), is the only one to be found wholly in this quadrant, showing negative values for shoot vigour and leaf dimensions. Cluster 4 comprises individuals which have a positive shoot vigour, comparable to Cluster 1, but unlike that cluster, they show a positive value for leaf dimensions. The trees that make up this cluster are, 1 from Butser Hill, 3 from Scout Scar, 1 from Yew Barrow, 2 from Overton Hall, 3 from Ravensdale, 5 from Guisborough, and 5 from Brantingham. Cluster 5 is found near the axis of the shoot vigour component; therefore within it there will be individuals with low positive values or low negative values for this characteristic. The same cluster shows a high value for leaf dimensions, and comprises 1 tree from Chichester Road, 1 from Yew Barrow, 5 from Overton Hall, 5 from Ravensdale, 2 from Guisborough, and 17 from Brantingham. Cluster 6 is close to the origin of both axes, and within it there are 6 trees from Chichester Road, 7 from Scout Scar, 13 from Yew Barrow, 13 from Overton Hall, 6 from Ravensdale, 5 from Guisborough, and 6 from Brantingham. The lowest cluster along the shoot vigour axis is represented by cluster 7, with a low positive leaf dimension characteristic consisting of 4 trees from Chichester Road, 1 from Scout Scar, 4 from Yew Barrow, 4 from Ravensdale, and 3 from Guisborough. Finally, cluster 8 can be found in the ++ quadrant, indicating high values for shoot vigour and high values for leaf dimensions. Within this cluster there are only 9 trees from two populations, namely 5 from Guisborough, and 4 from Brantingham.

(B) Fig 5.2.

This graph shows the mean coordinates and standard deviations of the eight clusters along component II and component III, i.e. leaf dimensions and tree dimensions. The number of individuals from each population in each cluster are shown in Table 5.6. It can immediately be seen by examining this graph that there is less spread across the tree dimension component than in the leaf dimension direction, suggesting that variation in tree dimensions between the clusters is less than the variation in the other direction. Along component III, the clusters have been combined into three groups. Cluster 4 on its own, with average leaf dimensions and the most highly positive tree dimensions, will be called group one. Group two comprises cluster 8, cluster 6, cluster 3, and cluster 1, representing positive tree dimensions, and in descending order, leaf dimensions; that is, cluster 8 has highly positive leaf dimensions; cluster 6, positive leaf dimensions; cluster 3, negative leaf dimensions; and cluster 1, highly negative leaf dimensions. Finally, group three consists of individuals all which show negative tree dimensions, with cluster 7 showing the highest leaf dimensions of the group, cluster 5 also positive but less so, and cluster 2 the lowest leaf dimensions of the group. Thus, group one consists of one cluster, cluster 4, which is identified as having average leaf dimensions with the most positive tree dimensions. The composition of this group and cluster is as follows; 1 from Butser Hill, 10 from Chichester Road, 5 from Scout Scar, 6 from Yew Barrow, and 1 from Guisborough. Group two, consisting of four clusters all with average tree dimensions but with decreasing leaf dimensions, from cluster 8 to cluster 6 to cluster 3 to cluster 1, are composed of the following individuals; cluster 8 has only four populations representing, 1 from Yew Barrow, 6 from Ravensdale, 5 from Guisborough, and 4 from Brantingham; cluster 6 has more of a mixture of individuals, with 3 from Chichester Road, 3 from Scout Scar, 6 from Yew Barrow, 10 from Overton Hall, 7 from Ravensdale, 5 from Guisborough, and 2 from Brantingham; Cluster 3 is comprised of 8 individuals from Butser Hill, 8 from Chichester Road, 6 from Scout Scar, 6 from Yew Barrow, 5 from Overton Hall, and 2 from Ravensdale; and the last cluster of group two, i.e. cluster 1, has 13 trees from Butser Hill, 7 from Chichester Road, and 2 from Scout Scar and Overton Hall and one from each of three populations, from Yew Barrow, Ravensdale and Guisborough. Finally, group three consists of three clusters with negative tree dimensions and with decreasing leaf dimensions, from cluster 7 to cluster 5 to cluster 2. The individual trees that comprise these clusters are as follows; cluster 7 has four populations represented in it, 2 from Overton Hall, 1 from Ravensdale, 4 from Guisborough, and 21 from Brantingham; cluster 5 is comprised of 2 from Butser Hill, 3 from Scout Scar, 4 from Yew Barrow, 3 from Overton Hall, 5 from Ravensdale, 5 from Guisborough, and 3 from Brantingham; in cluster 2, there are 6 trees from Butser Hill, 2 from Chichester Road, 11 from Scout Scar, 6 from Yew Barrow, 8 from Overton Hall, 3 from Ravensdale, 4 from Guisborough, and 3 from Brantingham.

(B) Fig 5.3. This graph shows the mean coordinates and standard deviations of the eight clusters along component I and component III, i.e. shoot vigour and tree dimensions. It is of interest to note here that cluster 3, which shows the trees with the highest shoot vigour, has average tree dimensions, whereas individuals with average shoot vigour have displayed the highest tree dimensions (cluster 6) and even some trees with a low shoot vigour as in cluster 7 show tree dimensions comparable to cluster 2. However, in contrast, trees that show comparable shoot vigour as with cluster 4 and 7 can also show contrasting tree dimensions, and trees that have roughly the same shoot vigour as in clusters 5 and 6 can show either low or high values along the tree dimension axis.

The individuals that make up the clusters are as follows; cluster 2, having high shoot vigour and average tree dimensions comprises 12 individuals from Butser Hill, 2 from Scout Scar, 1 from Ravensdale, 5 from Guisborough and 2 from Brantingham; cluster 1, having average values along both axes, has 6 trees from Butser Hill, 4 from Chichester Road, 7 from Scout Scar, 9 from Yew Barrow, 14 from Overton Hall, 7 from Ravensdale, 4 from Guisborough and 3 from Brantingham; cluster 6, having average shoot vigour and the highest tree dimensions has 1 tree from Butser Hill, 7 from

Chichester Road, 4 from Scout Scar, 4 from Yew Barrow, and 1 from each of Guisborough and Brantingham; cluster 5, showing a low positive value for shoot vigour and a negative value for tree dimensions has, 4 trees from Butser Hill, 3 from Scout Scar, 1 from Yew Barrow, 3 from Overton Hall, 1 from Ravensdale, 1 from Guisborough, and 11 from Brantingham; cluster 4, with low shoot vigour and average tree dimensions has, 1 tree from Butser Hill, 16 from Chichester Road, 2 from Scout Scar, 6 from Yew Barrow, 1 from Overton Hall, 8 from Ravensdale, 2 from Guisborough, and 2 from Brantingham; cluster 7, showing the lowest shoot vigour and negative tree dimensions has, 2 trees from Chichester Road, 4 from Scout Scar, 7 from Yew Barrow, 1 from Overton Hall, 7 from Ravensdale, and 5 from Guisborough; cluster 8, having comparable tree dimension values as cluster 7, but a higher shoot vigour has, 1 tree from Chichester Road, 8 from Scout Scar, 3 from Yew Barrow, 11 from Overton Hall, 2 from Ravensdale, 4 from Guisborough, and 11 from Brantingham; and finally, cluster 3, showing the highest shoot vigour and average tree dimensions has, 6 trees from Butser Hill, 3 from Guisborough and 3 from Brantingham.

Discussion of results.

The overall conclusion that can be drawn from the three cluster diagrams is that there are no distinct differences between populations, only trends. This means that although there are some indications of individuals from one population lying in a particular area of the graphs, some of the trees from all the populations are similar to individuals from other populations, and therefore fall within the same clusters. Fig 5.1 shows eight clusters of individuals in a comparison between shoot vigour and leaf dimensions. It is clear from these results that the overall trends indicated in the last chapter and in Table 5.5, are confirmed. Butser Hill shows a positive shoot vigour and a negative leaf dimension identified here by the majority of trees from this population falling in clusters 1 and 2. Chichester Road is negative for both characteristics, with 19 out of 30 trees measured lying in cluster 3. Scout Scar was identified as being variable for shoot vigour and negative for leaf dimensions; here, 19 out of the 30 trees measured are found in clusters 1, 2 and 3. Yew Barrow was shown to be negative for shoot vigour and variable for leaf dimensions, and this is confirmed by the majority of trees lying in clusters 3 and 6. Overton Hall was shown to be variable for both characteristics, and here the majority of trees from this population lying in clusters 3, 5 and 6. Ravensdale was shown to be negative for shoot vigour and positive for leaf dimensions; this is confirmed by this analysis, with the majority of the trees lying in clusters 5, 6 and 7. Guisborough was variable for shoot vigour and positive for leaf dimension; this is confirmed by the trees falling in clusters 4, 5, 6, 7 and 8. Finally, Brantingham was considered variable for shoot vigour and positive for leaf dimensions; this breakdown is confirmed by the cluster analysis, as the majority of trees from this population are found in clusters 4, 5, 6 and 8. The remaining trees from populations that lie in other clusters rather than the clusters describing the general trend can be considered as outliers of that trend. In the case of Butser Hill 1 tree is found in cluster 3 and 1 in cluster 4. Therefore, although the general trend is clearly demarcated there are clearly some individuals that show variation from this trend. Outliers in Chichester Road can be found in clusters 5, 6 and 7, and in Scout Scar there is one tree in cluster 2, three in cluster 4, seven in cluster 6 and one in cluster 7. Similarly, in Yew Barrow, there are two in cluster 1, four in cluster 7, and one in each of cluster 4 and 5. In Overton Hall, there are four outliers falling in cluster 1. In Ravensdale, three outliers lie in cluster 4 and one in cluster 1, and six in cluster 3. In Guisborough there are five in cluster 3, and in Brantingham there is one individual in cluster 1. These outliers to the general population trends indicate that variations from that trend are clearly present.

The more compact pattern shown in Fig 5.2 along component III indicates that there is little variation of tree dimensions throughout the sample set. However, as in Fig 5.1, there is a mixture of individuals from different populations within each cluster, as also shown in Table 5.6. In this graph, the majority of individuals from the Butser Hill population can be found in clusters 1, 2 and 3, showing a negative leaf dimension characteristic and a variable tree dimension characteristic. The majority of the individuals from the Chichester Road population can be found in clusters 1, 3 and 4, showing positive tree dimensions; indeed, cluster 4 shows the most highly positive tree dimensions of the whole sample, and in this cluster 10 out of the thirty trees sampled from this population can be found. Also this cluster crosses the positive-negative boundary along component II (i.e. leaf dimensions), so the general trend found in Table 4.13 in the preceding chapter of negative leaf dimensions is not incompatible with this result. The same is true for Scout Scar, as in this population the majority of individuals lie in clusters 2, 3 and 4, that is with negative leaf dimensions and variable tree dimensions. Yew Barrow was said to be variable for both these characteristics, and indeed this can be seen as the majority of the individuals in this population can be found in clusters 2, 3, 4, 5 and 6. The same is true for Overton Hall, lying in clusters 2, 3 and 6. It should be noted however that five individuals from Yew Barrow can be found in cluster 4, along with five from Scout Scar and ten from Chichester Road, as the cluster showing the highest tree dimensions. The majority of individuals from Ravensdale are found in clusters, 5, 6 and 8, i.e. with a positive leaf dimension characteristic and a variable tree dimension characteristic. The majority of the Guisborough individuals can be found to have positive leaf dimensions as they are found in clusters 5, 6, 7 and 8. Also, the variable tree dimensions suggested in Table 4.13 in the preceding chapter are confirmed by this result. For the Brantingham population twenty one of the trees measured fall in cluster 7 and therefore the majority of the individuals fall in the negative tree dimension sector and positive leaf dimension sector as suggested in Table 4.13.

Trends along component II of increased leaf dimensions towards the north are not easily visualised in this graph; however, it should be noted that the most negative cluster is cluster 1 and in it there are thirteen individuals from Butser Hill, and seven from Chichester Road, with two from Scout Scar and Overton Hall and one from all the other populations apart from Brantingham. So it can be said that in the south, individuals can be found with low leaf dimensions as compared with northern populations. At the other extreme, cluster 8 showing the highest leaf dimension characteristic, is made up of six trees from Ravensdale, five from Guisborough, four from Brantingham and one from Yew Barrow, suggesting that there are some northern individuals that show high leaf dimensions in comparison to the south and that it is possible for trees in the northeast to have leaf dimensions of comparable value to their northwestern counterparts. Another interesting cluster is number 7, where the majority of trees are from Brantingham (21 individuals), the rest being made up of four from Guisborough, one from Ravensdale and two from Overton Hall. This cluster shows the next highest leaf dimensions to cluster 8, therefore suggesting that the northeastern yew can have higher leaf dimensions than yews from other regions. In the rest of the clusters there is a mixture of individuals from different sources, suggesting that there are no apparent differences between populations, apart from the ones just described. Looking at the graph along the other component, that is the tree dimension component, three groups of clusters 1, can be seen, clusters 2, 5 and 7 have similar values, and clusters 3, 6 and 8 have similar values, leaving cluster 4 on its own. There is no trend at all shown by this result, as individuals from all sources can be found in the first two cluster groups; however, cluster 4, as mentioned above, is made up of ten trees from Chichester Road, five from Scout Scar, six from Yew Barrow, one from Butser Hill, and one from Guisborough, so that the majority of the trees in this group are from the south and northwest. It should also be noted that twenty four trees from the Brantingham population have low tree dimensions, twenty one in cluster 7 and three in cluster 5. This result suggests that although there are no overall geographic trends, high tree dimensions can be found in trees in the south and the northwest as compared with other sources and that the lowest tree dimensions are found in one northeastern population, namely Brantingham.

In Fig 5.3 the clustering of individuals along component I and component III is shown. As in the other graphs, the clusters are made up of individuals from different sources; however, it should be noted that the majority of Butser Hill individuals can be found in clusters 1, 2, 3 and 5, with clusters 2 and 3 showing the highest shoot vigour values in the graph. In cluster 3, which is the cluster showing the highest shoot vigour, only three populations are represented, Butser Hill with 6 individuals, Guisborough with 3, and Brantingham with 3. It should be pointed out that although this cluster displays the highest shoot vigour it shows only average values for tree dimensions. To emphasise this point, cluster 2, the next highest for shoot vigour, with twelve trees from Butser Hill, two from Scout Scar, one from Ravensdale, five from Guisborough and two from Brantingham, shows the same tree dimension trend as cluster 3.

In an attempt to identify definable areas of the graph, the remaining clusters are grouped together along the shoot vigour axis, with clusters 5, 1 and 6 being considered as one group, cluster 8 left on its own, and clusters 4 and 7 being grouped together. Combining clusters 1, 5 and 6, eleven trees from Butser Hill are represented, eleven from Chichester Road, fourteen from Scout Scar, fourteen from Yew Barrow, seventeen from Overton Hall, eight from Ravensdale, six from Guisborough, and fifteen from Brantingham. These trees show the next highest shoot vigour after clusters 3 and 2 respectively. After them comes cluster 8, in which all the populations are represented apart from Butser Hill, i.e.

one from Chichester Road, eight from Scout Scar, three from Yew Barrow, eleven from Overton Hall, two from Ravensdale, four from Guisborough and eleven from Brantingham. The trees in this cluster show negative shoot vigour and negative tree dimensions. Finally, clusters 4 and 7 show the lowest shoot vigour of all, and in this seventeen trees from Chichester Road can be found, six from Scout Scar, eleven from Yew Barrow, two from Overton Hall, fourteen from Ravensdale, seven from Guisborough and two from Brantingham. An overall shoot vigour pattern from these results is difficult to discern, although Butser Hill's high shoot vigour individuals suggest that in the south it is more possible to find high shoot vigour than in the rest of the sample.

When studying the graph along component III, representing tree dimensions, cluster 5 shows the most negative value and cluster 6, the most positive value. Within cluster 5, Brantingham is represented by eleven trees, Butser Hill by four, Scout Scar by three, Yew Barrow by one, Overton Hall by three, Ravensdale by one and Guisborough by one. In cluster 6, Butser Hill is represented by one tree, Chichester Road by seven, Scout Scar by four, Yew Barrow by four, Guisborough by one and Brantingham by one. It is interesting to note that in the cluster representing the highest tree dimensions there is an absence of trees from one of the regions in the sample, namely Derbyshire. It must be pointed out that the majority of the individuals from all sampled populations are found around the middle of the graph and that if there is any trend to be seen, it is that there is a tendency for the Brantingham population to have a generally lower tree dimension than other populations; but this is a population characteristic and not a regional one as Guisborough, its regional neighbour, is represented by only one tree in cluster 5, as opposed to eleven from Brantingham.

Summary conclusions of chapter 4 and 5.

The main purpose of this analysis and of that in the previous chapter, has been to investigate the patterns of variation in morphological characteristics of Taxus baccata, in three regions in northern England, and also to compare these populations with two from the south of England.

This was achieved by measuring a number of trees for thirteen variables within selected populations and subsequent analysis. Two populations per region were measured, and four replicates of each variable were taken for each tree, except where there was a single expression of the variable. The means of each variable for each tree were subjected to Principal Components Analysis so as to compress the variables measured in order to give more general dimensions of the original variables. The analysis in chapter 4 showed that the first four resulting from the PCA components should be considered as the eigenvalue drops below one after this. These were component I, shoot vigour; component II, leaf dimensions; component III, tree dimensions; and component IV, leaf angle. The overall population coordinates were then calculated to give an idea as to where along the four components they would lie, in respect to each other. From this it was found that the southern population of Butser Hill showed the highest value along the shoot vigour component and the lowest leaf dimensions. However, the conclusion drawn from the rest of the population coordinates was that there were no regional differences between the northern populations along the shoot vigour axis, and that all that could be discerned was an apparent variation in shoot vigour between the group consisting of Scout Scar, Overton Hall, Guisborough, and Brantingham and the group consisting of Yew Barrow, and Ravensdale, with Chichester Road showing the lowest value for vigour, for reasons outlined in page 139. As mentioned above, Butser Hill shows the lowest value for leaf dimensions, with all the northern populations showing higher values, suggesting that there is a south-north difference in this characteristic. Within the northern populations, it was noted that the northwestern populations showed a lower value for leaf dimensions than the populations from Derbyshire, and these showed a lower value in turn than those from the northeast. The information derived from the population coordinates along component III seemed to suggest that there were no differences between regions at all, as six out of the eight populations measured had very similar values. However, Chichester Road and Brantingham showed the highest and lowest values for this character respectively. Finally, component IV (leaf angle) gave very little more information, apart from a suggestion that Yew Barrow had a lower leaf angle than the general pattern. However, it did not indicate any regional patterns that had not already been extracted from the other components.

The next stage of the analysis considered individual trees along the several components to see if the overall mean coordinate pattern is further confirmed. From the study of the scatter diagrams for the first three components, it became clear that no distinct differences between populations could be found, and that there was a mixture of individuals from different sources along all three components. So as to promote some order in these diagrams, general trends for each population were worked out, to find where the majority of individuals from each population could be found, and when they were given a positive, negative, or variable value. It is clear that the conclusions drawn from the population mean coordinate analysis, along the shoot vigour axis, are confirmed by this analysis, as Butser Hill shows consistently higher values than the northern populations. Also within the north, the variable nature of Scout Scar, Overton Hall, Guisborough and Brantingham (which made up one group in the former analysis) and the negative ratings for Yew Barrow and Ravensdale (making up another group in the former analysis) indicates that there are no distinctive between-region trends to be seen here. However, the suggestion of an east to west cline in the north of England in the population mean coordinate analysis has been shown here not to be very clear, as two populations, namely Yew Barrow and Overton Hall show a variable rating along this component. Thus the trend for this characteristic has been described as a weak cline. The highly variable nature of the majority of populations along the tree dimension axis confirms the conclusions drawn from the previous analysis, i.e. there are no distinctive regional differences for tree dimensions. However, the positive rating for the southern population, Chichester Road, suggests that trees from the south can be larger than those in the northern regions.

As a way of further confirming these conclusions, and to make the overall picture even more clear, a cluster analysis then was performed (chapter 5) on the individual coordinates, to find out how individual trees would group as compared to the eight populations measured. As expected, there was a mixture of individuals from different populations within each cluster. It was found that no cluster contained individual trees solely from a single population, but that in each cluster there were trees from various sampled populations, confirming the suggestion that the populations measured showed no discrete differences in morphological variation. However, trends could be identified, and especially along the shoot vigour component; here, the majority of trees from Butser Hill were found to lie in two clusters, i.e. clusters 1 and 2, both of which lay in the positive area of the graph, for shoot vigour. They also were found along the leaf dimension axis to lie in the negative area; therefore, the conclusion was that the trees from this population showed a positive shoot vigour characteristic and a negative leaf dimension characteristic, so confirming what had been indicated from the previous stages of the analysis. All the other populations were found to lie in areas of the graph which confirmed the conclusions made at the previous stages of the analysis. The Chichester Road population was found to show a negative trend in both characteristics, Scout Scar was variable for shoot dimensions and negative for leaf dimensions, Yew Barrow was negative for shoot dimensions and variable for leaf dimensions, Overton Hall was variable for both characteristics, Ravensdale was negative for shoot vigour and positive for leaf dimensions, Guisborough was variable for shoot vigour and positive for leaf dimensions, and Brantingham was variable for shoot vigour and positive for leaf dimensions. In the case of the third component (tree dimensions), six of the populations were found to be variable for this characteristic, namely Butser Hill, Scout Scar, Yew Barrow, Ravensdale, Overton Hall and Guisborough, with Chichester Road and Brantingham being positive and negative respectively. These results confirm the conclusions made in the previous stages of the analysis, but the major conclusion from the latter analysis is that individual trees from different populations can be seen to be more similar to trees from other sampled populations than trees from the same population; accordingly, the trees that do exist do so not in a discrete fashion, but only as a trend based on the majority of trees.

To sum up, therefore, there seems to be no distinct differences between populations from the northern regions measured in this analysis along the shoot vigour component, and the variation between the northern populations can not therefore be described as ~~random~~ clinal; however, in comparison to the southern population of Butser Hill, all the northern populations show a lower value for this characteristic suggesting a broad clinal trend. Although it is difficult to see any regional trends along the leaf dimension axis, both the northeastern populations, i.e. Guisborough and Brantingham, show a positive value, while in the other northern regions there is no agreement for this characteristic, and in comparison to the southern populations which show a negative value it can be suggested that there is an increase of leaf dimensions towards the northeast, but within the north this can only be described as a weak cline. Finally, the extremely variable nature of the third component (tree dimensions) throughout all regions suggests that there are no differences between regions for this characteristic; however, the southern population of Chichester Road, in which the majority of trees have a positive value, suggests that tree dimensions in the south can be higher than those in the north, and the negative value found in the northeastern population of Brantingham, suggests that in this region it is possible to find the smallest trees of all.

CHAPTER 6.

Variation in seed weight, germination percentage, and seedling vigour in Taxus baccata L.

It has been previously pointed out in this dissertation, that the seed of the yew takes eighteen months to germinate naturally (chapter 1) and that the most recent work on the breakage of dormancy noted that at least ten months are needed, using controlled temperature stratification techniques to succeed in artificially germinating the yew seed (chapter 2). At the outset of this project it had been hoped to establish a common garden experiment to compare between-seedling characteristics of morphological traits, so as to supplement the information obtained from studies of the adult tree. This would have given some indication of genetic variability in the measured traits. However, in the time allotted, it was found that only very young seedlings could be grown, and that the work had to be foreshortened due to the germination problem. It was therefore decided that a comparison of three variables, that of seed weight, germination percentage, and seedling vigour, would form a preliminary investigation into the between-population variation from selected English seed sources.

Evidence from other workers.

Burgar (1964) and Burley (1965) have noted that seed size or weight may influence germination and initial seedling size. Burley (1965) has commented that it is generally accepted that at germination a large seed tends to produce a large seedling, even though Ashby (1939) had stressed that in some species the seeds are largely filled with the maternal tissue, so that embryo differences are small. However, Burgar (1964) noted that although several authors had reported that in some species large seeds germinate more completely than small seeds, and produce seedlings whose initial growth is better than seedlings from small seeds, in other species, the seed size affects only germination, or early survival, or the initial growth but not all three. For example, Hough (1952) established that heavy seed produced a significantly heavier red pine (*Pinus resinosa*) seedling than did light seed. Langdon (1958) reported a similar result for South Florida slash pine (*Pinus elliottii*), and Shoulders (1961) found that small slash pine seed produced a smaller seedling than did medium and large seed. On the other hand, Lavender (1958) recorded that Douglas-fir (*Pseudotsuga menziesii*) seed size did not affect the size and weight of seedlings, but heavier seed resulted in about 50% more live seedlings than did light seed. According to Wycoff (1962), there is no difference in the germination of large and small white pine (*Pinus strobus*) seed, but seedlings from small seeds are smaller, and do not start to grow as rapidly as seedlings from large seeds.

In a study using cross-bred pines, designed to find out whether seed and seedling size are controlled by heredity, Righter (1945) established that seed weight is correlated in a positive manner with seedling size, but interestingly went on to conclude that seed and seedling size cannot be indicators of inherent vigour in pines, commenting that the initial advantage of large seed is not permanent in pines. Stockwell (1942) found that there was no correlation between seedling height and seed characteristics in *Pinus jeffreyi*. Burgar (1964), using seed length as an indicator of seed size, found that there were significant differences in one-year-old seedling height and weight among three seed size classes in a sample of white spruce (*Picea glauca*). He noted that the seed size does not affect either the total germination or the rate of first-year survival of seedlings; however, seed size did affect total growth in the first-year seedling, with the height and weight of the seedlings increasing directly with the size of seed. Ackerman & Gorman (1969) studied seed weight, germination percentage and seedling weight of lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*), and found that a "relatively small part" of the total variation in the size of individual seedlings could be explained by seed weight. Also they found that there were significant differences in percentage germination between the lightest and heaviest seed in lodgepole pine, with the larger seeds having the higher percentage. However, there were no significant differences in the case of white spruce. It was also shown that seed weight contributed significantly to seedling weight in both species, i.e. heavier seeds gave heavier seedlings. It can be seen therefore that tree seed characteristics, germination, and seedling size in some cases can be correlated, although it is also evident that each species reacts differently.

Genecological experiments based on tree provenances begin with the collection of seeds from various locations, and therefore seed characteristics, germination and seedling characteristics may be thought of as being preliminary stages in a between-provenance study. Andersson (1965) studied cone and seed characteristics of provenances of Norway spruce (Picea abies), and found that there were significant between-population differences and between-tree differences within populations for cone length, cone weight, total number of seeds per cone and seed weight. He also found that there were differences between populations for seed germinative capacity, and that characters such as cone weight, cone length, seed weight and total number of seeds per cone, both seperately and in combination, could effect seed germinative ability between populations. He went on to note that the associations of seed weight per cone, cone weight, and breadth, with seed germination ability indicate that seed weight represents a very important component in determining seed germinative capacity. Palmberg (1975) looked at various aspects of geographic variation of Pinus halepensis from European seed sources, including seed weight and germination percentage. He found that there was a statistically-significant correlation between seed weight and elevation of seed source (altitude), and that the germination percentage was positively correlàted with seed weight, thus indicating that the heavier the seed, the higher the germination percentage. Birot (1978) studied geographic variation of seed weights of Pinus contorta collected throughout its natural range. He found that seed was heaviest in the subspecies Pinus contorta subp. murrayana from the Cascades (Oregon) and from the Sierra Nevada (California). Interprovenance variation was explained according to latitude, elevation and longitude. However, the differences between the patterns of the different subspecies were not consistent. For example, the subspecies bolanderi (which has a restricted range in California) had very light seed considering its southern latitude of origin. Burley (1966), studying the seed characteristics of Sitka spruce (Picea sitchensis), noted that seed weight was not significantly related to latitude but there was a tendency for northerly provenances to have heavier seed. He also found that the northerly seed lots had lower germination capacity than southern lots, i.e. the lighter seeds had a better germination percentage than the heavier seed.

From these examples from the literature, therefore, it seems that there are no general rules as far as the relationship between seed weight, percentage germination and initial seedling growth of conifers is concerned. It was therefore of interest to see whether there might be significant differences in these relationships between regions and populations in the yew; however, before entering into aspects of these relationships, it will be useful to restate the extent of our knowledge on the germination of the yew, in somewhat greater detail than hitherto.

The germination of the yew seed.

It has been previously pointed out, in chapter two, that the seed of the yew is surrounded by an aril, and that it reaches maturation in August to October of the same year as fertilisation (Favre-Duchartre, 1962). Although it is ready for dispersal at this time, the seed is still in a deep state of dormancy, with the embryo being very small in relation to the endosperm mass (Suszka, 1975). It is noted by Heit (1969) that, due to this deep dormancy, yew seeds germinate very unevenly, and some can take a few years to germinate naturally. This dormancy was studied by Le Page-

Degivry (1973 a,b) using isolated embryos, and she found that the inhibitor of growth was abscisic acid; if this was removed, embryo growth would take place.

It is well documented that once the seed is on the ground it will not germinate until the second spring, i.e. 18 months after falling from the trees (des Abbayes et al., 1963; Lawralree, 1952, S.W.P.U.S., 1974). Optimal germination conditions in the tree nursery have been worked out for many trees. Heit (1968) worked on "approximately" 500 species of trees and shrubs, including Taxus baccata, which he suggested needed a two to six month prechilling before normal germination would occur. Schopmeyer (1974) reported that yew seeds are slow to germinate and that natural germination does not take place until the second year. He also suggested that most of the natural germination in the yew comes from seed that has passed through a bird's digestive tract first. Heit (1969) and Mitiska (1954) wrote that yew seeds have a strong and variable dormancy, suggesting that this can be broken by a warm plus cold stratification. But the actual details seem confused. Heit (1969) and S.W.P.U.S. (1974) suggested that the seeds be held at 60°F for 90 to 210 days, followed by 60 to 120 days at 36°F. However, the International Seed Testing Association (ISTA) (1966) specified prechilling the seed for 270 days at 37°F to 41°F.

Devillez (1976) attempted to find the optimal conditions of yew seed germination by subjecting different seed lots to different stratification regimes. All the tests were carried out in darkness. The temperature regimes used were constant, 12-hour thermoperiodic regimes, and regimes with different warm and cold periods. He also X-rayed the seeds before and after stratification. Table 6.1 shows the control results of the relative sizes of embryo, embryonic cavity, endosperm and seed. It can clearly be seen that the embryo is small in relation to the quite large seed, and as Devillez remarked, "embryo length only reaches 31 per cent of the endosperm length and 45 per cent of the embryonic cavity length". This result agrees with work completed by Zenkteler & Guzowska (1970), who showed

Table 6.1. **Embryo, embryonic cavity, endosperm and seed lengths of seeds collected in Autumn 1971.**

	MEAN	STANDARD DEVIATION
EMBRYO	1.5	0.03
EMBRYONIC CAVITY	3.3	0.08
ENDOSPERM	4.9	0.02
SEED	6.0	0.06

After Devillez, 1976.

that the mature seed contains a small embryo surrounded by a massive female gametophyte. According to Le Page-Degivry (1973a) the embryo length is hardly equal to half of its final size, but it is completely morphologically differentiated. She concluded that it is only the growth that has stopped at the moment of seed maturation.

Of the many tests carried out by Devillez (1976), the warm-cold stratification of temperature gave the best results in increasing embryo length, and it was the only regime that produced germination, confirming the above nursery results (Heit, 1969; Mitiska, 1954). To find out the stratification regime that gave the best results, and further the length of time that would give the best results, he carried out a series of experiments. For the warm phase the test temperatures used were 10°C to 20°C, 15°C to 25°C, 20°C to 30°C, 20°C to 35°C, and 20°C to 40°C.. The cold periods were set at 0°C, 5°C, 10°C, and 15°C. The experiments were designed so that the periods of warmth and cold were of equal length, i.e. one month plus one month, two months plus two months, three months plus three months, and six months plus six months. He found that there was an increase of embryo length in all cases, although the most substantial increase was found to be over the longest time period. He also found that at the six month time period, the embryo length in the warmth is not bigger than 45 per cent of the gametophyte length, and that it is during the cold period that the maximum increase occurs, when the embryo length ratio reaches 61 per cent. When comparing the germination results of the different warm-cold stratification regimes for six months, he discovered that the best germination was reached at either 10°C to 20°C, or 15°C to 25°C, followed by 4 to 5 months at 5°C or 10°C, and concluded that the stratification must begin with the warm phase, and that the sequence warm-cold was needed to achieve after-ripening and dormancy breakdown; he finally suggested that it is this phenomenon that may explain the 18-month period which precedes germination in the field.

Suszka (1975) summed up the findings of dormancy breakage as follows; soaking the seeds in cold water is a necessary first step of breaking dormancy. It leads to a migration of the inhibitor contained in the embryos into the endosperm. Warm stratification should follow in order to increase the permeability of seed coats and remove the inhibitors from the embryos. A repeated period of cold (cool stratification) would be necessary after warm stratification to enable embryos to increase in length, and to put an end to the dormancy, followed again by a period of moderately-increased temperature, which would enable not only the root (breaking the seedcoat) but also the hypocotyl (raising seeds to the soil surface) and the cotyledons to grow at the expense of gradually used food reserves of the endosperm.

Since the above is the most recent information available on dormancy breakage in the yew, this procedure was followed in this study.

Variation of seed weights, percentage germination and seedling vigour.

From the results obtained from the study of the variation of morphological characters of the adult yew, it has been suggested that populations from the south of England tended to show a higher shoot vigour than their northern counterparts. This, in turn, might suggest that there would be equivalent variations in the reproductive characteristics of the yew, the working hypotheses being that there should be a decrease in reproductive characteristics along a south to north gradient, and that there will be no regional trends when comparing the northern seed samples *per se.*

Variables.

The variables seed weight, percentage germination, and seedling vigour were selected to give an overall preliminary comparison of regional differences in reproductive capacity in the species.

Statistical analysis.

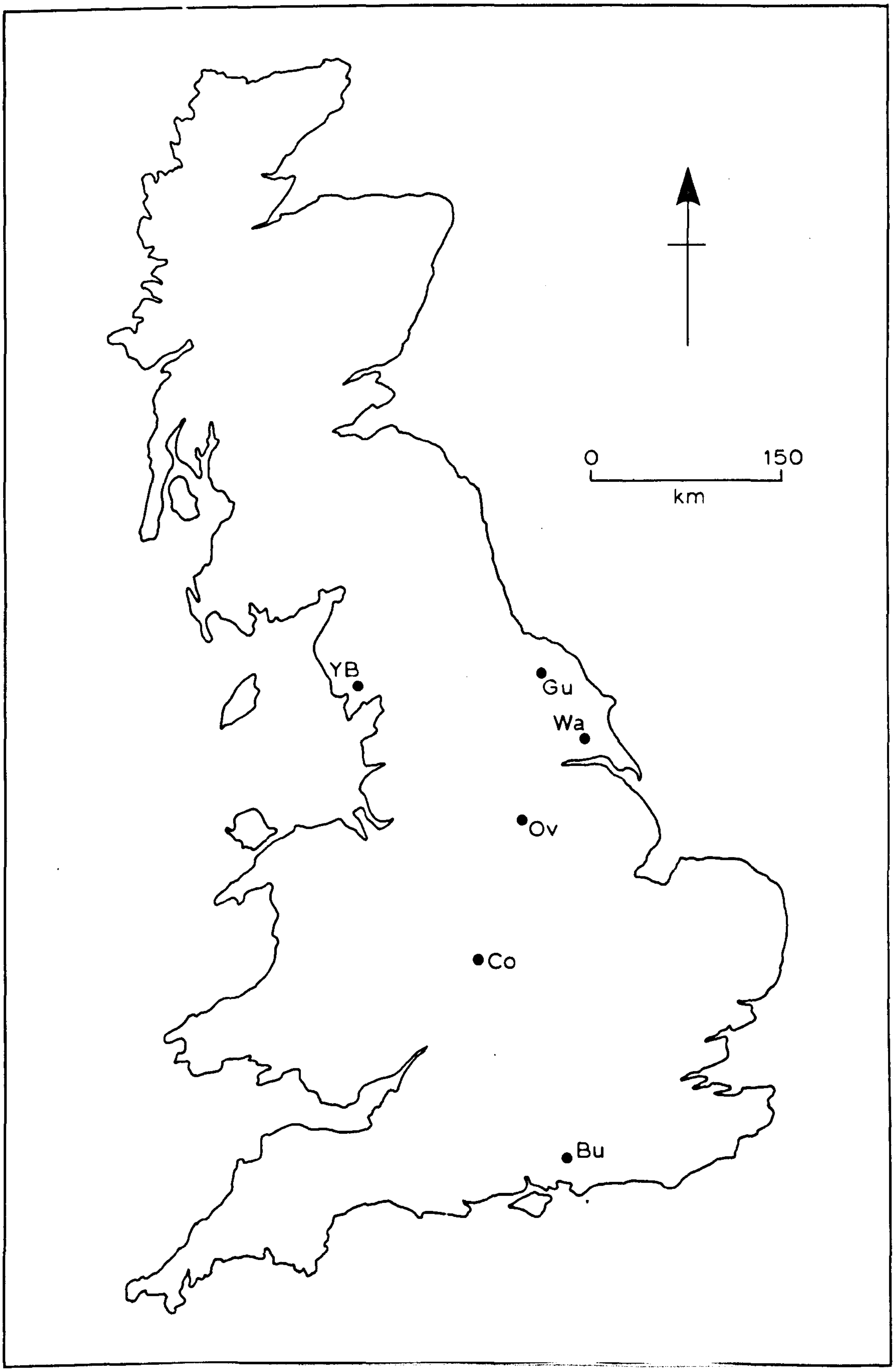
It should be pointed out at the outset that univariate analysis was employed, so as to study variables singly. For this, the analysis of variance technique was used to compare between-population differences for the single variables. This is achieved by discovering whether there are significant differences between the means of the populations in the study for each particular variable. If significant differences are found, an additional test is needed to indicate where these differences lie. The method used in this dissertation for this purpose was Duncan's multirange test (1955). The analysis of variance was performed on ICL 1904S computer at Hull University, the programme name being Anova 1, and the multirange test was done by hand calculator. More details about these statistical tests will be given in the appropriate places in the text.

Materials and methods.

The populations selected for seed collection were Butser Hill (Bu), Coughton Hall (Co), Overton Hall (Ov), Yew Barrow (Yb), Warter (Wa), and Guisborough (Gu), as shown in Fig 6.1. Four of these populations were used in the preceding study of variation in the morphological characteristics of adult trees, namely Bu, Yb, Ov and Gu. The inclusion of Co NGR SO 083605 was thought necessary to see whether, in the light of information gained from the work displayed in chapters four and five, one could distinguish a distinct south-north trend for these variables. Warter was included as very few seeds were found at the Brantingham site at the time of seed collection; thus, another site was required from this region. From the table shown in chapter 4 (Table 4.1) which lists the yew tree populations in the three northern regions of study, it can be seen that there is only one other site in this region, and that is Warter. The site lies only 20 km from Brantingham, and has similar environmental conditions.

The reason for the absence of seeds from the Brantingham site can only be speculative. It is, for example, possible that all the seeds had been taken from this site by birds; that there was an overall failure of seed set; or frost damage to the developing reproductive organs could have occurred. Whatever the reason, for the purposes of this experiment seeds were required from the region and thus the Warter population was selected

Fig 6.1. Populations selected for the collection of seed samples.



Legend: Bu = Butser Hill
Co = Coughton Hall
Ov = Overton Hall
Wa = Warter
Gu = Guisborough
Yb = Yew Barrow

as the alternative.

The seeds were collected from approximately twenty trees from each selected population during the period October-November 1977, with arils intact. They were then separated from the arils in the laboratory by soaking in water and removing them by hand. They were then counted (Table 6.2).

Table 6.2. The number of seeds collected from each population.

Wa	Gu	Yb	Bu	Co	Ov
531	547	636	624	603	586

When all the seeds had been counted, each seed population was put into a separate tray which had been previously lined with filter paper and wetted with distilled water. The trays were then covered with black plastic, and put into a growth room for the start of the warm phase of stratification; the growth room temperature was set at 15°C to 20°C. Each week, the trays were checked to make sure the filter paper was always moist. After six months, the trays were moved to a cold room (temperature at approximately 6°C), for the second stratification phase, and they were again checked regularly for moisture content.

Germination was said to have occurred when the radicle (seedling root) was as long as the seed. The germinated seeds were removed from the cold room and sown into trays, at a rate of 20 / tray, equidistant from each other. These trays were put into a glasshouse, so that the environment was conducive to growth. The soil used was a standard potting compost (John Innes potting compost No. 2), the daylength was controlled (sixteen hours daylength) and the temperature never fell below 15°C. These seedlings were watered every day.

Two months after sowing, the seedlings were cut at soil level using a sharp scalpel and taken to the laboratory where they were dried in an oven using a standard procedure, i.e. 60°C for 48 hours (Williams & Hanson 1974), for measuring seedling vigour.

Seed weight measurements.

Another sample of seeds was collected in October-November 1978 from the same populations for the determination of seed-weight differences. These were separated from the arils in the same way as before, and left to dry for five days at laboratory temperatures. Thirty seeds from each population were randomly selected for weighing, by assigning each seed a number and selecting the seeds to be weighed using random number tables.

(A) Analysis of data.

Analysis of variance was used on the seed weight and seedling vigour measurements to test whether there might be significant differences between populations for these variables at a probability level of 0.05. Details of the analysis of variance test are shown below.

Analysis of variance table.

Source of variation.	Degrees of freedom (df) Formula	S.S. Formula	M.S. Formula	F Formula
$\bar{Y} - \bar{\bar{Y}}$ (between groups)	a - 1	$\frac{1}{n}\sum^{a}\left(\sum^{n} Y\right)^{2}$ -CT	$\frac{\text{SS among}}{(a - 1)}$	$\frac{\text{M.S. between}}{\text{M.S. within}}$
$Y - \bar{Y}$ (within groups)	a(n - 1)	S Stotal^{-SS}groups	$\frac{\text{SS within}}{a(n - 1)}$	
$Y - \bar{\bar{Y}}$ (Total)	an - 1	$\sum^{a}\sum^{n} Y^{2}$ - CT		

Where: $\bar{Y}$ = mean of each group   a = the number of groups

$\bar{\bar{Y}}$ = grand mean of the group means   n = the number of observations within groups

S.S. = the sum of squares

M.S. = the mean square   Y = individual observations

C.T. = Correction factor $= \frac{1}{an}\left(\sum^{a}\sum^{n} Y\right)^{2}$

If the F ratio is found to be significant, it indicates that there is a significant difference between populations; if not, the null hypothesis can be accepted, i.e. there are no differences between populations.

To find out where the significant between-group differences occur, if the above analysis shows there to be between-group differences, a further analysis is undertaken, as below.

(B) The Duncan's multirange test.

This test shows which groups are significantly different from each other and which are not. The procedure is as follows:

(a) The means of the groups from highest to lowest are ranked; then

(b) Calculate $S\bar{x} = \sqrt{\text{the number of means (k) X the mean square (within) / N}}$

Where: N = the total number of observations; and

(c) Using the tables compiled by Duncan (1955), the values of the Significant Studentised Range (S.R.) for n-1 degrees of freedom are identified. The value for k means against the highest average is inserted, that for k-1 against the next highest and so on. Then

(d) Each S.R. value is multiplied by $S\bar{x}$, to give the Shortest Significant Range (S.S.R.) Then

(e) Starting with $\bar{X}$ max, subtract $\bar{X}$ min from it and place it in Col 1a (see below). Then subtract the next lowest X from X max and place it in Col 1b etc. Col. 2a is then the second highest mean minus X min. This is continued until all the differences have been calculated.

(f) A difference is significant at $p=0.05$ if it exceeds the appropriate S.S.R.

(g) According to convention, the results are stated by underlining pairs that are not significantly different from each other.

Thus:

	Mean	$S\bar{x}$	S.R.	S.S.R.		Col. 1	Col. 2	Col. 3	Col. 4
$\bar{X}$ DECREASING ↓	$\bar{X}$ max	Q	k	k Q	a	$\bar{X}$ max-Xmin	-	-	-
	next $\bar{X}$	Q	k-1	(k-1)Q	b	$\bar{X}$ max-next lowest $\bar{X}$	next $\bar{X}$-$\bar{X}$min	-	-
					c	etc.	etc.		
					d				

Where a is the probability level selected.

(A) Results.

(B) Seed weights.

The weights of the individual seeds were measured in grammes (Table 6.3). This data was analysed using an analysis of variance programme, Anova 1, on the ICL 1904S computer in Hull University and the results are shown in Table 6.4. The F ratio was significant at the 0.05 level. This indicates that there is a marked between-population difference in seed weight; therefore, Duncan's multirange test was applied to the means of the populations to identify where the differences lie (Table 6.5).

Table 6.5. The results of the Duncan's multirange test for the seed weight data.

Population	$\bar{X}$	$S\bar{x}$	S.R.	S.S.R.	a	b	c	d	e
Bu	0.0695	0.002	3.15	0.006	0.025*	-	-	-	-
Co	0.0653	0.002	3.09	0.006	0.022*	0.020*	-	-	-
Yb	0.0607	0.002	3.02	0.006	0.018*	0.018*	0.016*	-	-
Wa	0.0516	0.002	2.92	0.006	0.009*	0.014*	0.014*	0.007*	-
Gu	0.0472	0.002	2.77	0.005	0.004	0.005	0.009*	0.004	0.002
Ov	0.0449								

* = significant differences at the 0.05 level.

Therefore: Bu Co Yb Wa Gu Ov

0.0695 0.0653 0.0607 0.0516 0.0472 0.0449

This result separates the six populations into two distinct groups, with Bu, Co, and Yb forming one group and Wa, Gu and Ov the other. It can be seen that the former group includes the three populations with the heaviest seed weights and the latter the lighter. Looking at the two groups separately, in the group consisting of Bu, Co and Yb, there is a significant difference between Bu and Yb with the seed weights of the Bu population being heavier than Yb; also, Co is not significantly different

Table 6.3. Individual seed weights of the six populations in grammes.

	Population					
Seed weight gms	Butser Hill	Coughton Hall	Yew Barrow	Overton Hall	Guisborough	Warter
1	0.0708	0.0742	0.0744	0.0480	0.0524	0.0558
2	0.0698	0.0744	0.0525	0.0478	0.0426	0.0543
3	0.0722	0.0659	0.0504	0.0520	0.0489	0.0675
4	0.0622	0.0600	0.0630	0.0522	0.0555	0.0564
5	0.0702	0.0569	0.0647	0.0494	0.0654	0.0512
6	0.0754	0.0640	0.0690	0.0452	0.0610	0.0515
7	0.0576	0.0628	0.0648	0.0562	0.0641	0.0636
8	0.0759	0.0697	0.0618	0.0368	0.0370	0.0688
9	0.0835	0.0573	0.0575	0.0557	0.0586	0.0432
10	0.0830	0.0583	0.0510	0.0467	0.0663	0.0550
11	0.0708	0.0646	0.0534	0.0488	0.0296	0.0510
12	0.0644	0.0531	0.0610	0.0564	0.0341	0.0540
13	0.0738	0.0597	0.0480	0.0448	0.0530	0.0610
14	0.0685	0.0726	0.0616	0.0412	0.0578	0.0491
15	0.0700	0.0610	0.0578	0.0490	0.0406	0.0410
16	0.0724	0.0689	0.0584	0.0426	0.0502	0.0316
17	0.0592	0.0648	0.0661	0.0400	0.0574	0.0317
18	0.0780	0.0704	0.0656	0.0498	0.0460	0.0307
19	0.0543	0.0619	0.0632	0.0370	0.0454	0.0624
20	0.0714	0.0664	0.0534	0.0335	0.0276	0.0593
21	0.0731	0.0654	0.0624	0.0406	0.0478	0.0503
22	0.0602	0.0638	0.0504	0.0362	0.0432	0.0608
23	0.0668	0.0698	0.0716	0.0478	0.0392	0.0607

Table 6.3 (Cont). Individual seed weights of the six populations in grammes.

seed weight gms	Population Butser Hill	Coughton Hall	Yew Barrow	Overton Hall	Guisborough	Warter
24	0.0792	0.0650	0.0706	0.0393	0.0480	0.0555
25	0.0690	0.0586	0.0564	0.0476	0.0416	0.0292
26	0.0654	0.0700	0.0510	0.0379	0.0390	0.0547
27	0.0568	0.0640	0.0687	0.0309	0.0369	0.0592
28	0.0751	0.0892	0.0637	0.0438	0.0462	0.0592
29	0.0710	0.0593	0.0664	0.0450	0.0394	0.0494
30	0.0647	0.0674	0.0584	0.0442	0.0420	0.0295

Table 6.4. Analysis of variance results from the seed weight data.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio
Between Groups	5	0.1527^{10-1}	0.3054^{10-2}	42.19
Within Groups	174	0.1259^{10-1}	0.7238^{10-2}	
Total	179	0.2786^{10-1}	0.1557^{10-3}	

from either of these two. This is interpreted as meaning that within the Co population seed weights there are seeds that are as heavy as those found in the Bu population and some that are as light as those found in the Yb population. In the other group, of three populations, i.e. the group consisting of Wa, Gu and Ov, a similar pattern has emerged. Wa is significantly heavier than Ov; and Gu has seeds that are as heavy as those found in Wa, and as light as those found in Ov.

(B) Seedling vigour.

The standard test for measuring seedling vigour is the oven-dry weight of the seedling, as mentioned above. The results are shown for each population in Table 6.6, and an analysis of variance was carried out on this data as above. The results of this test are shown in Table 6.7. It was found that the F ratio was significant at the 0.05 level, and so as before the Duncan's test was carried out, shown in Table 6.8.

Table 6.8 The results of the Duncan's multirange test for seedling weight data.

Population	$\bar{X}$	$S\bar{x}$	S.R.	S.S.R.	a	b	c	d	e
Co	0.01978	0.001	3.15	0.003	0.004*	-	-	-	
Ov	0.01975	0.001	3.09	0.003	0.003	0.004*	-	-	
Bu	0.01911	0.001	3.02	0.003	0.002	0.003	0.003	-	
Gu	0.01730	0.001	2.92	0.003	0.001	0.002	0.002	0.002	
Yb	0.01679	0.001	2.77	0.003	0.000	0.001	0.002	0.001	
Wa	0.01566								

* = significant differences at the 0.05 level.

Therefore:	Co	Ov	Bu	Gu	Yb	Wa
	0.01978	0.01975	0.01911	0.01730	0.01679	0.01566

In this case there are no distinct groupings of the populations, with only three of the populations being significantly different, i.e. Co and Ov are significantly different to Wa. The other three populations, i.e. Bu, Gu and Yb are shown to be intermediate between these extremes.

Table 6.6. Individual oven-dry weights of seedlings from the six populations.

	Population					
seedling weights gms	Butser Hill	Coughton Hall	Yew Barrow	Overton Hall	Gainsborough	Warter
1	0.0236	0.0166	0.0228	0.0248	0.0184	0.0199
2	0.0141	0.0296	0.0165	0.0235	0.0122	0.0127
3	0.0218	0.0236	0.0124	0.0276	0.0195	0.0063
4	0.0248	0.0218	0.0186	0.0180	0.0212	0.0182
5	0.0203	0.0210	0.0145	0.0246	0.0282	0.0204
6	0.0259	0.0161	0.0122	0.0201	0.0192	0.0166
7	0.0201	0.0156	0.0145	0.0197	0.0140	0.0144
8	0.0212	0.0178	0.0115	0.0129	0.0128	0.0234
9	0.0176	0.0300	0.0082	0.0183	0.0153	0.0190
10	0.0172	0.0258	0.0180	0.0107	0.0066	0.0108
11	0.0139	0.0162	0.0219	0.0235	0.0099	0.0121
12	0.0180	0.0300	0.0212	0.0135	0.0142	0.0203
13	0.0213	0.0328	0.0171	0.0162	0.0175	0.0134
14	0.0165	0.0130	0.0170	0.0113	0.0104	0.0166
15	0.0176	0.0198	0.0108	0.0245	0.0102	0.0155
16	0.0190	0.0110	0.0109	0.0151	0.0272	0.0185
17	0.0180	0.0115	0.0201	0.0184	0.0179	0.0150
18	0.0169	0.0186	0.0238	0.0249	0.0171	0.0172
19	0.0189	0.0178	0.0185	0.0215	0.0140	0.0122
20	0.0148	0.0212	0.0232	0.0163	0.0260	0.0117
21	0.0170	0.0226	0.0196	0.0160	0.0186	0.0112
22	0.0148	0.0118	0.0218	0.0224	0.0242	0.0146
23	0.0250	0.0180	0.0195	0.0189	0.0198	0.0096
24	0.0208	0.0136	0.0089	0.0214	0.0221	0.0236
25	0.0186	0.0186	0.0162	0.0297	0.0160	0.0184

Table 6.7. Analysis of variance results from the seedling weight data.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F Ratio
Between Groups	5	0.3711^{10-3}	0.7421^{10-4}	3.06
Within Groups	144	0.3492^{10-2}	0.2425^{10-4}	
Total	149	0.3863^{10-2}	0.2593^{10-4}	

It should also be noted that, in comparison to the seed weight results, the order of the populations has changed, suggesting that there is no relationship between seed weight and seedling vigour.

(B) Germination.

The seeds were put into the cold room at the beginning of May 1978, after the warm stratification period. The first signs of germination in the yew seed is the splitting of the seed coat, and this occurred within three months of entering the cold phase. The first seeds germinated in the month of August 1978, i.e. the fourth month after entering the cold phase, thus confirming the experience of Devillez (1976). The results are summarised in Figs 6.2 and 6.3a to f.

(C) Description of Figures.

First it should be pointed out that the germination results are based on the first six months from the beginning of germination, and not from the beginning of the cold stratification period, as in Devillez's experiments (1976). Thus the seeds were in the cold stratification phase for considerably longer than for his experiments. This was found to be necessary as by the sixth month, although some populations had begun to germinate, other populations had not, even though these showed signs of seed-coat splitting. Also it should be pointed out that the yew seed will continue to germinate in the cold phase of stratification long after six months, albeit in small numbers.

Fig 6.2 is a summary of all the seed populations together, giving an overall description of seed germination of the yew for the six populations in the survey. The details are shown in the inset table, which shows the total number of seeds collected, the number of seeds that germinated in each of the six months in the test, the percentage of the total seed stock that this represents, and the total number and percentage of the seeds germinated in the six months of data collection.

Total number of seeds collected = 3527

Month	Aug.	Sept.	Oct	Nov	Dec.	Jan.	Total
	1978					1979	
No. of seeds germinated	45	98	110	213	161	144	771
Percentage of total	1·28	2·78	3·12	6·04	4·56	4·08	21·86

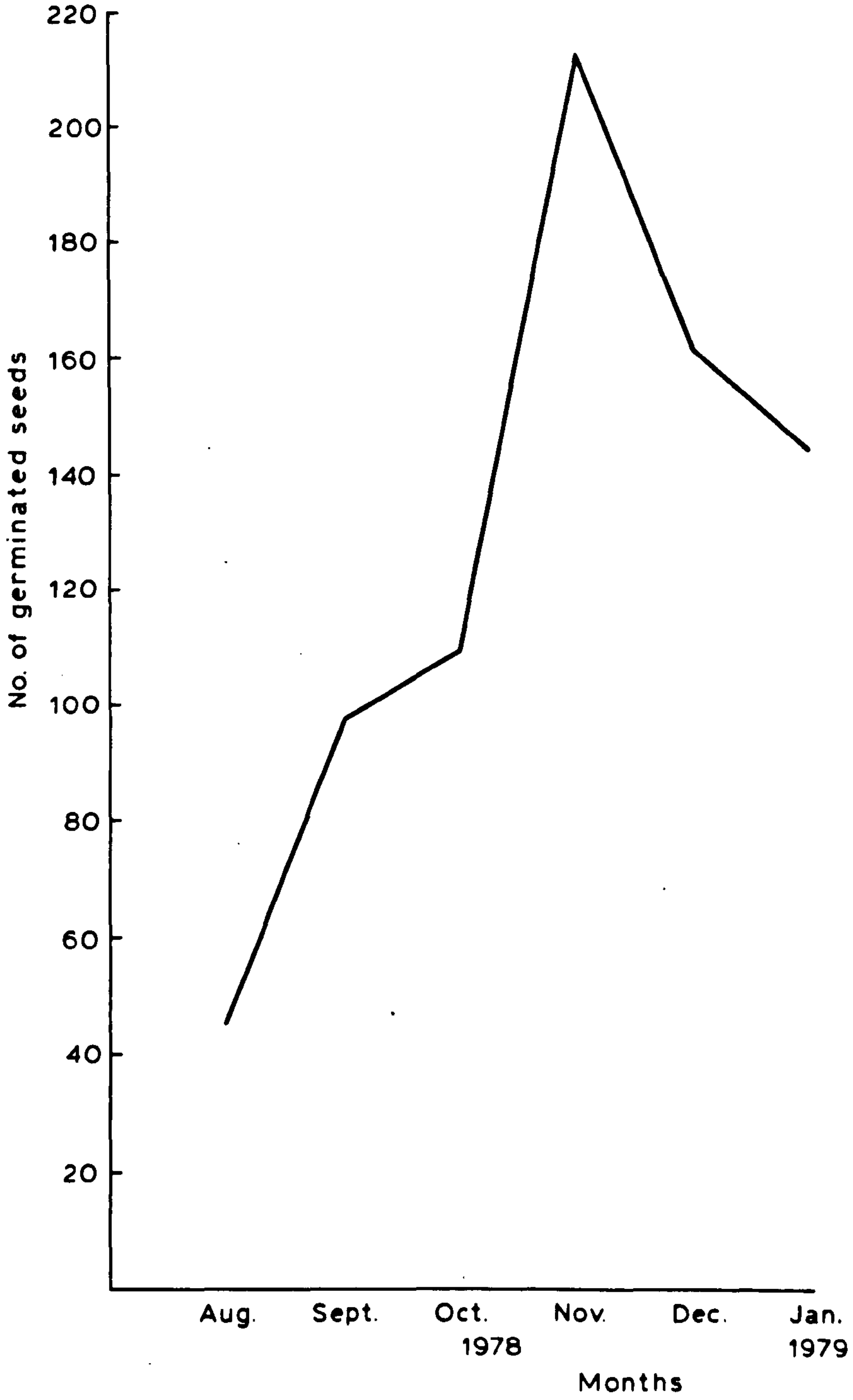


Fig 6.2: Number of seeds germinated in each of the test months for the entire seed sample.

Total number of seeds collected = 586

Month	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Total
	1978					1979	
No. of seeds germinated	37	18	6	17	21	33	132
Percentage of total	6·31	3·07	1·02	2·90	3·58	5·63	22·51

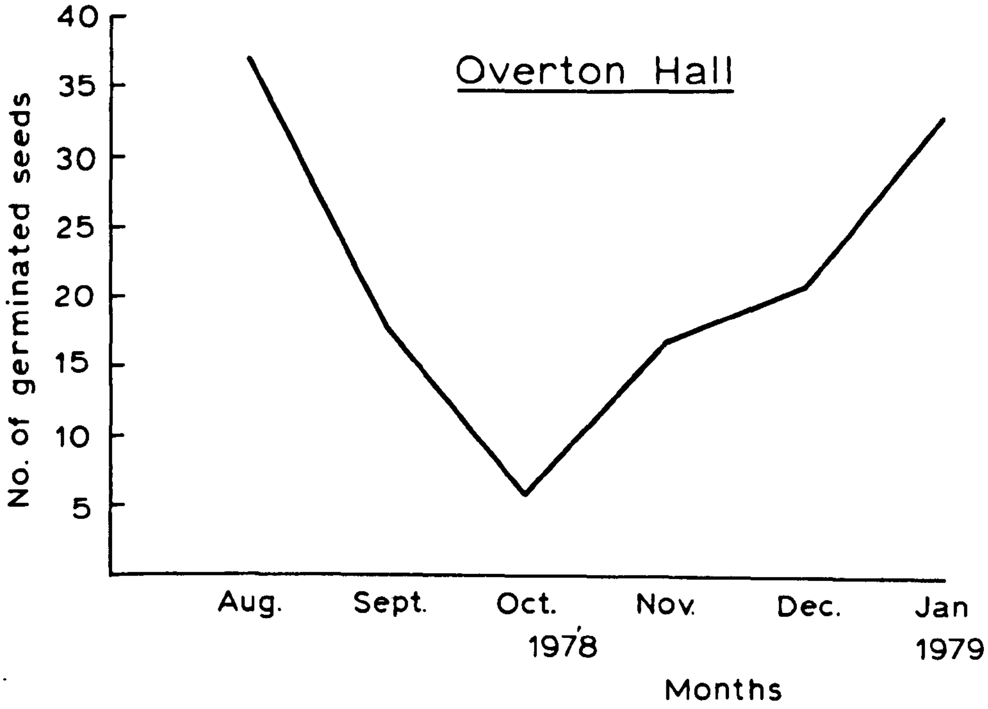


Fig 6.3a. Number of seeds germinated in each of the test months for the Overton Hall seed sample.

Total number of seeds collected = 624

Month	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Total
	1978					1979	
No. of seeds germinated	3	23	19	15	1	5	66
Percentage of total	0·48	3·69	3·04	2·40	0·16	0·80	10·57

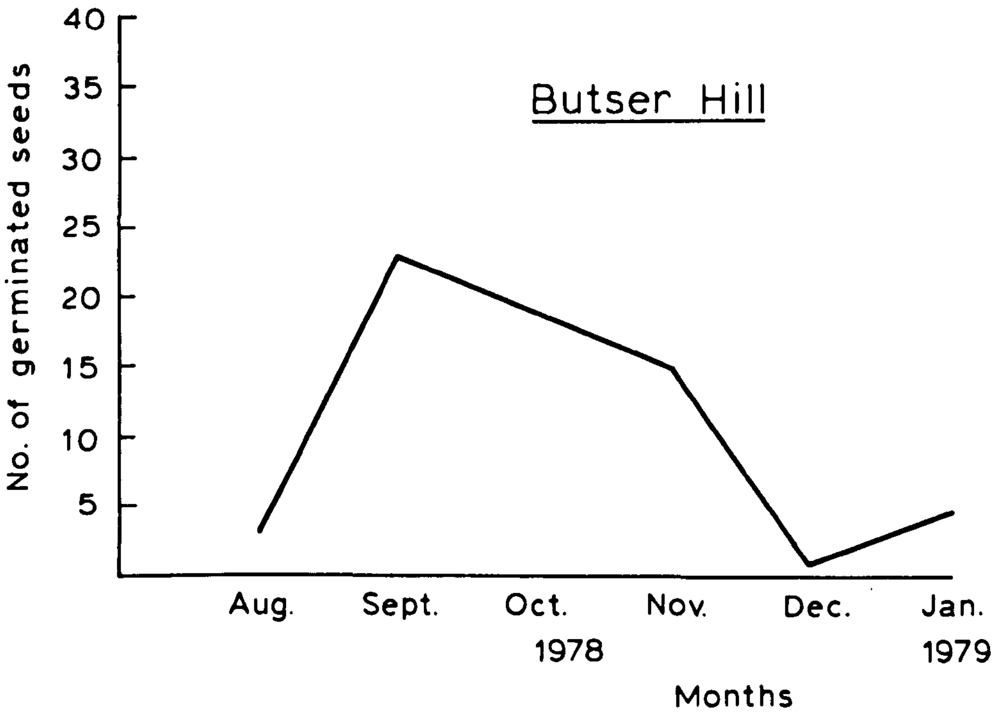


Fig 6.3b. Number of seeds germinated in each of the test months in the Butser Hill seed sample.

Total number of seeds collected = 636

Month	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Total
	1978					1979	
No. of seeds germinated	1	5	16	62	69	51	204
Percentage of total	0·16	0·79	2·52	9·75	10·84	8·02	32·09

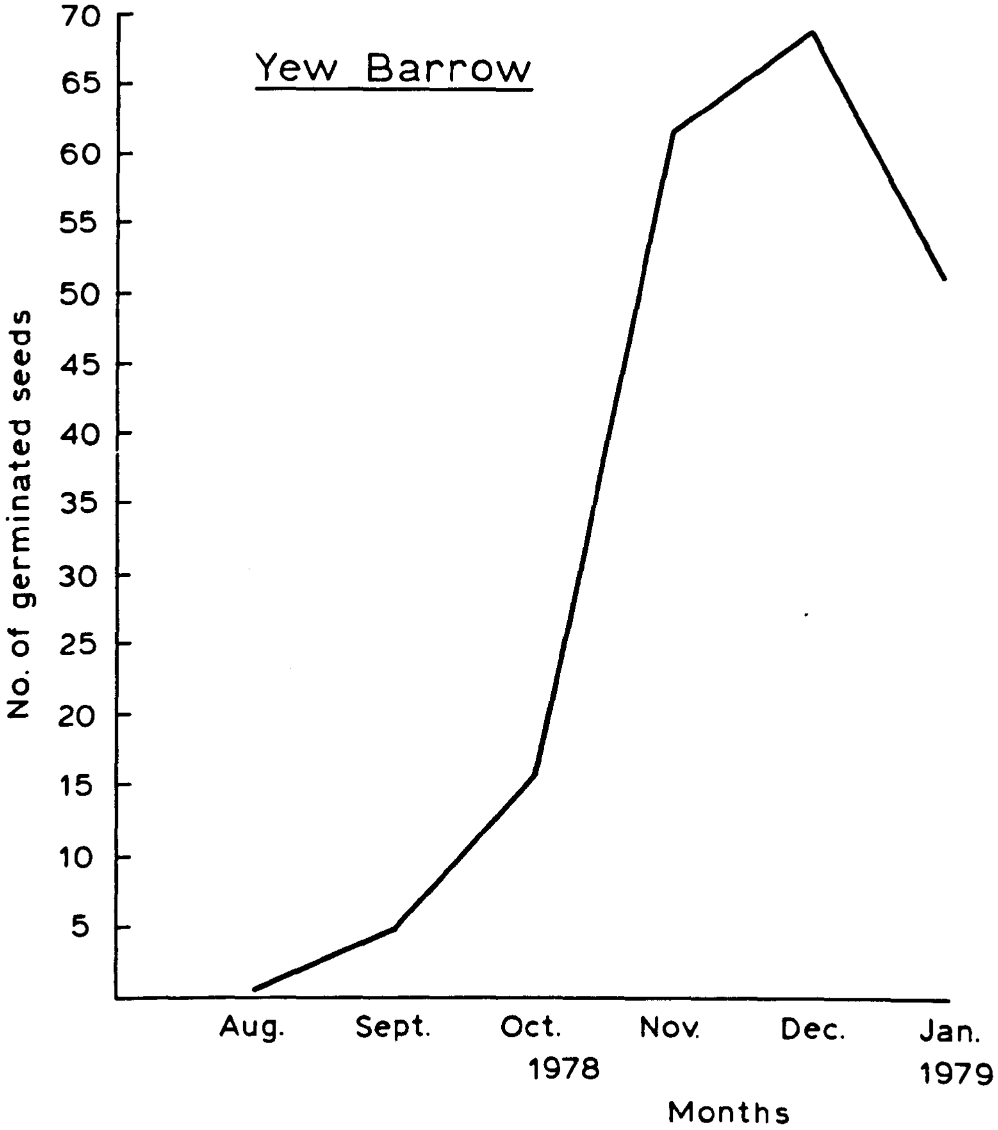


Fig 6.3c. Number of seeds germinated in each of the test months in the Yew Barrow seed sample.

Total number of seeds collected = 603

Month	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Total
	1978					1979	
No. of seeds germinated	1	2	7	64	47	30	151
Percentage of total	0·17	0·33	1·16	10·61	7·79	4·97	25·03

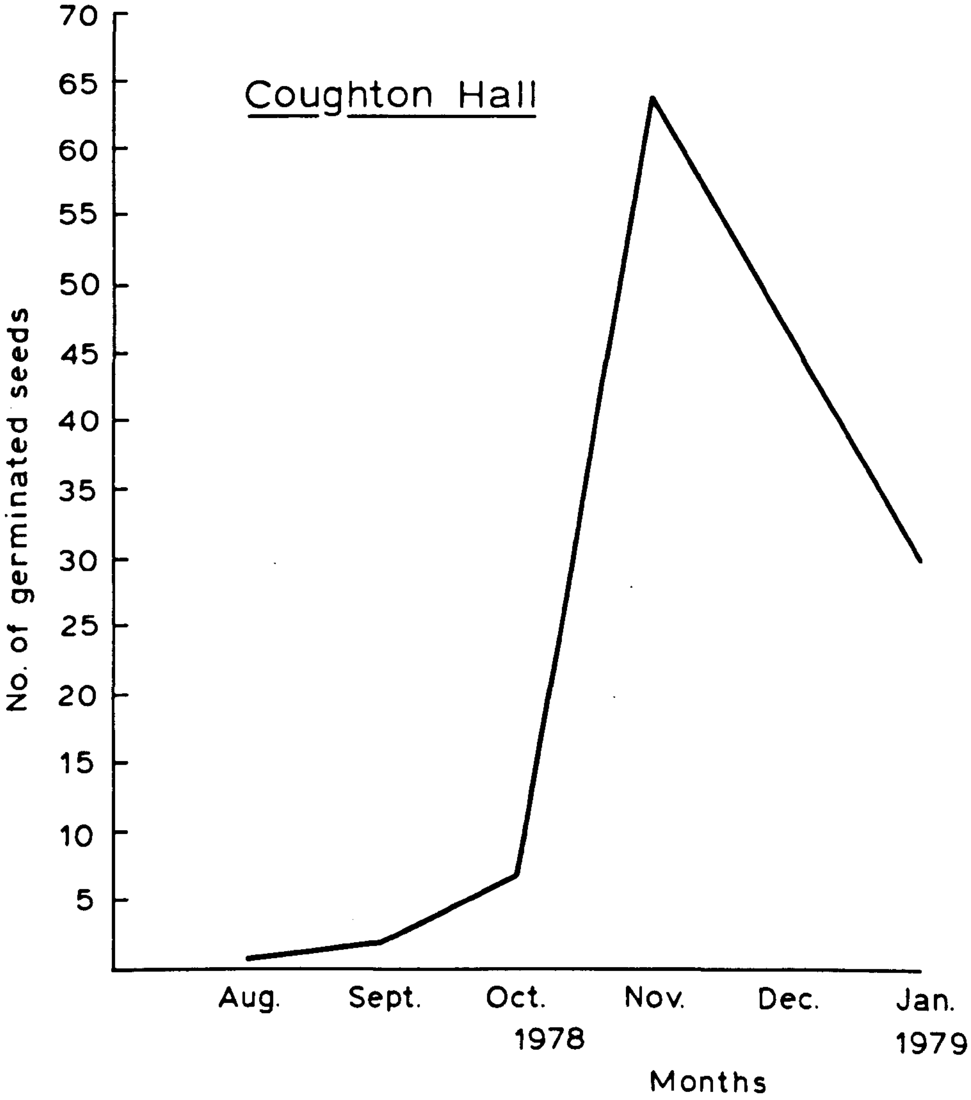


Fig 6.3d. Number of seeds germinated in each of the test months in the Coughton Hall seed sample.

Total number of seeds collected = 547

Month	Aug.	Sept.	Oct.	Nov.	Dec.	Jan	Total
	1978					1979	
No. of seeds germinated	0	22	23	17	9	10	81
Percentage of total	0	4·02	4·20	3·11	1·64	1·83	14·80

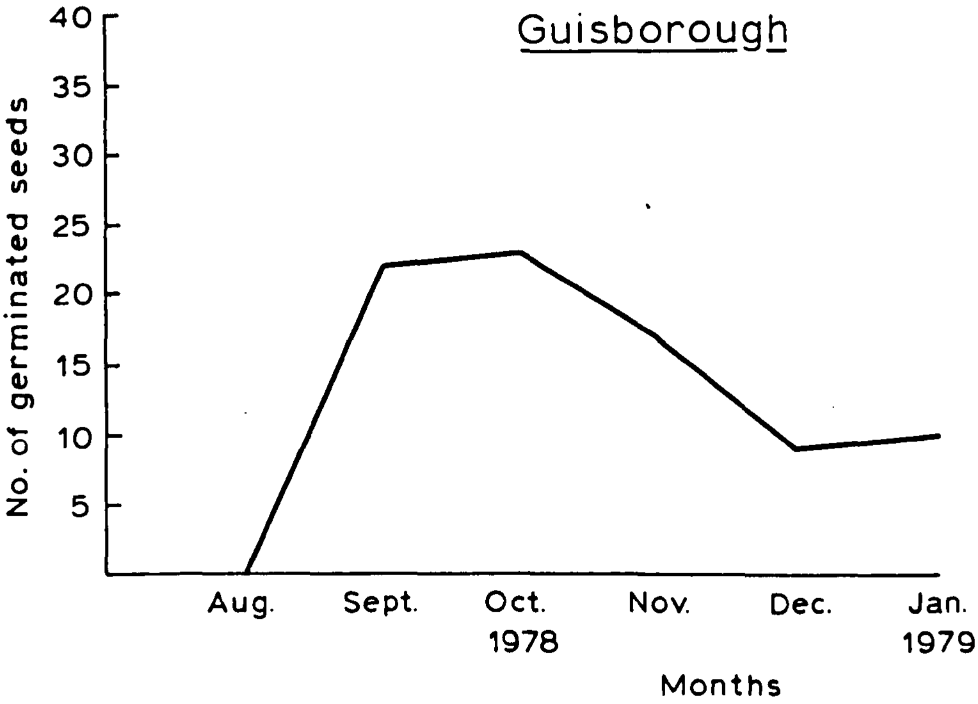


Fig 6.3e. Number of seeds germinated in each of the test months in the Guisborough seed sample.

Total number of seeds collected = 531

Month	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Total
	1978					1979	
No. of seeds germinated	3	28	39	38	14	15	137
Percentage of total	0·56	5·27	7·34	7·16	2·64	2·82	25·79

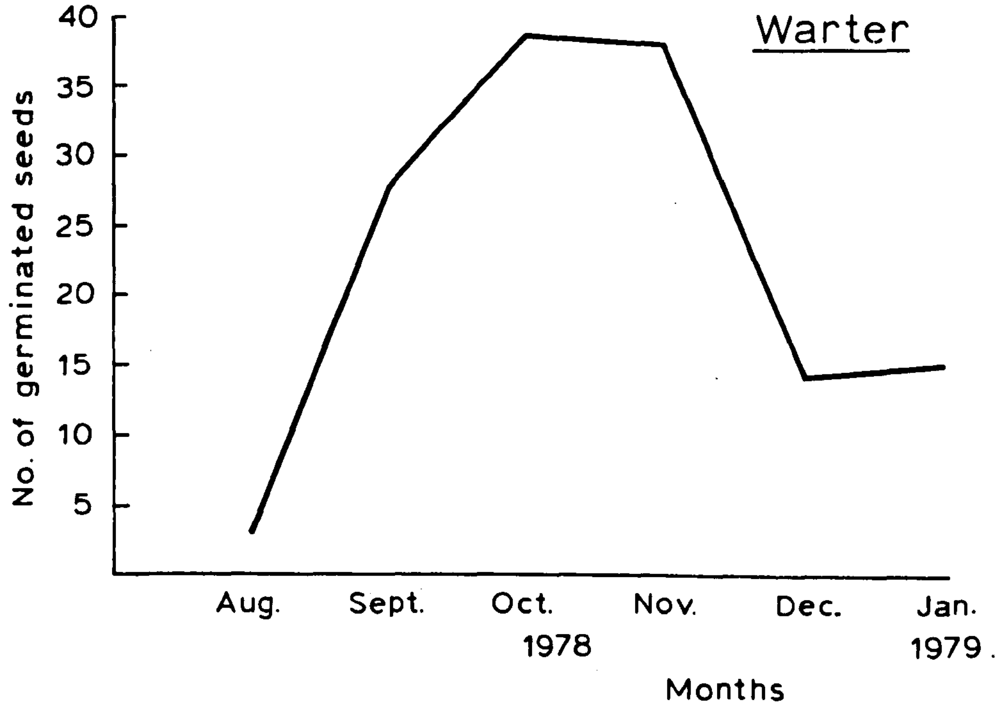


Fig 6.3f. Number of seeds germinated in each of the test months in the Warter seed sample.

As shown in Fig 6.2 the total number of seeds collected from the six populations in the study was 3527. In August 1978, 45 seeds, i.e. 1.28% of the total, germinated; in September 1978, 98 seeds (2.78%) of the total; in October 1978, 110 seeds, (3.12%); in November 1978, 213 seeds (6.04%); in December 1978, 161 seeds (4.56%); and in January 1979, 144 seeds (4.08%). Therefore, in the six months of data collection, 771 seeds germinated, i.e. 21.86% of the total number of seeds in the experiment, from the six populations. It can be seen from the figure that germination increased to a peak in November 1978, i.e. the seventh month after entry into the cold stratification phase, and then fell off to January 1979, the end of the experiment.

The number of seeds which germinated within population samples was then studied, with the results shown in Fig 6.3a to f. It can immediately be seen by comparing the six figures that there are population differences with respect to germination over time. Overton Hall (Ov), in Fig 6.3a, was the first population to show strong germination in August, subsequently dropping away in September and October and then increasing again in November, December and January. Butser Hill (Bu), in Fig 6.3b, increased to a peak in September, fell away slowly in October and November and then dropped considerably in December, showing a small subsequent increase in January, Yew Barrow (Yb), in Fig 6.3c, increased up to a peak in December and fell away in January, while Coughton Hall (Co), Fig 6.3d, reached peak germination in November before falling away in December and January. Guisborough (Gu), in Fig 6.3e, reached its peak around September October, before falling away in November and December with a slight increase in January. Finally, Warter (Wa), in Fig 6.3f, reached its peak in October and November, then falling away in December, but with a slight increase in January.

Not only does timing of germination vary between populations but also the number of seeds that germinate, the details of which are shown in the inset tables following along the same lines as in Fig 6.2. It can be seen from these tables that the total number of germinated seeds over the six month period of the test from the highest to the lowest were as follows; 204 seeds from Yew Barrow, i.e. 32.09% of the seeds collected from that site, 137 (25.79%) from Warter, 151 (25.03%) from Coughton Hall, 132 (22.51%) from Overton Hall, 137 (14.80%) from Guisborough, and 66 (10.57%) from Butser Hill.

The details are as follows. For Yew Barrow, in August 1 seed germinated, i.e. 0.16% of the total, with 5 in September, 0.79%, 16 in October, 2.52%, 62 in November, 9.75%, 69 in December, 10.85%, and 51 in January, 8.02%. For Warter, 3 seeds germinated in August, 0.56%, 28 in September, 5.27%, 39 in October, 7.34%, 38 in November, 7.16%, 14 in December, 2.64% and 15 in January, 2.28%. From Coughton, 1 seed germinated in August, 0.17%, 2 in September, 0.33%, 7 in October, 1.16%, 64 in November, 10.61%, 47 in December, 7.79% and 30 in January, 4.97%. From Overton Hall, 37 seeds germinated in August, 6.31%, 18 in September, 3.07%, 6 in October, 1.02%, 17 in November, 2.90%, 21 in December, 3.58% and 33 in January, 5.63%. There was no germination at all of seeds from Guisborough in August, but 22 seeds germinated in September, 4.02%, 23 in October, 4.20%, 17 in November, 3.11%, 9 in December, 1.64% and 10 in January, 1.83%. From Butser Hill, 3 seeds germinated in August, 0.48%, 23 in September, 3.69%, 19 in October, 3.04%, 15 in November, 2.40%, 1 in December, 0.16% and 5 in January,0.80%.

Discussion.

The working hypothesis in this experiment was first, that there would be a decrease in reproductive characteristics from the south to the north, thus indicating a higher reproductive success rate in the south; and secondly, that there would be no between-population differences in the northern populations.

According to the seed weight results, the populations can be split into two groups, with Butser Hill, Coughton Hall, and Yew Barrow making up the heavier group and Warter, Guisborough, and Overton Hall the lighter. Within these groups it was seen that there were significant differences between populations, i.e. Butser Hill was significantly heavier than Yew Barrow in the former group and Warter was significantly heavier than Overton Hall in the latter, with Coughton Hall and Guisborough having seeds that were as heavy and as light as found in their respective groups.

From the germination results, it was seen that the lightest SEEDS FROM Overton Hall began germination before those from all the other populations (Fig 6.3a), with a sudden burst of activity in the fourth month of the cold phase of stratification (August, 1978). In contrast, all the others showed little germination in this month, displaying an increase in germination up to a peak at various subsequent times during the test. In the case of Butser Hill, this was in September, although there was little change of % germination from September to November and October, 3.69% to 3.04% to 2.40%. In Guisborough and Warter the peak was in October and in Yew Barrow in December and in Coughton in November. This therefore shows that, although all these seed populations were in the same constant experimental conditions, they showed different germination peak times. Is there a relationship between seed weight and germination timing? From Figures 6.3a to f, it could be suggested that the Overton Hall curve is perhaps the most extraordinary shape, for the germination of seeds dropped markedly when all the other seed populations were increasing germination numbers, and then when they were all falling away there was another surge of germination at Overton Hall. It has already been mentioned that Overton Hall seeds were among the lightest of all the seeds and therefore this result might suggest a causal relationship between the erratic germination behaviour and seed weight. If this were so, one would expect to find more regular curves as the seed weight increases. This indeed is the case when the curves of Guisborough, Warter, Yew Barrow and Coughton are compared with Overton Hall. At the other end of the weight spectrum is Butser Hill, which has some of the heaviest seeds; the shape of the germination curve here is more or less opposite to that of Overton Hall, for there is an increase of germination and then approximate levelling off before dropping away in December. It could therefore be suggested that seed weight has an effect on germination patterns, and that the most erratic patterns will be seen in the heaviest and lightest seed populations. Is there any relationship between seed weight and percentage total germination? When comparing the seed weight results with the germination percentages (Table 6.9), it can be seen that the lowest germination percentage is found where the seed is heaviest (Butser Hill). However, the highest germination percentage is found in the same group, i.e. Yew Barrow with 32.07%, followed by Warter at 25.80%, the population having the heaviest seeds in the 'lighter' group, and Coughton Hall at 25.04%, which belongs to the same group as Butser Hill. There therefore seems to be no relationship between these two variables.

In the case of seedling vigour, it has already been noted that there does not seem to be any relationship between this variable and seed weight, (compare Table 6.5 to Table 6.8). The same conclusion has to be drawn in respect of comparisons between seedling vigour and germination percentage (Table 6.10). In this table, it can be seen that there are relatively high germination percentages at both ends of the table. For example Co, which is at one extreme when considering seedling vigour, has a relatively high germination percentage; however, although Wa is at the other extreme for seedling vigour, it has approximately the same germination percentage as Co. This tends to suggest that there is again no relationship between seedling vigour and germination percentage.

To emphasise the lack of any relationship between the three

Table 6.9. Comparison of seed weight and % germination for the six populations.

Population	Bu	Co	Yb	Wa	Gu	Ov
Seed weight	0.0695	0.0653	0.0607	0.0516	0.0472	0.0449
% germ.	10.58	25.04	32.07	25.80	14.81	22.53

________ = insignificant at the 0.05 level of probability.

Table 6.10. Comparison of % germination and seedling vigour for the six populations.

Population	Co	Ov	Bu	Gu	Yb	Wa
% germ.	25.04	22.53	10.58	14.81	32.07	25.80
Seedling vigour	0.01978	0.01975	0.01911	0.01730	0.01679	0.01566

________ = insignificant at the 0.05 level of probability.

Table 6.11. Correlation coefficients between thethree variables

	% germination	Seedling vigour
Seed weight	-0.62$^+$	0.27$^+$
% germination		-0.33$^+$

+ = insignificant at the 0.05 level of probability.

variables studied here, the correlation coefficients between them were calculated (Table 6.11). This shows that there is no significant correlation between seed weight and germination percentage, seed weight and seedling vigour, or germination percentage and seedling vigour. It can therefore be concluded that the collection of heavier seeds will not produce better germination percentages or higher seedling vigour than lighter seeds in the case of the yew.

As there are no relationships between the three variables in this study per se, any geographic patterns that might be inferred can only be discussed for each variable in turn. In the case of seed weights, the most southerly population, Butser Hill, had heavier seeds than the rest of the populations, with Coughton Hall, the next most southerly site, having some seeds that were as heavy as Butser Hill but also some which were as light as Yew Barrow, the Cumbrian site. Warter, one of the northeastern sites, shows the next heaviest seed weights with Overton Hall, the Derbyshire site, having the lightest seeds of all, and with Guisborough, the other northeastern site, having seeds which were as heavy as Warter and as light as Overton Hall. These results tend to suggest that there is a clinal pattern from the south to north of England, but that within the north of England there seems to be a random pattern, thus confirming the working hypothesis for this variable.

Perhaps the most surprising outcome of this study relates to germination percentage, as the most southerly site, Butser Hill, had the lowest value for this of all. Unlike the seed weight result, there does not seem to be any clinal pattern for this variable, as Coughton Hall, the next most southerly site, had one of the highest percentage germinations, with the highest being in the northwest, i.e. Yew Barrow. And if the populations are put in order with respect to this variable they are arranged as follows; Yb, Wa, Co, Ov, Gu and Bu. It can therefore be concluded that the pattern for this particular variable is random.

The same conclusion may be drawn from the results for seedling vigour, as although the order of the populations is different from that above, the pattern is still random.

Finally, although only 180 seeds were weighed in this experiment from six populations, it is interesting to extrapolate this to 1000 seed weight to compare it with the 1000 seed weight in the two other documented areas for this variable for the yew, mentioned in chapter two. Szczesny (1952) found that 1000 seed weight collected in Poland was 43 to 59 gm, while Detz and Kemperman (1968) found that the same amount of seeds from Holland weighed 77 gm. The extrapolation for the English yew shows that 1000 seed weight is 56.5 gm. This result suggests that Holland has heavier seeds than both Poland and England.

CHAPTER 7.

Cold hardiness: General considerations.

The next part of this dissertation deals with the variability of cold hardiness in the leaf of the yew. However, before the details of the experiment are presented some information about this phenomenon and its application to the study of variability is described.

Introduction.

Men have wondered for centuries how trees and shrubs of the temperate regions can survive the winter cold, subsequently to produce leaves and blooms each spring (Weiser, 1970). An early suggestion was that trees, like animals, possessed a vital heat that prevented them from freezing (Levitt, 1956). Tests have shown, however, that water does freeze in hardy plants during the winter, and that such plants can survive freezing in liquid nitrogen at -196°C (Sakai, 1960). This ability to withstand low temperatures in the winter has been variously named; it is called cold resistance by Weiser (1970), frost hardiness by Kozlowski (1971), and cold hardiness by Flint (1972). Kozlowski (1971) noted that trees show a "remarkable periodicity throughout the year" in this phenomenon, with the cold hardiness increasing during the autumn as the temperature falls, reaching a maximum in winter, and then decreasing in the spring to a summer minimum. Weiser (1970) commented that a plant which is killed at temperatures just slightly below freezing in the summer may survive -196°C in the winter.

Due to frost hardening being featured by seasonal change, even the most hardy of plants may be severely injured by light summer frosts (Pomerleau & Ray, 1957). Very tender species (e.g. those from tropical climates) usually never develop any frost resistance, no matter what the stage of growth or time of year (Levitt, 1972). It was found by Sakai (1970) that, under artificial conditions, tropical species of willow (*Salix*) are exceptions to this rule. He noted that when such species are hardened in the same manner as the northern species of willow, they develop as high a degree of tolerance to cold, surviving -50°C or even exposure to liquid nitrogen. Levitt (1956) noted that when hardiness is at its maximum, it varies from species to species and from variety to variety. He went on to say that it does not follow that a species or variety with the maximum tolerance at its full development necessarily is also the most tolerant of a series of species or varieties at all times of the year. The rates of hardening may vary independently of the maximum attained. An example of this can be seen in the case of varieties of apple (Malus)in which it was found that a hardy variety showed far greater resistance in the autumn than a less hardy variety, but the differences between the two in midwinter were slight (Siminovitch & Scarth, 1938).

A further complication is the difference in hardiness exhibited by adjacent tissues or parts of a plant (Weiser, 1970). In stems, for example, the living cells in the wood (xylem, parenchyma and pith) are often several degrees less resistant in midwinter than are neighbouring cells in the bark tissues (cambium, phloem, cortex and epidermis) (Potter, 1939). Scheumann (1962) found that the cambium and bark tissue of larch (Larix) were less resistant than needles during the spring. Day & Barrett (1963) noted that the buds and lower part of the previous year's growth were injured on Douglas-fir (Pseudotsuga menziessii), Sitka spruce (Picea sitchensis), and Corsican pine (Pinus nigra var. maritima) in the spring, whereas only needle injury occurred outdoors in the winter.

Some plants are "resistant stable", a term which means that their hardiness fails to change much with external conditions (Larcher, 1954). These may, therefore, be the most freezing tolerant of their community in summer and the least tolerant in winter. The most extreme examples of resistant stable plants are found among the lower orders. Rieth (1966) has shown that Porphyridium cruentum shows normal optimum growth above 27°C, and that no damage results from rhythmic alternation of periods of frost at -22°C in the dark with periods of 27°C in the light. Whole taxonomic groups may be resistance stable. Thus, the freezing tolerance of artic mosses and liverworts was not found to differ from that of tropical mosses (Biebl, 1957). Many algae, however, are resistance labile, i.e. unstable (Scholm, 1968). But in the case of higher plants of temperate climates, the autumn rise in freezing tolerance is a universal phenomenon (Levitt, 1972).

Plant range and cold hardiness.

The ability of plants to survive subfreezing temperatures is of interest to the study of distribution, succession, and migration, in that climate is generally considered to be the most important environmental factor affecting these phenomena (Alden & Hermann, 1971). However, seasonal subfreezing temperature, as a single environmental factor, may not limit natural altitudinal and polar migration of plants in cold climates. Daubenmire (1959) for example, has stated that inadequate heat during the growing season appears more limiting to plant distribution than cold, and Dunbar (1968) has noted that large seasonal oscillations of other environmental factors, such as low productivity, and the young age of ecosystems in polar climates are more limiting to the adaptation of plants than subfreezing temperatures. However, seasonal subfreezing temperatures can force many plants to develop a greater tolerance to cold than the minimum temperature of their ecological range, as with the case of the tropical species of willow mentioned above. From this evidence, Sakai (1970) concluded that willows native to warm climates have an inherent mechanism for cold hardiness that is never fully developed, because the plants are not exposed to hardening temperatures in their natural habitats. It has been found that other species are capable of developing cold tolerance greater than the minimum temperature of their ecological range. For example, Posey (1967) found that the sub-tropical loblolly pine (Pinus taeda) is fully established in an artificial situation in Oklahoma, USA, 230 miles northwest of its nearest natural habitat; in so doing, it has survived a minimum air temperature of -28°C.

Further studies show that plants can be conditioned to develop greater cold resistance in controlled environments than they display in their native habitats appear to indicate that climates which have seasonal subfreezing weather do not necessarily limit the distribution of particular plant species. Thus, Smithberg & Weiser (1968) found that there was no difference in the maximum cold tolerance of red osier dogwood (Cornus stolonifera) from twenty one locations between latitudes 40° and 65° in North America, "although each genotype ceased growth and developed resistance to cold at a different time". Salazar (1965) has noted that cold resistance in Citrus plants may be increased beyond their accepted level of tolerance by preconditioning treatments which depress the growth rate. Although this and other evidence suggests that injury from cold does not limit the natural migration of plants in regions of annual subfreezing weather, Campana (1964) has commented that low temperature, nevertheless, is the most significant natural environmental factor causing direct plant injury in cold climates. Cold injury also may be the most limiting factor to agricultural production (Johnston, 1964; Dexter, 1965) and may cause more damage to crops in some areas than parasitic diseases (Brown & Fitzsimmons, 1964), as well as reducing growth and quality of forest products (Tyron & True, 1966; Hurd, 1963; Strain, 1966).

Parker (1965) demonstrated that commercial forest trees native to the southeastern USA were unable to adapt to low temperatures in New England. He found that the foliage of longleaf pine (Pinus palustris) seedlings grown outside in southern Connecticut from summer into winter increased in hardiness from -10°C to only -15°C, when cooled and rewarmed at a rate of 4°C per hour. He also found that seedlings grown in the greenhouse developed the same degree of hardiness as those outside, indicating that the hardening mechanism failed to respond to low temperatures of the natural environment of the area. The foliage of loblolly pine (Pinus taeda) seedlings, on the other hand, hardened little, from -12°C to 14°C, and only in the outside environment. Growers of

Christmas trees (Gerhold, 1965) and landscape designers(Barker, 1963; Mower, 1964) have found the same general weakness in the hardiness mechanism of other southern plants moved to northern latitudes, and in coastal plants moved inland. From this and other evidence, Weiser (1968) concluded that although many plants have an inherent ability to develop high resistance to cold, they lack the correct biological timing for this in new climates. Alden & Hermann (1971) commented that plants from warm climates introduced to a cold environment may be susceptible to cold injury because they fail to develop sufficient protection from early cold weather, or deharden too rapidly, which makes them vulnerable to freezing temperatures in late winter, or are subject to a combination of these causes.

The same authors also noted that although cold hardening ability, synchronised to environmental low temperature minima, is essential to plant survival in climates with seasonal subfreezing temperatures, differences in the degree of cold tolerance between species may determine plant distribution in areas where frosts often occur sporadically, such as topographic depressions and forest openings, while the surrounding terrain is above freezing. Berntsen (1967) found that seedlings of lodgepole pine (Pinus contorta) were more tolerant than seedlings of ponderosa pine (Pinus ponderosa) during the period of emergence in spring. He commented that this difference may explain the abrupt transition zone between pure lodgepole pine in topographic depressions and pure ponderosa pine on adjacent higher ground in eastern Oregon. Minimum night temperatures during the spring near the soil surface were about -9°C on the lodgepole pine flats and about -6°C on the ponderosa pine slopes. He also showed that there was an almost total mortality of ponderosa pine seedlings at -9°C, but only slight mortality at -6°C. Mortality of the lodgepole pine seedlings, however, began at -9°C. Mracek (1966), when working with Norway spruce (Picea abies), concluded that direct reforestation in frost hollows at medium elevation in the mountains of Czechoslovakia is impossible without nurse crops such as birch (Betula), for these reasons.

Hard (1963) noted that conelets of red pine (Pinus resinosa) in the lower half of crowns and in trees on low ground may also be subjected to lower temperatures and injured more frequently from spring frosts, than conelets in the upper half of crowns in trees on high ground.

Growth and cold hardiness.

During the period of rapid growth in the spring, plants are exceptionally susceptible to frost injury (Alden & Hermann, 1971). Thus Van Huystee et al., (1967) have noted that maximum resistance to cold can be induced in red osier dogwood (Cornus stolonifera) in seven weeks at any stage during its annual cycle of development, except during one or two months after growth resumes in the spring. Tumanov et al., (1964) have studied the relationships between dormancy and cold hardiness in white birch, (Betula populifolia) and Acacia seedlings and found that plants growing vigorously under continuous light could develop some cold hardiness when exposed to chilling temperatures. However, they found that this increase in cold hardiness was not substantial. Salazar (1965, 1966) discovered a similar inverse relationship between growth rate and cold hardiness in Citrus. He found that the growth rates of varieties capable of hardening were more depressed when the plants were subjected to preconditioning treatments. Sakai (1962, 1966) has reported that cold hardiness of growing twigs of woody plants that are extremely sensitive to frost injury cannot be improved by chilling to 0°C, however, frost resistance developed even without exposure to low temperatures after growth had stopped. Huber & Kohn (1962) failed to harden four- to six-year-old Norway spruce (Picea abies) and silver fir (Abies alba) by chilling in June when growth occurred. However, both species developed increased frost resistance at temperatures between 0°C and -5°C in only four days during September.

That development of cold hardiness in woody plants is inversely proportional to growth rate has been well established (Levitt, 1966). Glerum et al., (1966) have tested the frost hardiness of six nursery-grown conifer species during a five-week period in August and September, and found a decrease in frost injury from the first week through to the fifth week. The decrease indicates that resistance of the seedlings to cold injury develops as growth processes cease. They found that rapidly-growing seedlings were more severely injured than those which grew slowly. The cold resistance of red osier dogwood increased from -7°C to -18°C with the beginning of rest in mid-September. Absence of the rest period under long-day conditions prevented slowly lowered temperatures from inducing cold hardiness (Van Huystee et al., 1967).

Schonbach et al., (1966) found provenance differences in the resistance of Japanese larch (Larix leptolepis) to early and late frosts and low winter temperatures. They noted that resistance to early frost was related to the termination date of the growing season, and the critical freezing temperature correlated with the percentage of plants that formed terminal buds by mid-September. Buds of the todo fir (Abies sachalinensis) and white spruce (Picea glauca) can tolerate -3°C and -5°C respectively in September. Their twigs were less hardy then until mid-November, when twigs became more hardy than the buds (Takatoi et al., 1965). In Douglas-fir (Pseudotsuga menziesii) development and the loss of resistance to cold was related to cessation and commencement of cambial activity, but not to the formation of terminal buds and budbreak (van den Driessche, 1969). Mair (1968) observed that in ash (Fraxinus ornus) cold resistance was lost most quickly in those buds that were the earliest to break. Oksbjerg (1966) reported that Douglas-fir (Pseudotsuga menziesii) and Sitka spruce (Picea sitchensis) flushed earlier than, and completed their shoot growth later than Norway spruce (Picea abies) in Denmark, and were more susceptible to frost damage. Provenance studies on Scots pine (Pinus sylvestris) in Norway by Dietrichson (1964) have shown that frost damage reduced growth in the height of trees from sources where growth begins early, and ends late. Tumanov et al., (1964) suggested that many southern species can overwinter in the north if they develop dormancy early enough to allow sufficient time for the completion of the initial phase of hardening. They noted that low temperatures in the autumn may impede the dormancy inducing photoperiodic response of plants adapted to warm habitats, because southern plants do not become dormant at day lengths that induce dormancy in northern plants.

Seasonal changes in cold hardiness.

In 1913, Winkler studied seasonal cold resistance in woody plants in Germany, and found that the resistance of tree buds sharply increased in November and decreased in March. The lower the temperature that the trees were exposed to, the more rapid their "accommodation" to cold. Hardiness in Elberta peach bark (Prunus persica) may vary from -16°C in winter to only -5°C in summer according to Chandler (1913). Hildreth (1926) showed that the cold resistance in apple (Malus) twigs increased steadily from July to January. In late March, the curve changed sharply as tissues lost hardiness into early May (Fig 7.1). Seasonal changes of hardiness have been demonstrated for cortex, pith and bracts of tung twigs (Aleurites fordii) by Fernholz & Potter (1941). Meader & Blake (1943) found a steady increase in cold resistance from November to February in the percentage of live peach buds that survived treatment. Then in March there was a decrease. Pisek (1958) found that Ontario apple bark reached a resistance of about -33°C in January in Austria, while cherry and apricot (Prunus) were resistant to -25°C and -21°C respectively, after which they all began to loose their hardiness.

Ulmer (1937) made the first thorough study of the hardiness of several wild woody plant species. He found that near the tree line in the Austrian Alps, species had resistances which were somewhat different from one another at almost any time of the year. For example, Pinus cembra in December could not be killed by subjecting it to -45°C, while

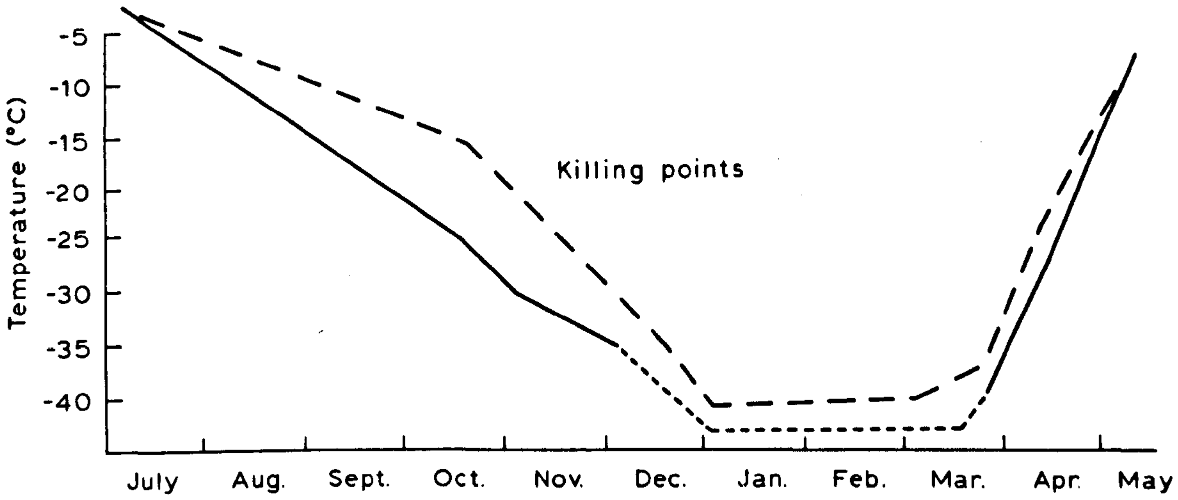


Fig 7.1. Seasonal variations in frost killing points of Duchess (solid line) and Jonathan (broken line) apple twigs.

(after Hildreth, 1926).

Rhododendron was resistant to about -28°C and Loiseleuria to about -35°C. His curves showed that the spring decline in hardiness is steeper than the autumn increase. Parker (1963) further suggested that this situation appears to be common in woody plants of cold climates. Ulmer's findings were subsequently verified by Pisek (1950) and Pisek & Schiessl (1947), when they found that Pinus cembra could withstand -47°C and that Rhododendron ferrugineum never tolerated more than about -15°C.

Parker (1963) has noted that very little work had been undertaken on seasonal changes in cold resistance in North America up to 1955. An exception to this was the study by Clements (1938) on ponderosa pine (Pinus ponderosa) and the large-coned Douglas-fir (Pseudotsuga macrocarpa), in which he found that the ponderosa pine was less hardy than the fir, although seasonal changes occurred in both. A study was therefore undertaken (Parker, 1955) which showed that northern Rocky Mountain conifers underwent the same autumnal changes in hardiness exhibited by the Austrian trees. Parker found that none of the native Rocky Mountain conifers could be injured by treatments in winter down to -60°C. Later studies of the eastern white pine (Pinus strobus) showed that the leaves were hardy down to -196°C in the late winter (Parker, 1959); however, when looking at more southerly species, like the long leaf pine (Pinus palustris), he showed that only slight hardening occurred in autumn and that it was practically incapable of responding to low temperatures by further hardening beyond its "endogenous capability" (Parker, 1961). The hardiness changes of the eastern white pine, however, are fairly typical of other native northern conifers in the USA (Parker, 1961). Glerum (1973) has tested the seasonal trends in frost hardiness in potted 3- to 4-year-old seedlings of white, red, and jack pine (Pinus strobus, P. resinosa, and P. banksiana), white, black, and Norway spruce (Picea glauca, P. mariana, and P. abies), and tamarack (Larix laricina). All the seedlings were obtained from the same area in Ontario, Canada. He found that differences in frost hardiness between the species at different times of the year were small, finding that the minimum frost hardiness in the summer was between -3°C and -5°C, and the maximum frost resistance in the winter was below -40°C for all the species except Norway spruce, which had its maximum around -40°C.

Deciduous broadleaved trees go through much the same seasonal changes in cold hardiness as conifers, in the colder regions of the world (Tumanov & Krasavtsev, 1955; Till, 1956; Parker, 1962).

Parker (1963) noted that one of the astonishing facets of such seasonal studies is that there appears to be no lower limit down to absolute zero for the hardiness tolerance of some tissues of certain woody plants. Sakai (1958a,b) has determined that mulberry bark can withstand -183°C, Parker (1962) that hardwood twigs can withstand -196°C, and Krasavtsev & Khvalin (1959) and Tumanov (1960) showed woody buds withstanding -253°C.

(A) Environmental factors affecting cold hardiness.

(B) Inorganic nutrients.

The availability of nutrients essential for plant growth is also important for the development of maximum resistance to cold (Kawana *et al.*, 1964), although the reasons for improved resistance to frost by increased availability of nutrients is not known (Smith, 1964).

In this respect Atterson (1967) noted that frost damage to lodgepole pine and Sitka spruce in soils deficient in magnesium could be correlated with the degree of yellowing caused by the lack of magnesium, and was alleviated by the application of magnesium sulphate and other magnesium fertilisers. Cooling (1967) found that the cold resistance of *Eucalyptus grandis* was improved by the addition of borate fertilisers. Peynado & Young (1963) noted that solutions of calcium chloride, sodium sulphate, and sodium chloride which caused deficiencies of boron, magnesium, and potassium as well as reduced growth, bronzing, and chlorosis of grapefruit trees, also increased the severity of frost injury. White & Finn (1964) found less frost injury in foliage of tulip poplars (*Liriodendron tulipifera*) previously fertilised with potassium, although unfertilised trees abscissed at a much earlier date than did leaves of fertilised trees. Viart (1965) commented that although potassium and phosphorus fertilisers reduced the incidence of frost cracks in Populus spp., ammonium phosphate increased it. Benzian (1966) said that a late top dressing of nitrogen applied to seed beds, so that the nitrogen accumulates in the seedlings without increasing further growth, decreased the frost damage in Sitka spruce and Western hemlock (Tsuga heterophylla), and that potassium applied in the same manner almost eliminated frost damage to Sitka spruce. Li et al., (1966) found that the total inorganic phosphorus content of red osier dogwood decreased as frost hardiness increased, while total organic phosphorus increased with increasing frost hardiness. They suggested that a high level of inorganic phosphorus may predispose plant cells to freezing injury and that certain organic phosphorus compounds may enhance cold hardiness "by means other than serving as an energy source".

(B) Soil moisture.

The ultimate tolerance of plants to cold, and their ability to overwinter successfully in climates with seasonal subfreezing temperatures, may also depend on the available moisture in the soil during the growing season. For example, Holmgrem (1963) noted that abnormally low temperatures during the winter period, preceded by a drought in the autumn, are believed responsible for the severe winter damage and disappearance of Ceanothus velutinus from the mountains of northern Utah. Borzakivs'ka & Majka (1965) have reported considerable winter damage to the shoots and branches of Juglans regia and Acer velutinium after a severe drought in the summer of 1963 in Russia. Eiche (1966) pointed out that a summer drought may combine with other environmental factors to weaken the cold tolerance development in young Scots pine, leaving the cambium, phloem, and cortex of the stem susceptible to injury from low temperatures. It was observed by Schnetter (1965) that frost resistance in Bellis perennis was about 3°C higher in dry and hot weather than in rainy weather. But the above results have not been entirely confirmed by other workers on other plants. For example, Calder et al., (1965) found that alfalfa hardened when soil moisture was at field capacity and had a higher rate of recovery after freezing than plants hardened in fully saturated soil. Kilpatrick et al., (1966) reported that clover plants were more resistant to cold when frozen in dry soil than in moist soil, after hardening for two weeks at 2°C. Temperatures of the dry soil decreased gradually during the freezing, whereas temperatures of the wet soil remained at 0°C for six hours, and then dropped rapidly. The rates of thawing were similar for both these conditions of soil moisture. It was concluded that soil moisture may determine survival at the time of freezing. Valmari & Valmari (1966) found that clover survived temperatures of -10°C if the soil remained unfrozen, but was killed at -5°C as the soil froze. Horn (1966) noted that crops on dry and coarse textured soils are more likely to be injured by frosts than crops on moist soils, because water increases the conductivity of heat, stores heat during the day, and releases 80 calories of heat per gramme as it freezes.

(B) Temperature and light.

A decrease in freezing tolerance occurs during winter when plants are exposed to warm weather for two weeks (Goppert, 1830) or even a few hours in the cases of mosses (Irmscher, 1912) and evergreens (Pisek, 1950), and an increase in freezing tolerance occurs when they are exposed to low temperatures (Haberlandt, 1875; Schaffnit, 1910; Irmscher, 1912; Chandler, 1913; Gassner & Grimme 1913).

Harvey (1922) has stated that in general the threshold temperature above which hardening does not occur is usually 5°C - 10°C. Levitt (1972) qualifies this by saying that the precise temperatures for hardening or dehardening are difficult to determine, and vary with the species and probably the variety. Le Saint (1966) noted, when working with cabbage (Brassica), that some hardening may occur at 12°C, while none occurred at 18°C. Sakai (1967) showed that any temperature above

13°C led to a loss in freezing tolerance in some young trees, although poplars (Populus) held at 15°C increased in tolerance from a killing temperature of -2°C to -30°C over a two-month period, (Sakai & Yoshida, 1968).

Levitt (1972) noted that a temperature of 0°C to 5°C will induce greater hardening than one of 5°C to 10°C, and that once the maximum hardening possible at this temperature has been attained, a second stage increase may still occur at a temperature of just below 0°C. This second stage temperature is -4°C in the case of barley (Hordeum) (Dantuma & Andrews, 1960), and -2.5°C to-5°C in the case of mulberry (Sakai, 1955). Tumanov (1969) has emphasised that this second-stage hardening may occur at temperatures well below freezing. He lists three periods in the preparation of plants for hibernation: (a) the onset of dormancy; (b) the first stage of hardening at about 0°C; and (c) the second stage of hardening during a gradual lowering of the temperature below 0°C. An example of this can be seen in the work of Krasavtsev (1969) on the freezing tolerance of cherry and apple twigs. He showed that there was a marked increase in tolerance when these were subjected to prolonged (5-20 day) exposure to -5°C, and subsequently -10°C. Further hardening occurred during one day at -20°C, and -30°C. He also found that birch (Betula) and poplar (Populus) twigs did not require this preliminary gradual greezing treatment, surviving temperatures of -60°C if cooled gradually, and -30°C(in the case of birch) and -50°C (in the case of poplar) if cooled rapidly.

Some results have indicated that alternating warm and cold temperatures are at least as effective in producing hardening as constant low temperatures (Harvey, 1918, 1930; Tumanov, 1931; Tysdal, 1933; Angelo *et al.*, 1939), although others have failed to obtain hardy plants by this method (Peltier & Kiesselbach, 1934, Suneson & Peltier, 1934; Day & Peace, 1937).

The prevailing temperature under natural conditions also markedly affects the freezing tolerance within individuals. Till (1956) has shown that above-ground parts of a plant may have 11.5°C greater freezing tolerance than the below-ground parts. Even among the above-ground parts, the most exposed and therefore colder parts of the plant are more freezing-tolerant than parts covered by snow (Brierley & Landon, 1954). Among roots, the deeper ones are killed by freezing temperatures that fail to injure the shallower ones (Smirnova, 1959). Similarly, a colder winter has frequently been observed to result in greater freezing tolerance and midwinter thaws to result in a partial loss of freezing tolerance (Kohn, 1959). Sakai (1966b)has found that the cortical cells on the south, and therefore warmer side, of trees are less tolerant of freezing than those on the north side. In general, freezing tolerance has been found to fluctuate throughout the winter, increasing as the temperature drops, and decreasing as it rises.

When alternating low and high temperatures are present, the hardening of plants has been shown to occur only if light is supplied during the high temperature period (Dexter, 1933; Tysdal, 1933). Even continuous low temperatures in the absence of light are incapable of inducing hardiness in winter annuals (Tumanov, 1931; Dexter 1933; Pfeiffer, 1933; Andersson, 1944). Many workers have found a reduction in hardiness results from darkening the plants (Lidforss, 1907; Weimer, 1929; Angelo et al., 1939). No hardening occurred in cabbage seedlings in the dark at 4°C or in the light at 18°C (Le Saint, 1966), but normal hardening occurred when they were exposed to both low temperatures and light. A threshold illumination of about 1000fc was required for the hardening of young conifers (Mcguire & Flint, 1962; Scheumann & Bortitz, 1965). Douglas-fir (Pseudotsuga menziesii) seedlings failed to harden in the dark at 2.5°C even after several weeks (van den Driessche, 1969b), but they did harden at low light intensities (40 to 100fc). Light enhances the rate of hardening of Hedera helix, but it is not essential for the hardening process (Steponkus & Lanphear, 1968). However, the second stage of hardening on exposure to temperatures below 0°C, may occur in the dark (Tumanov & Trunova, 1963; Kohn & Levitt, 1965). Even at this stage, however, light is necessary in the case of conifers (Scheumann & Bortitz, 1965).

The need for light is apparently due to a need for photosynthesis, since if the leaves are chloritic, the plants are unable to harden even when exposed to light, although when allowed to become green by spraying with ferrous sulphate, they harden normally (Rosa, 1921). Similarly, if exposed to CO_2 free air, hardening does not occur even in light (Dexter, 1933).

Interestingly, Dexter (1933) also pointed out that plants with abundant organic reserves are exceptions to this rule, as they will harden markedly at 0°C, even in the dark. However, this was not found to be true of cabbage seedlings kept in the dark at hardening temperatures (Le Saint, 1966). Nevertheless, once hardened in the light, they did maintain their hardiness in the dark for at least two weeks. Furthermore, if the part of the shoot that is capable of hardening is kept in the dark, and the remaining leaves are illuminated, the darkened part will harden, due to translocation from the illuminated part. Since only the younger leaves are capable of hardening, this method works if the upper leaves are darkened and the remaining leaves are illuminated; if this is reversed, the darkened (older) leaves do not harden. Steponkus & Lanphear (1967a), in agreement with Le Saint, found that light results in the production of a promoter of hardiness in Hedera helix, which could be translocated to a darkened receptor.

Temperature and light thus seem to be the two main environmental factors controlling the development of freezing tolerance in plants. Artificial hardening by control of these two factors is capable of producing a degree of hardiness equal to that under natural conditions, as in the cases of cabbage (Kohn & Levitt, 1965) and Hedera helix (Steponkus & Lanphear, 1967b). Further to this, Aronsson (1975) has commented that although the influence of photo-and thermoperiod on the hardening of plants has had some attention by workers, their influence on dehardening is far less well studied. Zehnder & Lanphear (1966) have reported that, for Taxus cuspidata, hardiness was lost at high temperatures approximately twice as rapidly as it could be developed even under the most favourable conditions. Van den Driessche (1969) found that for Douglas-fir, dehardening depended much more on temperature than on photoperiod. An investigation carried out by Aronsson (1975) dealt with dehardening in Scots pine (Pinus sylvestris) and Norway spruce (Picea abies) seedlings. Before the dehardening experiments started, these seedlings were exposed to a hardening and chilling period at short photoperiod and low temperatures, (the length of this period was 8 or 11 weeks). In the eleven week treatment time it was found that it was sufficient to increase the temperature and maintain the same photoperiod (8 hours) to obtain rapid dehardening, while in the shorter treatment (eight weeks) dehardening was "far slower". If the photoperiod was increased to 18 hours, dehardening was very fast for both chilling periods. It was found that the higher the temperature, the more rapid the dehardening, and that there was no difference between the two species in this respect. Parker (1963) has reported that for different species dehardening is a much faster process than hardening; this was confirmed for pine and spruce in this experiment, where dehardening was about twice as fast as hardening "under the prevailing conditions". Van den Driessche (1969) found that for Douglas-fir, loss of hardiness is not influenced by photoperiod, and is dependent on temperature. Aronsson (1975) remarked that although dehardening for the plants with the longer chilling period did not go as fast at eight hours' light as at eighteen hours' light, the results indicate that dehardening for pine at least, as for Douglas-fir, depended more on temperature conditions than on the light period.

Cold hardiness, and its relationship to plant growth and plant development.

Low temperatures and adequate light intensity are not always able to induce the hardening of potentially hardy plants. For example, the newly-formed buds of evergreens fail to harden at low temperatures and with normal light, even though they might survive -30°C during the subsequent winter (Winkler, 1913). They also lose their ability to harden when they begin to develop into shoots during the spring (West & Edlefsen 1917, 1921; Roberts, 1922; Knowlton & Dorsey, 1927; Field, 1939; Geslin, 1939). Similarly, the changes in tolerance may not follow temperature changes at certain times of the year (Ulmer, 1937), and this was demonstrated clearly by Pisek (1953) when he exposed plants to low and high temperatures for one day at different times of the year.

Even if kept constant at the hardening temperature, plants do not retain their maximum hardiness indefinitely. Sprouting winter wheat, for instance, reaches its maximum hardening at 1.5°C in the dark after about 5 weeks, and then hardiness decreases rapidly between the seventh and the eleventh week (Andrews et al., 1960). Although this drop in hardiness may sometimes be due to loss of reserves, as suggested by Jung & Smith (1960), it has been shown that it can occur without an appreciable loss of these. For example, Sergeeva et al., (1959) noted that early spring growth in less tolerant species or varieties may be indicated by an earlier appearance of starch. The metabolic changes that occur in preparation for spring growth apparently lead to a loss of freezing tolerance, even though the plants are exposed to optimum hardening temperature and light. In contrast, in some plants, the mere cessation of growth in the autumn may confer some hardiness without the aid of hardening temperatures (Larcher, 1954; Sakai, 1955).

In many cases the plant actually enters into a non-growing "rest period" and freezing tolerance has frequently been related to the depth or length of this period (Levitt, 1956). Thus the reduction in freezing tolerance of plants brought indoors during the winter occurs only if they are no longer in their rest period (Lidforss, 1907; Meyer, 1932; Kessler, 1935). Irving & Lanphear (1967b) have confirmed this for Acer negundo and Viburnum plicatum, in finding that when the plants were in a naturally hardened state, their dormancy condition retarded the loss of tolerance on exposure to 70°F.

The correlation between rest period and freezing tolerance does not occur in all plants (Pojarkova, 1924). Some may be dormant, although possessing no freezing tolerance (Clements, 1938), and others may survive the winter period without a rest period (Walter, 1949). Even in some hardy woody plants, such as Acer negundo and Viburnum plicatum development of tolerance occurs independently of bud dormancy (Irving & Lanphear, 1967b). And in the case of very hardy plants, such as dogwood, the high degree of freezing tolerance may be maintained in winter long after its rest period is over (van Huystee et al., 1967). In many cases, the importance of the rest period is believed to be due to prevention of growth and the accompanying loss of freezing tolerance during winter warm spells (Brierley & Landon, 1946). These and other observations therefore suggest that it is the growth per se, rather than the stage of development, which is the main factor that prevents hardening. It is generally found that if plants are growing rapidly they cannot be frost-hardened (Rivera & Cornelli, 1931; Dexter, 1932), whereas treatments that retard growth increase hardening (Chandler, 1913; Harvey, 1918; Rosa, 1921; Collison & Harlan, 1934; Kessler & Ruhland, 1938), although exceptions may occur, as found by Kuksa (1939) in the case of wheat.

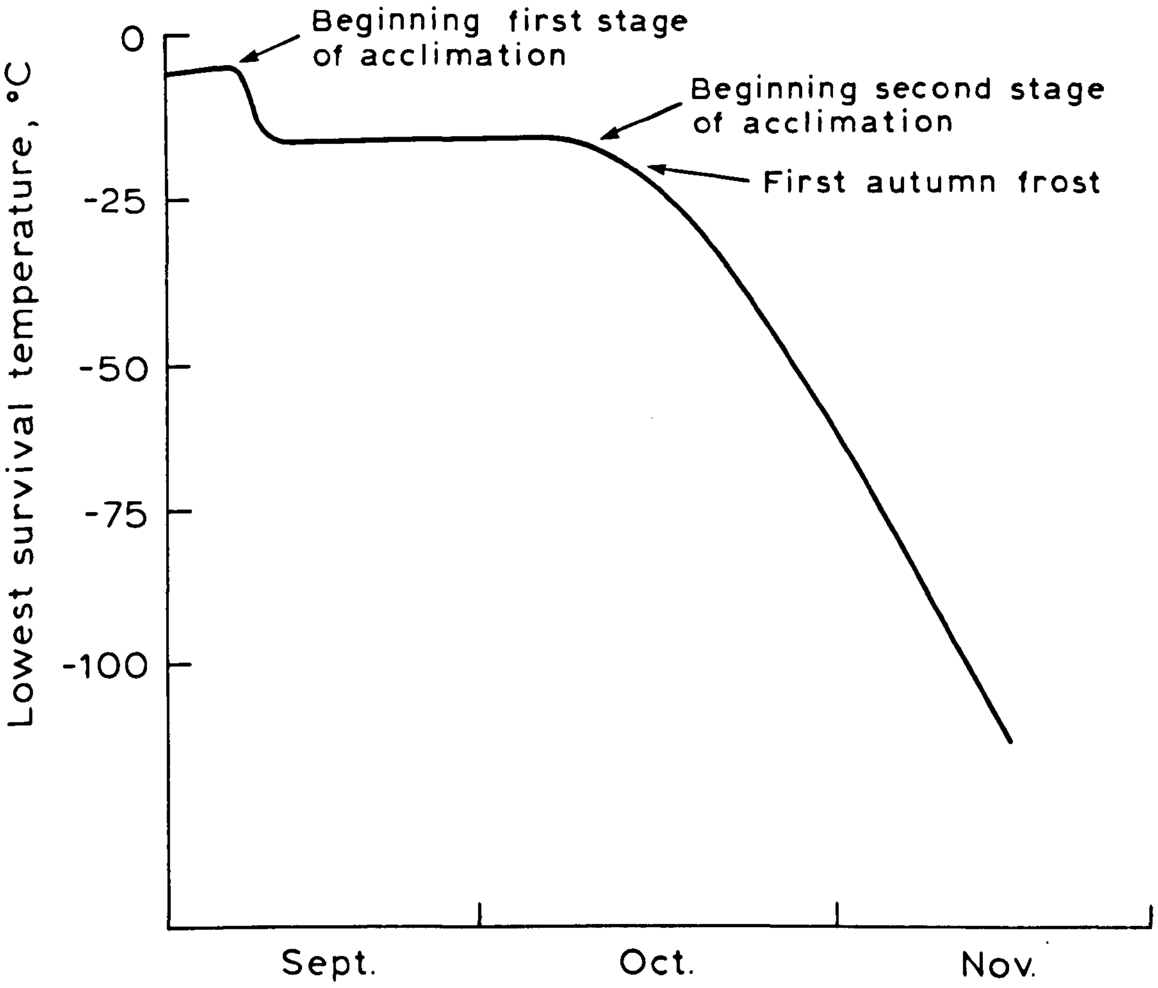
The relationship of freezing tolerance to growth and development is clearly seen by controlling the photoperiod. Hardening is improved by short days, both in the case of woody plants (Moshkov, 1935; Bogdanov, 1935) and herbaceous plants (Dexter, 1933; Smith, 1942; Ahring & Irving, 1969). Thus, in some cases the normal autumn hardening can be prevented if the plants have previously been induced to continue their growth by maintaining them in a long photoperiod (Levitt, 1972). Kramer (1937) has pointed out that this can be observed when introduced trees and shrubs are growing next to artificial lighting, as in city streets, where shoots growing near the lights may be winter-killed whereas the other parts of the plant may be uninjured due to their distance from the light. Biebl (1957) has concluded that the autumn increase in freezing tolerance is dependent primarily on the shortening of the day length, and only secondarily on the decrease in temperature. When different species or varieties are compared, a direct correlation frequently exists between length of the critical photoperiod and freezing tolerance (Rimpau, 1958), and an inverse correlation between the growth effect of a long photoperiod and hardiness (Schmalz, 1957). But exceptions do exist, as when hardening will occur in spite of long photoperiods (Kneen & Blish, 1941). Thus, cabbage seedlings harden equally as well when grown before and during hardening at any photoperiod from 8 to 24 hours, provided that optimum temperature and light regimes are used for hardening (Kohn & Levitt, 1965). In the case of Douglas-fir seedlings, day length, temperature and light are important for the development of freezing tolerance, but only temperature affected the loss of tolerance (van den Driessche, 1969).

The stages of hardening acclimation.

It has already been briefly noted that hardening occurs in two to three stages in woody plants native to temperate zones, (Tumanov & Krasavtsev, 1959; Krasavtsev, 1967; Weiser, 1970; and Glerum, 1973). According to Levitt (1972), Tumanov lists three periods or stages in the preparation of plants for winter, (a) the onset of dormancy, (b) the first stage of acclimation (hardening) at about 0°C, and (c) the second stage of acclimation, during a gradual lowering of temperature below 0°C. This is in agreement with Weiser (1970), who suggested that the first stage is induced by short days, noting that decreasing photoperiods cause growth cessation in many northern deciduous species by triggering the onset of the rest period (dormancy). For example, Fig 7.2 shows a typical seasonal pattern of cold resistance in the living bark of red-osier dogwood (Cornus stolonifera) stems. In nature, acclimation in this hardy shrub and in a number of other woody species proceeds in two distinct stages, as shown. The beginning of the second stage of acclimation characteristically coincides with the first autumn frost (Weiser, 1970). Glerum (1973) found that there were two stages of acclimation when studying the hardiness of seven coniferous species, and that the transition between the two stages was approximately at -18°C. He also suggested that there are two stages in the dehardening process, but pointed out that since dehardening in the spring occurs so rapidly, it is difficult to identify separate dehardening stages.

Studies have been undertaken on the environmental and chemical controls of cold acclimation by (a) dividing plants with light or temperature barriers (called a split plant study), so that branches of a single plant may be simultaneously exposed to different environments (Irving & Lanphear, 1967a;and Timmis & Worrall, 1974), (b) by partially or completely defoliating plants at different times of acclimation (Irving & Lanphear,(1967a), and (c) by removing a band of bark around a stem (girdling) to interrupt the transport of substances in the phloem (Siminovitch & Briggs, 1953). The major results of these experiments have been summarised by Weiser (1970). The studies indicate that (a) growth cessation is a prerequisite to cold acclimation in woody plants; (b) plants severely depleted in photosynthetic reserves cannot acclimate; (c) leaves are the site of perception of the short-day stimulus which initiates the first stage of acclimation; (d) low temperatures inhibit the short-day induced phase of acclimation; (e) long-day induced leaves are a source of a translocatable factor(s) which inhibits cold acclimation; (f) short-day induced leaves are a source of translocatable factor(s) which promote acclimation; (g) a hardiness- promoting factor

Fig 7.2. Seasonal cold acclimation of red osier dogwood (Cornus stolonifera).



Description of Fig 7.2. As it can be seen the first stage of acclimation starts in September. The graph shows that the red-osier dogwood stems can withstand below freezing temperatures even when there is no hardening. Then there is a drop in September to a stage when the stem can be said to be hardened completing the first stage of acclimation. This plateau continues into October when there is another increase in hardening; this is called the second stage of cold acclimation and as noted by Weiser (1970) this coincides with the first autumn frost. From then on these stems continue to harden into November and by the middle of November they can withstand temperatures less than -100°C.

moves from the leaves to overwintering stems through the bark; (h) frost triggers the second stage of acclimation; (i) the frost-induced phase of acclimation does not involve translocatable factors; and (j) plants exposed to long days and frost will eventually become fully hardened, but plants exposed to short days and relatively high temperatures only reach the first stage of acclimation.

Weiser concluded that short days probably function as an early warning system in nature, and that the first stage of acclimation seems to involve two distinct events, namely growth cessation and the initiation of metabolic changes, thus facilitating the plant's response to low temperatures during the second stage of acclimation. It should be pointed out that, although the increase in hardiness during the first stage is relatively minor (see Fig 7.2) it may be very significant since just a few degrees of resistance can make the difference between life and death.

Physiological factors involved in cold hardiness.

There is a vast literature regarding different physiological factors involved in freezing tolerance, although the total number of factors involved is unknown. Levitt (1972) has noted that the most common factor chosen for study is the quantity of a specific substance, that is its accumulation, in relation to freezing tolerance. For example, the accumulation of total solutes (Thompson & Taylor, 1968; Pisek et al., 1935), sugars (Sakai & Yoshida, 1968; Steponkus & Lanphear, 1968; Sawano, 1965, water (Pellet & White, 1969; Kappen, 1969; Le Saint & Catesson, 1966), amino acids (Wilding et al., 1960a,b; Smith, 1968; Durzan, 1969), Proteins (Siminovitch et al., 1967; Li & Weiser 1967), nucleic acids and simpler nucleotides (Li & Weiser, 1967; Jung et al., 1967; Baker & Jung, 1970), and lipids (Kuiper, 1969; Yoshida, 1969a,b). Although an interesting part of the overall problem of the nature of freezing resistance, this has little relevance to the present discussion, and therefore it is only mentioned in passing.

(A) Intraspecific variation in cold hardiness.

In this section, details of intraspecific variation in cold hardiness are given as they relate to various tree species. Also, within the following account, information about the methods used in the testing of this phenomenon is given, as it is clear from the reading of the literature that there are many and varied ways to test hardiness in the organs of a plant, and that no standard method has yet been accepted amongst workers in this field.

(B) Visual observations of damage.

Studies of various 'strains' of *Pinus sylvestris* have been made in Europe, and these have clearly revealed geographical varieties which change colour in the autumn at different times. Thus, the eastern European races of Scots pine, lose their green colour easily and become yellow, while the western races (i.e. those in France and Belgium) retain their green colour (Kienitz, 1922). This latter fact seemed to Kienitz to be a "protective colouration", since the French races of pine, which remained largely unchanged in colour, tended to be uninjured by a late spring frost. Langlet (1936) has also noted intraspecific differences in the hardiness of Scots pine, saying that those from the north or from high altitudes seem to be the hardiest.

Hardiness in Scots pine has also been studied in the USA by Gerhold (1959). He concluded that in spite of the genetic variation which produced different yellowing effects, the intensity of illumination as well as the length of day influenced hardiness. He found that long-day treatments tended to prolong the normal green colour into December, while short-day treatments (i.e. shorter than normal for that season) tended to speed up discolouration. It was suggested by Gerhold that discolouration might be inversely related to the development of hardiness. He further suggested that discolouration is the result of chloroplast clumping although this has not been substantiated by other workers (Parker, 1963).

A study of colour change from green to purple in Jack pine (Pinus banksiana) was made by Stoeckeler & Rudolf (1956), in which they found good correlations between latitude and the extent of discolouration of the foliage, with the more northerly individuals showing the most purplish colour. They also found a good correlation between discolouration, and the average mean January temperature in the place of origin. On the other hand, Mirov et al., (1952), while seeking an answer to the question as to whether low altitude seed of Pinus ponderosa could be used at high altitudes in the Sierra Nevada, California, concluded that there was no relationship between seed origin and foliage injury, at least for this species.

Among deciduous tree species, Wright (1944a) found that white ash (Fraxinus americana) from a southern source was usually killed in the seedling stage when planted in a more northerly site. He also identified three ecotypes of red ash (Fraxinus pennsylvanica) in a common garden experiment in which he found that the northern ecotype was slow growing, winter hardy and lost its leaves in the autumn, the southern coastal plain ecotype was fast growing, sensitive to the cold and retained its leaves through two killing frosts, and a third ecotype from the New York area was intermediate between the two, Wright (1944b). Further, in silver maple (Acer saccharinum), Wright (1949) found three biotypes, one of which was very winter hardy, another moderately hardy, and the third not very hardy. Kriebel (1957) studied varieties of sugar maple (Acer saccharum) from various parts of the eastern United States. He found that, although the day length response was about the same in all varieties, there was a certain amount of variation among varieties for winter hardiness. Shoots of young trees from the south sub-species (floridanum) were very sensitive to autumn frost injury. Trees from a more northerly origin were subject to stem killing from late spring frosts, because of premature bud break. This same early bud break problem was found by Ozol (1953), who reported that hardy Juglans mandshurica and J.cinera were poorly adapted to southern Russia, since they tended to bud out too early in spring, and were then injured by frost.

More recently, Campbell & Sorenson (1973) have studied the cold hardiness of Douglas-fir and its relationship to the tree's phenology and provenance. The questions asked were: (a) is frost sensitivity related to time of bud set among individual seedlings within seed sources and between seed sources: (b) what proportion of differences in frost sensitivity among seed sources can be attributed to differences in bud set date: (c) what proportion of the differences in frost damage can be attributed to differences in frost sensitivity at the stage of bud sets: and (d) can differences in frost sensitivity among seedlings be related to location or climate of origin? Seedlings were examined from ten provenance seed sources, with damage being scored one month after a heavy frost on a scale of: 0, no damage; 1, yellowed needles; 2, dead needles; 3, terminal bud and stem damage. They noted that the frost-damaged seedlings appeared to be differentially frost sensitive on a continuous scale. There was a highly significant linear regression of height and diameter with the score which indicated that injured seedlings had grown less than uninjured ones. The loss in growth was directly related to the score. It was found that ninety per cent of the variation in frost damage among sources was related to the week of the mean bud set, "a very close relationship indeed". Also, when determining whether seedlings from the various seed sources suffered equivalent damage if frosted at an equivalent stage of bud development, it was noted that seedlings within source populations set buds over a period of several weeks, and therefore some seedlings from every source set buds within the same week. Thus, if in any bud set group, some sources sustained more damage than others, it was concluded that they were more frost sensitive. It was indeed found that the southern source material suffered more damage than the northern source material. It was noted that normal autumn frost acclimation of the sources appeared to have two components. The first can be closely tied to bud set. Although the rate of development toward frost resistance seemed to be similar for all sources, frost sensitivity at points in time measured from a phenological checkpoint need not be. The second component accounted for these discrepancies in sensitivity. This latter effect appeared to be a function of latitude of the seed source. This supposition was confirmed by examining, by means of regression, the average bud set dates and latitudes of sources on the proportion of seedlings damaged. It was found that frost damage was more related to latitude than to bud set; for example, correlation coefficients between latitude and bud set, and between latitude and frost damage were 0.19, 0.62 and -0.66, -0.80 respectively. They concluded their work by advancing "two of many possibilities" for this effect; (1) a relatively tighter photoperiodic control of hardiness in comparison to control of growth cessation; or (2) different adaptational strategies among sources for hardiness and growth cessation, both based on a photoperiodic timer, but using different critical daylengths.

Lester et al., (1977) have recently studied freezing injury in seedlings of balsam fir, (Abies balsamea) by comparing the effects of freezing on shoot elongation. Seeds were collected from three provenances in the USA, and grown in a common garden for one year, after spending two years in a glasshouse. In February, the seedlings were thawed out in a glasshouse in a uniform environment, after which half from each provenance were scored for shoot development, exposed to freezing temperatures and returned to the glasshouse. Ten days later the remaining seedlings were similarly scored and exposed. The workers scored shoot development on a scale of 1 to 9, where 1 represented a bud for which there was no external evidence of shoot growth. For score 3, buds had expanded to a point where green leaves were visible through the transparent bud scales; at 5, shoots had elongated to produce vase like structures; at 7, leaves still masked the stem of an elongated shoot; and at 9, the leaves were arranged perpendicularly to the stem. Intermediate stages were assigned intermediate scores.

Using this system, the seedlings were exposed to four test temperatures, -3.3°C, -4.5°C, -6°C and -8.5°C, at two different times during shoot elongation. It was found that exposure at -3.3°C resulted in no bud, shoot, or leaf injury, while exposure at -8.5°C resulted in injury to 53% of the buds and shoots tested. Differences in provenance, and the timing of exposure were significant at the lower temperatures. It was found that freezing injury was largely a function of the developmental stage of buds and shoots at each temperature of -4.5°C or lower, as between-provenance differences in frost injury were not significant when buds of a similar developmental stage were compared. They therefore concluded that, at least for balsam fir, phenological measurements may serve as an index of frost hazard during the period from shoot growth initiation to nearly complete shoot elongation.

Sakai & Weiser (1973) have looked at the freezing resistance of trees in North America, with reference to tree regions. In this study, dormant one-year-old twigs of some seventy tree species from mature trees in the five major tree regions in the USA, were collected. Induced maximum freezing resistance was then induced by holding twig samples of uniform length at -3°C for two weeks, -5°C for one week, and -10°C for three days. After this hardening, the twigs were cooled at 5°C increments each day to -30°C, and then to -80°C in 10°C increments. At selected test temperatures during this procedure, twig samples were removed from the freezer, after equilibrium for 20 hours, and thawed in air at 0°C. Freezing injury was evaluated visually, where browning was used as a criterion for rating injury. Hardiness of the vegetative buds, leaves (in the case of evergreens), and the living tissue of the twig was expressed as freezing resistance, i.e. the lowest test temperatures at which no injury was sustained. The authors go into some detail as to the hardiness of tree species within the major tree regions and, as might be expected, the northern or more extreme (cold) areas produced hardier tree species, although not all species were as hardy as each other. The main interest for this dissertation lies in the results of comparisons between provenances of single species. The authors found that the winter twigs of Betula papyrifera, Populus tremuloides, Populus balsamifera and Larix laricina, at the southern limits of their range in the north-central United States, were uninjured down to -80°C, and that twigs of the same species were equally as hardy in Alaska. However, freezing resistance in buds of "climatic races" of Picea mariana and Picea glauca from central Alaska survived freezing to at least -70°C, whereas those from Ontario and Northern Wisconsin survived only to -50°C. They found similar differences in freezing resistance in Pseudotsuga menziesii, Thuja plicata, and Tsuga heterophylla. The winter buds of Douglas-fir from the Pacific Coast resisted freezing to only -20°C, but those native to Idaho and Colorado survived freezing to -50°C. Buds of Tsuga heterophylla from Alaska were more resistant than those from Oregon and Washington. Similar trends were observed in Thuja plicata. The authors remarked that these variations in hardiness generally appeared to be closely related to the winter minimum temperatures of their native habitats.

The triphenyl tetrazolium test.

Demos (1973) looked at frost tolerance among populations of Acer negundo, commenting that "the purpose of the study was to investigate frost tolerance in geographically-diverse populations and answer the question, does each member of a species possess a broad range of frost tolerance or do local populations have frost tolerance mechanisms that are in harmony with the local winter conditions?"

In this study of frost tolerance variation, a different method of measuring damage was employed, which was first suggested by Steponkus & Lanphear (1967b). This is based on the staining of samples with triphenyl tetrazolium chloride (TTC), which enters into a chemical reaction in living cells, turning from a colourless liquid to red formazan, but not in dead cells. From this, Steponkus & Lanphear (1967b) suggested that if the red pigment was extracted and determined by calorimetric methods, quantitative values of damage might be obtained. After freezing, the method is used as follows; (a) previously frozen material is measured to a standard weight, e.g. 100 mg; (b) tissue samples are placed into graduated test tubes, and 3.0 ml of 0.6% (w/v) TTC in 0.05 M Na_2hPO_4-KH_2PO_4 buffer (pH 7.4) 0.05% (v/v) wetting agent (Ortho X-77) is added, and infiltrated under vacuum conditions; (c) samples are then incubated at 30°C for 15 hours; (d) then the TTC solution is drained and the tissue is rinsed once with distilled water. The samples are extracted with 7 ml of 95% (v/v) ethanol in a boiling water bath. The water insoluble formazan is extracted using 95% ethanol. A five-minute period of extraction is required for leaf samples, while woody samples must be sliced and then extracted for ten minutes. (e) The absorbance is then recorded at 530 mµ.

In the case of <u>Acer negundo</u>, Demos (1973) tested for frost tolerance, in two experiments. First, he tested for population differences in seedlings grown outdoors, in a common garden. Secondly, seedlings were compared after being grown in a greenhouse, the environmental conditions of which mimicked the outdoor experiment, except that the average night temperature was "considerably higher". Both these seedling lots were tested for frost hardiness using the above method, in the "early autumn". It was found that within each treatment there was an increase in frost resistance with a decrease in the length of growing season, in respect of the origin of the parent population. However, it was also found that a comparison of mean values between treatments was significant, indicating that the seedlings grown outside were more frost resistant than those grown from the same population within greenhouses.

The comparative weight method.

Another method of testing for frost hardiness has been suggested by Paton (1972), who considered frost injury in altitudinal provenances of Eucalyptus viminalis. The method was based on the examination of loss of water and possibly other volatile substances when injured leaf tissue finally dies, to develop a dry, papery texture. He goes on to say that, for an assessment, all dead, injured, and unaffected leaves of each seedling should be rapidly stripped, and the wet-weight determined immediately. Care must be taken to prevent the occurrence of free water on the leaf surface that could affect the wet weight as collected. Dry-weight was determined several days later, when loss of weight in a drying oven at 92°C had ceased. Both wet and dry weights were determined with an accuracy of ± 1 mg. The basic assumption in this method is that the percentage ratio of dry weight to wet weight is determined, within limits, by the relative amounts of dead and living leaf tissue at the time of assessment. Unfrosted control plants were found to have a ratio of 30%, and this indicates that uninjured leaves of Eucalyptus viminalis have a water and volatiles content of C.70%. A ratio of 85% in frost-killed plants indicated that the water content of dead tissue was reduced to 15%, in equilibrium with atmospheric moisture. Paton found that intermediate ratios between these two extremes agreed with the visual assessments of intermediate frost damage. He concluded that the ratio thus appeared to provide a good objective and quantitative measure of frost injury for individual seedlings. Using this method, he grew seedlings of Eucalyptus viminalis under controlled environmental conditions and exposed them to single frost treatments between -1°C and -5°C. He found that in general frost resistance increased with an increase in altitude of seed source above 1000 feet, but that the sea level provenance proved to be as frost resistant as the provenance at 3600 feet, which suggested that more than a simple altitudinal cline for frost resistance is involved. Furthermore, variation in frost resistance within half-sib families and within provenances was often significant and of the same order as the variation between provenances. He concluded that frost resistance in Eucalyptus viminalis appears to involve several different mechanisms.

Awe & Shephard (1975) studied another species of Eucalyptus using the same method of determining frost injury. In their case, Eucalyptus camaldulensis was studied. Four widely-dispersed provenances were used for collection of seed, from which two series of experiments were conducted. First, unhardened plants were raised in a glasshouse, these then being subjected to frost treatment as seedlings, and again a second time as coppice plants (experiments Ia and Ib); secondly, plants were raised in a phytotron and subjected to frost treatment either as unhardened plants or following a temperature hardening treatment (experiments IIa and IIb respectively).

In the first experiment seedlings were subjected to freezing temperatures directly, in a frost room after three months growth. At the end of the experiment Ia, all the plants were cut back and most produced coppice shoots. These were then subjected to the same frost treatment as the original plants. In the second experiment, after two months growth in the controlled conditions of the phytotron, half the seedlings from each provenance were put into a temperature regime to produce hardening and the others remained unhardened. Both sets were then transferred to the frost room.

The results from the first experiments, where no hardening treatment was applied, displayed differences between provenances. It was found that the northern provenances "tended to be the least damaged and the most southerly provenance from Nathalia the most damaged". In experiment Ib, it was determined that the coppice plants of the northern provenance were the least damaged at -4.5°C, but the leaves of these same plants had been completely killed by frost at -5.5°C as seedlings. The authors suggested that perhaps the absolute minimum temperature which the unhardened plants can survive when raised in the glasshouse is between -4.5°C and -5.5°C. The phytotron-raised material of experiment II was less severely damaged than the glasshouse plants of experiment I, but the same trends emerged. The authors noted that of particular interest is the apparent lack of a need for frost hardening by the northern and western provenance to be able to withstand a mild frost. Where seedlings are not hardened to low temperatures the northern, and to a lesser extent, the western provenance, are best able to withstand a sudden artificial frost to -4.5°C. At -5.5°C the leaves of the northern provenance were completely killed on seedlings which were raised under similar conditions.

The conductivity method.

Another approach to the study of cold hardiness variation between provenances is by the use of a conductivity measurement. For example, Flint (1972) has compared the cold hardiness of twigs of Quercus rubra, using this method. He indicates that "this study was conducted on individual trees of Quercus rubra grown from seeds collected from the native stands over the natural range of the species...These trees had been planted as one year old seedlings in 1950-1952...". The randomly selected twig segments from the different provenances were equilibrated at 5°C overnight and the following morning a control group was removed. The other samples were subjected to a lowering of temperature at the rate of 3°C per hour and at four selected test temperatures samples were removed. All the samples were allowed to thaw slowly. This is a test of naturally hardened twigs as compared to the artificial hardening mentioned above. The test for damage at the four test temperatures was carried out quantitatively using the conductivity method first suggested by Dexter.

In was in 1930 that Dexter first wrote about a "new" method for determining hardiness in plants. This was based on the degree of exosmosis of electrolytes from tissue after freezing. He tested the method on alfalfa roots from varieties of which the hardiness was known. Determinations of exosmosis were made at weekly intervals throughout the autumn, measuring the outward diffusion of the electrolytes into distilled water by the change of the conductivity in the water. This showed a progressive development of hardiness throughout the autumn in the hardy varieties, while the tender varieties showed no such change. He remarked that "calorimetric tests for chlorides and nitrates in the exudate from the frozen roots correlate very well with the conductivity measurements". Flint *et al.*, (1967) commented that in these earliest studies using the electrolytic method, as well as in many later ones, specific conductance of leachates from frozen and unfrozen samples were compared. Such comparisons were useful, but not strictly quantitative, because total electrolytes varied in different samples. Stuart (1939) overcame this limitation by expressing the amount of cell electrolyte released by freezing as a percentage of the total electrolytes released after heat killing. Rollins *et al.*, (1962) expressed the degree of injury as the difference in quantity of electrolytes released between frozen and unfrozen samples, expressed as a percentage of the total electrolytes by heat-killing them. Thorsrud & Hjeltnes (1963) divided the percentages of total electrolytes released by freezing by the percentage released from similar unfrozen samples, and used a quotient as an expression of that injury. Flint *et al.*, (1967) commented that a more useful alternative to these methods is to convert the percentage release of the electrolytes to a scale where the unfrozen sample is given a value of zero and the heat-killed sample a value of 100. They called the scale the Index of Injury, calculated from the equation;

$$It = 100\,(Lt\,Ld - Lo\,Lk)/\,Lk\,(Ld - Lo)$$

Where:

It = The index of injury from exposure to temperature, t.

Lt = The specific conductance of the leachate from sample frozen at temperature, t.

Lk = The specific conductance of leachate from sample frozen at temperature, t, and then heat killed.

Lo = The specific conductance of leachate from unfrozen sample.

Ld = The specific conductance of the leachate from the unfrozen sample, which is heat killed

After the determination of It for a series of freezing temperatures, the temperature required to give any selected It can be found by interpolation, giving a single expression of cold hardiness.

In a study of Quercus rubra, Flint (1972) represented differences between geographic origins by extrapolating the temperature when It was equal to 10, which he called the killing temperature, "even though it represents the killing of only a fraction of the sample". These killing temperatures were compared to four climatic variables namely, the average annual minimum temperature (AAMT), the extreme minimum temperature (EMT), the length of the frost free period (FFP) and the mean annual biotemperature (BIOT). The first three of these parameters are self explanatory, BIOT is an approximation of the temperature regime of the growing season first worked out by Holridge (1947); it is calculated by summing the normal monthly mean temperatures of all months with a mean temperature of above 0^{o}C, and dividing the sum by twelve, (the number of months in a year); or it could be done more accurately by summing the normal daily mean temperatures above 0^{o}C and dividing the sum by 365/6 (the number of days in a year).

Along with these four parameters, Flint (1972) compared the killing temperatures with the latitude, longitude and altitude of the sources of the material. He found that twig hardiness was closely related to latitude of origin, that longitude and altitude had significant but secondary effects in the autumn, and that all four of the climatic parameters were strongly related to the cold hardiness of the twigs in the autumn. However, he also noted that cold hardiness in all the cases was greater than that required by the climate of the area of origin, suggesting that twig hardiness in established trees is not an important factor currently in natural selection.

Maronek & Flint (1974) looked at the variable nature of cold hardiness between populations of Pinus strobus from different localities in the United States, using this same methodology. They found that there was a difference in the amount of hardening between the southern populations in comparison with the northern. "Variation in killing temperature with latitude is clinal, consistently significant only between the northern and southern range extremities". They found that in midwinter, all needles had attained levels of hardiness of 3°C or more below the extreme minimum temperature of their respective seed sources, suggesting that this was probably sufficient for long term survival in the native habitat. They concluded that from this result cold hardiness was at a satisfactory level at all latitudes for the survival of Pinus strobus and that it is not the primary limiting factor in the limitation of its range.

Differential thermal analysis.

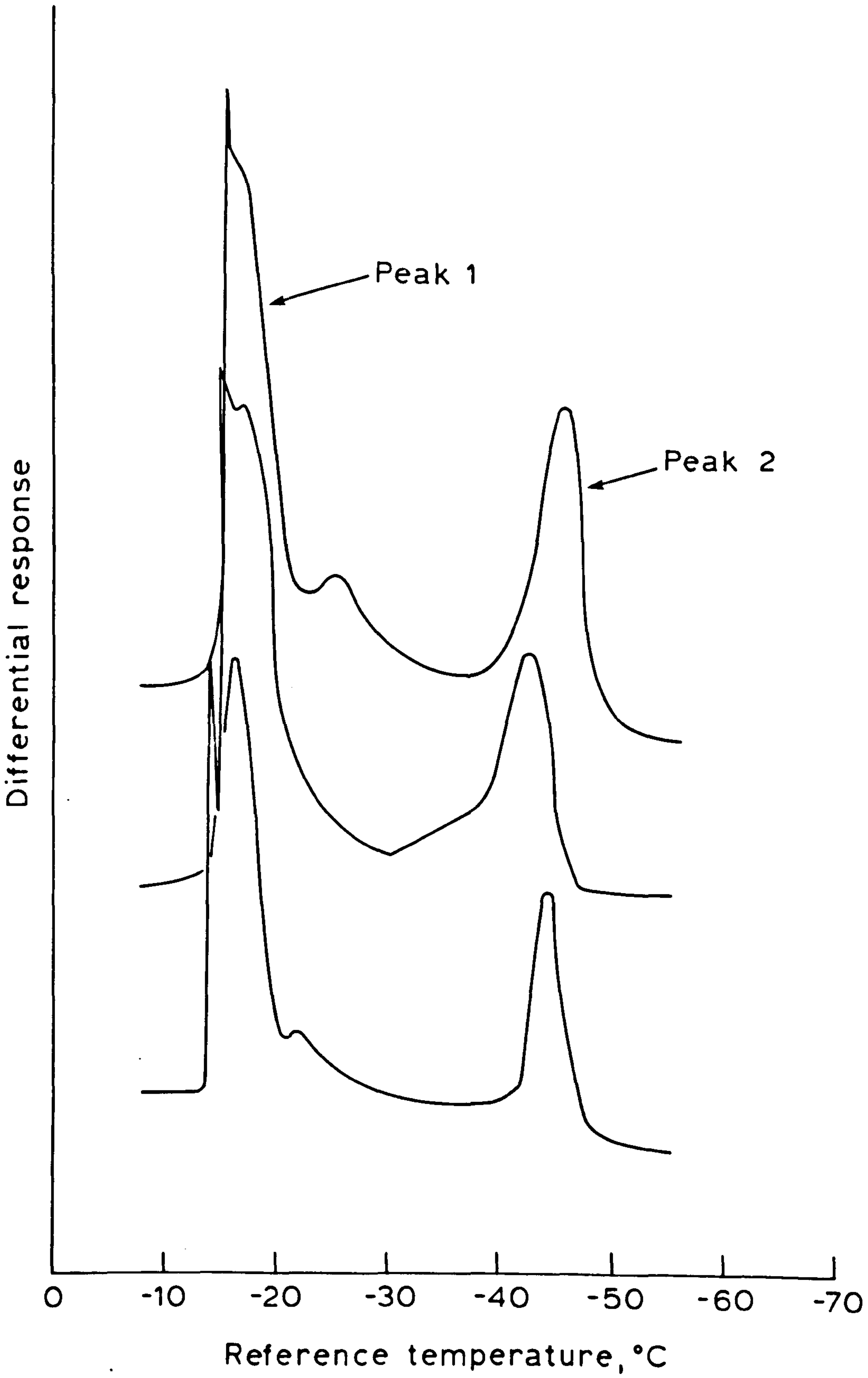
Since Flint's study, the mechanism of injury to stems of certain species has been elucidated. It has been found that the injury results from freezing of deep super-cooled water in the stem xylem and pith (George et al., 1974; Burke et al., 1975). George et al., (1977) studied this injurious freezing of deep super-cooled xylem water in relation to geographic source in the red oak (Quercus rubra), yellow birch (Betula lutea), black walnut (Juglans nigra), and wild black cherry (Prunus serotina).

A super-cooled solution is one that is completely liquid, containing no ice, exist~~ed~~ing at temperatures below its thermodynamically defined equilibrium freezing point (Glasstone, 1946). For plants, this is typically between 0°C and -5°C (George et al., 1977). A deep super-cooled solution is a super-cooled solution existing at temperatures approaching the homogeneous nucleation temperature, i.e. the theoretical low temperature limit for super-cooling. The homogeneous nucleation limit is found to be between -40°C and -50°C for plant solutions thus far studied, and is at -38.1°C for pure water (Rusmussen & Mackenzie, 1972; George & Burke, 1976). For the four species named above, the objective was to determine whether the injurous freezing of deep super-cooled stem water existed in each species regardless of geographic origin, and to determine the correlation, if any, of geographic origin to the freezing temperature, and the quantity of deep super-cooled stem water.

The analysis of stem freezing was undertaken using a differential thermal analysis, described by George <u>et al</u>., (1974) and Burke <u>et al</u>., (1976). Stem sections and an aluminium reference sample, were cooled at a constant rate, and the temperature differences between the two were monitored. Examples of this analysis are shown in Fig 7.3, in which the differential temperatures between the stem section and aluminium reference sample are plotted against the reference temperature. In Fig 7.3 the peaks (exotherms) indicate freezing points and result from the exothermic heat release during the freezing of water. This warms the stem section relative to the aluminium reference sample. However, the warming is temporary, and when the freezing is complete the stem sample again cools to the reference temperature.

In order to measure the hardiness of stem samples in this method, twigs were placed in a freezing chamber, and the temperature was lowered at 15°C / hour to -20°C. They were then removed at three-degree intervals to -47°C. They were then allowed to thaw overnight, stored in an incubator for six days, and then removed and examined for visual browning. It was noted that the bark remained uninjured in this experiment, and that only the xylem and pith showed injury. The exotherm temperatures demonstrated that nearly all trees from the provenance collections of the four species attained stem hardiness in the vicinity of -40°C, and they were able to show that there was almost no variation in either the exotherm temperature of the

Fig 7.3. Typical differential thermal analysis profiles of three samples of red oak (Quercus rubra).



Peak 1 results from water freezing extracellularly in the bark, pith, and xylem vessels and does not cause injury. Peak 2 is from water freezing intracellularly in the xylem and parenchyma, causing injury.

visual killing points. They also found that there was no correlation between the exotherm temperature and the geographic origin or climatic data. The only strong correlation involving the exotherm position was the average annual minimum temperature for wild black cherry, in which the exotherm temperature always remained below the average annual minimum temperature at each local source. It was pointed out, however, that these results do not indicate that the overall hardiness of plants in these provenances would be the same at all times, as they only indicated hardiness attainable in midwinter.

In conclusion George et al., (1977) remarked that the data showed that cold hardy trees in provenance collections of red oak, yellow birch, black walnut, and wild black cherry have low temperature exotherms in the xylem near the homogenous nucleation temperatures for dilute aqueous solutions (-38°C to -47°C), regardless of geographic origin. Generally, no correlation is found between exotherm temperature and geographic range within a species at midwinter. In the red oak the more northern plants had smaller low temperature exotherms.

It can be seen that a variety of methods may be used in the evaluation of intraspecific variation in cold hardiness. These methods are indeed not the only ones that have been used in the determination of cold hardiness per se, although to date none of the others have been used in respect of intraspecific variation. However, it is considered that for completeness, a few brief remarks on the other methods should be given.

As a modification of the conductivity value of electrolyes diffusing from damaged cells, Siminovitch et al., (1962) have noted that these substances were not the only ones that diffuse from damaged cells, and they have considered the release of amino acids and other ninhydrin reacting substances in the determination of cold hardiness. Greenham & Daday (1957, 1960) have noted that the ratio of conductance of a high frequency to that of a low frequency current drops from ten in a living plant, to one when tissue is killed. They therefore inserted a fine electrode directly into plant tissue, and injury was determined repeatedly at different times after thawing. McLeester et al., (1969), made use of the multiple freezing point of plant tissues as a test of viability in evaluating cold hardiness. They noted that living stem sections revealed two freezing points while dead tissue only exhibited one; thus, the presence or absence of two freezing points in a second freezing of the material was used as a criterion for establishing viability.

Levitt (1972) has also noted that for many years investigators have searched for an indirect "measuring stick" to evaluate hardiness, without having to freeze the plant. To this day the search continues, as sometimes methods that work beautifully for one series of plants, do not for another. For example Akerman (1927) found that sugar content is directly proportional to hardiness in a series of twelve wheat varieties; while Babenko & Gevorkyan (1967) found that other varieties and other grains did not accumulate sugars at hardening temperatures. Impedence has been correlated with hardiness of forty three peach bearing trees (Weaver et al., 1968) and with increases in the apparent freezing resistance of alfalfa (Hayden et al., 1969). However, it was found that scion diameter was also correlated with the hardiness in the same forty three peach trees, and that impedence was not correlated with hardiness in nonbearing trees (Weaver et al., 1968). Similarly, impedence readings did not separate the winter hardy from the tender cultivars of red raspberry (Craig et al., 1970).

Another method of determining cold hardiness has been to evaluate the sulphydryl (SH) content in wheat and barley varieties (Schmuetz et al., 1961; Schmuetz, 1969). These workers found that there was a correlation between the SH content of the homogenate, and winter hardiness. Schmuetz (1969) also found an equally good correlation between ascorbic acid and winter hardiness, in several wheat varieties.

When discussing these various methods Levitt (1972) concluded that "past experience indicates that no one "measuring stick" can be trusted as a measure of relative freezing in all plants, and in the final analysis direct freezing tests are essential for fully reliable measurements of freezing resistance.

Cold hardiness in the yew.

No study relating to cold hardiness had ever been attempted in the case of the yew tree; even the simplest questions relating to it are significant. For instance, does the yew tree possess the physiological apparatus involved in cold hardiness? Since populations of this tree species exist in temperate regions the working hypothesis must be that it does. Does the cold hardiness show periodicity, as has been shown to be the case in other tree species? The hypothesis again must be that it does, as Levitt (1972) noted that in the case of higher plants of temperate climates, the autumn rise of freezing tolerance seems to be a universal phenomenon. Apart from these questions, however, the main purpose of this section of the study is to find out whether there are differences in frost resistance between northern and southern populations of the yew in England. A qualitative suggestion that the yew's northern limit is perhaps set by its intolerance to winter cold has been mentioned by Godwin (1956), but no other equivalent reference exists. I shall aim to establish whether cold hardening in the yew in England is present, is periodic, and is sufficient to ensure its survival in all regions.

CHAPTER 8.

Variation of cold hardiness in Taxus baccata L.

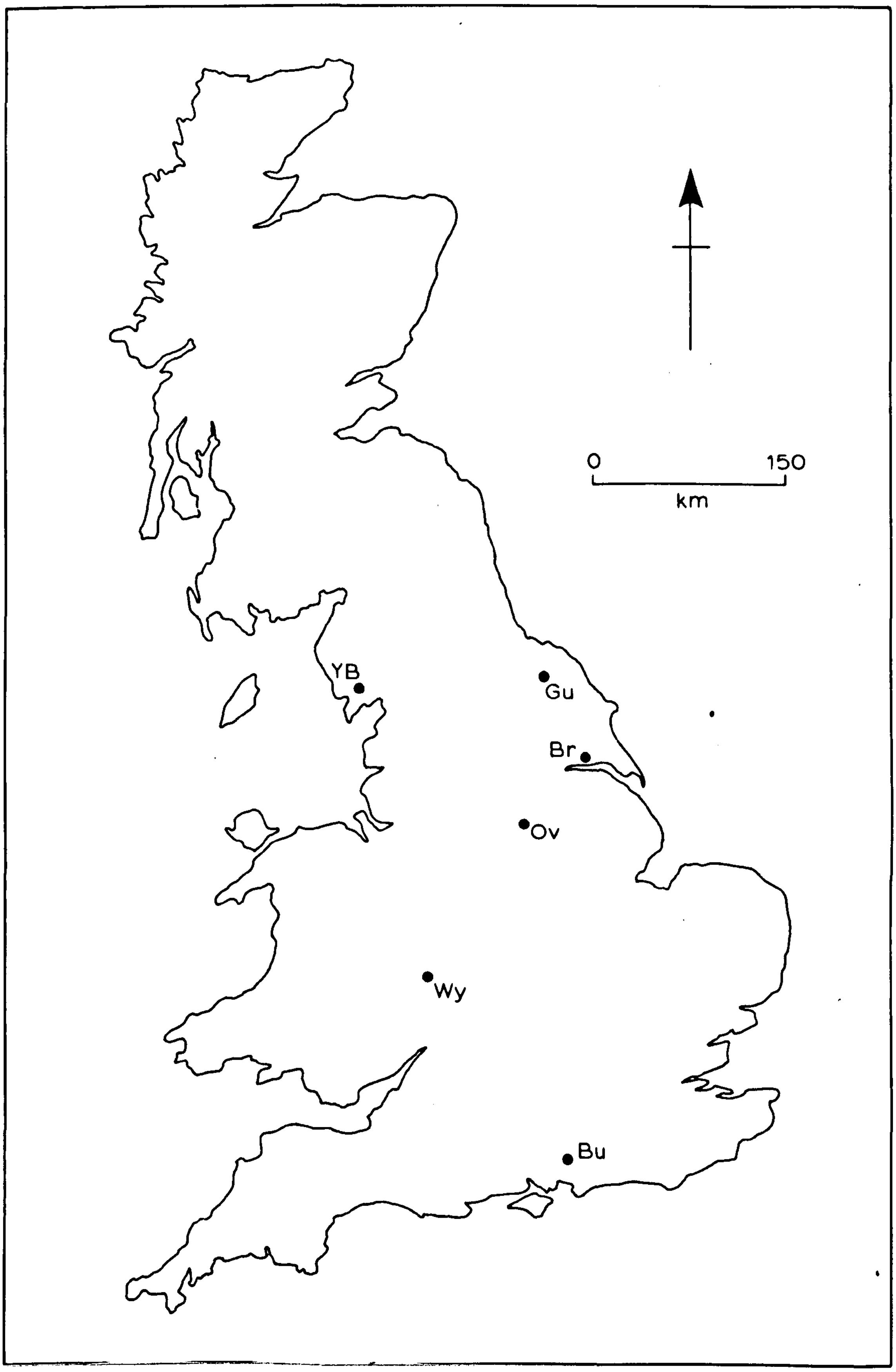
In England, populations of yew trees become rarer to the north, and especially towards the northeast. Although it is not at the most northerly point of its range in these parts (it exists in Scotland and Scandinavia), a study of variation in cold hardiness is likely to give an indication of the overall survival potential of the tree with respect to winter and other cold temperature conditions. Accordingly, this study will also look at the periodicity of this phenomenon. Although periodicity has been seen to be present in other trees, it has never yet been confirmed in the yew tree. By looking at these two aspects of cold hardiness in the yew simultaneously it is hoped that more understanding of the phenomenon itself, with respect to the yew, and regional variation within it, will be forthcoming.

Material and methods.

Six populations were selected from five regions of the country (see Fig 8.1). They were Butser Hill (Bu), Sussex; Wyre Forest (Wy), Worcestershire; Overton Hall (Ov), Derbyshire; Yew Barrow (Yb), Cumbria; Brantingham (Br), East Yorkshire; and Guisborough (Gu), The North York Moors. As there was no information on cold hardiness in the yew available and the time factor and apparatus capacity in this particular study did not allow for a within-region study of variability, the populations studied were assumed to be representative of their place of origin.

Shoots were removed from five or six reproductively mature trees from the north-facing side at a height of five to seven feet (1.5m to 2.1m) from ground level. For transit to the laboratory the shoots were put into polythene bags, which were themselves housed in insulated containers so as to keep their surrounding temperature constant. The leaves from the most recent shoots were removed and the rest of the shoot discarded. The leaves from each population were then randomly mixed, weighed out in either ½ or 1 gm measures, diced and put into clean and labelled test tubes. Approximately

Fig 8.1. Populations sampled for the cold hardiness experiment.



Legend: Bu = Butser Hill
Wy = Wyre Forest
Ov = Overton Hall
Br = Brantingham
Gu = Guisborough
Yb = Yew Barrow

0.2 ml of deionised water was added to each before freezing to reduce the chances of undercooling. The test tubes were then stoppered, placed in a freezer at +2°C ± 0.2 and allowed to equilibrate for two hours. Control samples (five replicates per population) were then removed and the temperature was lowered at a rate of 2°C per hour, to -18°C. At each of five preselected test temperatures, (-2°C, -6°C, -10°C, -14°C, -18°C), another five replicates per population were removed from the freezer and immediately placed in an insulated container along with the control samples to permit slow thawing.

The conductivity test.

After this freezing and thawing, the viability of the samples was determined by the electrolytic diffusion method, described in the last chapter (Dexter, 1930). The method is based on the principle that the ability of live cells to regulate their contents is quickly lost upon membrane damage, resulting in the diffusion of solutes into the bathing solution. Hence, deionised water (25 ml) was added to each test tube, which was then stoppered to prevent evaporation, and returned to the insulated container. The leaves were then allowed to soak for twenty-four hours, after which they were brought quickly to constant temperature in a water bath (20°C), shaken vigorously and the specific conductance of the leachate was measured immediately with a conductivity meter and probe. The leaf samples and leachate, still in the original test tube, were then subjected to 120°C for 20 minutes in an autoclave, thus killing the remaining viable tissues. The samples were cooled for four hours, adjusted to the same constant temperature as before, shaken vigorously, and the specific conductance was measured as before. This experiment was repeated three times per month, as there was only room in the freezer for two population samples at a time, and for five months, i.e. November 1977, to January 1978, March 1978, May 1978, and July 1978. The conductivity measurements are shown in full in Appendix 2. From these measurements the Index of Injury (It) for all the samples was calculated, using the equation formulated by Flint et al., (1967), and elaborated in the last chapter.

To recapitulate;

It = 100 (Lt Ld - Lo Lk) /Lk (Ld - Lo), where:

It is the index of injury from exposure to temperature t;

Lt is the specific conductance of the leachate from the sample frozen at temperature t;

Lk is the specific conductance of the leachate from a sample frozen at temperature t, and then heat killed;

Lo is the specific conductance of the leachate from the unfrozen sample; and

Ld is the specific conductance of the leachate from the unfrozen sample which is heat killed.

Results.

The Index of Injury was calculated for all samples at all test temperatures and for the five test months. The results are shown in Tables 8.1 to 8.5.These were then plotted onto graphs (Figs 8.2 to 8.6). Each individual graph therefore shows five points for each test temperature, indicating the It for each sample, and the ways in which the samples behave in the five test temperatures. Although all measurements were obtained from individual samples, the linking of the five 'sample sets' by straight lines was considered acceptable, as at the beginning of the experiment all the leaves were rendomly mixed and all the test tubes were randomly assigned to the different experimental temperatures. When examining and comparing the individual graphs, it can be seen that without exception the general trend is for an increase of the Index of Injury at the lower test temperatures. In Fig 8.2, which shows the results for all the leaf samples in November 1977, all the graphs show an increase up to a maximum It at 18°C. In Fig 8.3, showing the leaf samples measured in January 1978, the same general trend is shown, with the exception of Overton Hall, which seems to have similar overall damage at -14°C as at -18°C. Fig 8.4 shows samples measured in March 1978, at which time the trend is again repeated,

Table 8.1. The index of injury for the five replicates at the five test temperatures for the six populations in November 1977.

Population	Replicates	-2	-6	-10	-14	-18
		Test temperature (°C).				
Br	1	1.39	7.84	11.25	17.07	21.11
	2	0.15	9.47	13.79	21.94	16.22
	3	5.62	8.79	12.28	16.58	22.64
	4	3.36	4.41	16.24	10.11	12.53
	5	2.63	6.14	17.74	13.89	20.97
Gu	1	0.00	0.00	0.83	19.66	20.60
	2	0.00	0.00	2.22	9.32	21.35
	3	1.67	1.74	3.65	9.96	25.75
	4	0.26	2.69	3.18	13.64	22.91
	5	0.00	0.00	1.43	14.95	17.55
Wy	1	0.00	1.04	2.06	5.50	9.07
	2	0.00	0.00	0.17	2.86	8.53
	3	0.00	1.39	2.35	6.64	9.30
	4	0.00	0.96	2.83	7.17	10.44
	5	1.16	0.77	1.45	3.30	13.65
Bu	1	0.00	0.42	1.23	6.76	13.95
	2	0.00	1.37	2.58	5.44	11.68
	3	0.00	0.00	2.21	5.65	19.95
	4	0.00	0.00	0.32	8.78	9.70
	5	0.00	0.12	1.58	6.59	13.76

Table 8.1 (Cont). The index of injury for the five replicates at the five test temperatures for the six populations in November 1977.

Population	Replicates	Test temperature (°C). -2	-6	-10	-14	-18
	1	0.00	0.21	2.63	9.60	18.44
	2	0.30	2.54	4.49	8.99	11.77
Ov	3	1.15	2.10	5.42	11.47	17.20
	4	1.29	1.78	5.99	10.99	21.17
	5	1.12	1.26	5.90	15.16	24.18
	1	0.00	1.44	5.07	18.15	-
	2	0.00	0.14	4.14	15.27	24.89
Yb	3	2.39	3.11	6.12	17.46	23.01
	4	0.00	0.00	7.33	15.31	27.79
	5	0.08	2.13	3.67	20.15	43.28

Table 8.2. The index of injury for the five replicates at the five test temperatures for the six populations in January 1978.

		Test temperature (°C).				
Population	Replicates	-2	-6	-10	-14	-18
	1	0.00	0.83	1.67	4.62	3.23
	2	0.54	0.00	4.71	2.63	4.52
Br	3	1.37	1.24	4.93	5.11	5.97
	4	0.00	2.28	2.31	4.51	6.96
	5	0.00	0.00	0.00	1.52	2.56
	1	4.31	0.37	0.91	2.57	22.57
	2	0.00	0.37	3.40	3.34	15.32
Gu	3	0.00	0.00	0.88	6.97	10.62
	4	0.37	1.38	4.79	4.74	11.90
	5	0.00	2.38	5.87	3.24	14.56
	1	0.34	0.69	3.33	9.23	19.12
	2	1.81	3.35	3.88	10.38	13.33
Wy	3	0.00	1.94	2.86	10.21	17.78
	4	0.00	0.00	1.00	10.62	15.14
	5	0.00	0.57	1.99	9.05	14.40
	1	0.00	0.00	0.00	1.02	4.36
	2	0.00	0.00	0.00	0.00	4.21
Bu	3	0.00	0.00	0.67	4.95	5.33
	4	1.24	0.00	2.15	3.77	6.81
	5	0.57	1.60	0.17	3.16	5.63

Table 8.2 (Cont). The index of injury for the five replicates at the five test temperatures for the six populations in January 1978.

		Test temperature (°C).				
Population	Replicates	-2	-6	-10	-14	-18
Ov	1	0.00	0.00	0.62	6.59	1.92
	2	1.17	0.00	0.98	1.44	5.76
	3	0.35	0.00	0.42	5.29	4.41
	4	0.00	0.00	0.00	1.15	3.40
	5	0.00	0.00	0.00	4.03	4.78
Yb	1	0.00	1.14	3.30	8.47	7.88
	2	0.00	0.00	3.75	8.19	11.64
	3	0.00	0.00	0.36	4.41	4.42
	4	0.00	0.49	4.87	3.12	10.57
	5	0.61	-	1.37	1.15	11.42

Table 8.3. The index of injury for the five replicates at the five test temperatures for the six populations in March 1978.

		Test temperature (°C).				
Population	Replicates	-2	-6	-10	-14	-18
Br	1	4.37	3.75	3.97	10.40	14.44
	2	1.97	4.02	3.12	7.05	14.37
	3	2.00	4.14	4.25	12.30	13.75
	4	4.00	3.69	5.08	11.75	16.04
	5	2.04	3.57	5.51	9.93	16.26
Gu	1	4.23	13.23	14.67	20.11	38.74
	2	0.00	6.66	11.91	30.20	52.06
	3	0.00	2.75	2.57	18.76	22.86
	4	14.48	5.25	10.50	28.87	-
	5	0.00	4.89	7.72	21.42	-
Wy	1	1.94	2.11	5.40	17.41	28.33
	2	2.99	1.46	5.79	16.85	31.07
	3	0.88	0.46	2.32	14.03	33.00
	4	2.23	1.27	7.02	12.87	28.72
	5	0.00	0.74	3.39	10.21	31.79
Bu	1	2.30	5.04	5.23	18.74	48.00
	2	4.58	2.71	3.34	10.20	37.58
	3	4.97	2.99	6.19	14.02	42.42
	4	0.00	0.00	2.13	14.58	44.62
	5	0.00	0.00	0.00	11.87	-

Table 8.3 (Cont). The index of injury for the five replicates at the five test temperatures for the six populations in March 1978.

		Test temperature (°C.).				
Population	Replicates	-2	-6	-10	-14	-18
Ov	1	0.00	0.00	0.00	19.12	44.58
	2	1.77	2.07	1.77	20.72	38.50
	3	0.00	0.00	2.54	17.34	32.63
	4	0.00	0.00	3.86	16.40	41.02
	5	0.00	0.00	3.17	14.26	50.66
Yb	1	1.48	1.86	5.13	15.16	26.91
	2	1.41	2.12	2.94	10.14	28.34
	3	0.00	0.00	2.25	17.40	26.73
	4	3.92	1.19	3.48	17.02	29.94
	5	1.17	3.77	3.23	13.25	22.73

Table 8.4. The index of injury for the five replicates at the five test temperatures for the six populations in May 1978.

Population	Replicates	Test temperature (^{o}C).				
		-2	-6	-10	-14	-18
Br	1	5.0	1.72	34.79	84.14	87.28
	2	2.96	5.95	38.16	82.59	84.08
	3	0.03	2.74	41.84	77.76	81.18
	4	0.00	13.46	42.31	78.85	86.42
	5	1.04	1.37	67.97	83.14	85.68
Gu	1	0.00	1.37	37.11	79.69	89.77
	2	1.96	3.61	36.37	78.79	86.74
	3	0.00	0.94	39.74	77.35	89.10
	4	0.00	1.59	42.63	69.12	90.15
	5	0.00	0.00	38.82	78.46	87.91
Wy	1	0.22	12.89	71.49	79.27	90.02
	2	0.35	12.12	69.37	85.27	90.64
	3	0.00	12.89	59.49	85.56	89.63
	4	0.00	6.64	61.29	84.28	86.06
	5	0.00	11.84	66.79	87.14	91.93
Bu	1	0.00	23.27	66.43	86.72	88.65
	2	2.36	23.52	69.65	83.53	88.18
	3	0.00	24.85	75.11	87.89	89.11
	4	1.54	26.05	72.20	80.95	89.47
	5	0.58	23.22	70.97	89.02	91.53

Table 8.4 (Cont). The index of injury for the five replicates at the five test temperatures for the six populations in May 1978.

Population	Replicates	Test temperature (°C). -2	-6	-10	-14	-18
Ov	1	2.12	7.00	39.91	85.26	91.11
	2	2.38	3.28	47.73	85.98	93.06
	3	6.39	2.69	39.59	85.00	91.61
	4	0.98	6.74	43.17	85.15	92.89
	5	2.75	5.82	42.11	84.47	92.23
Yb	1	0.72	21.16	63.01	84.87	90.14
	2	0.15	21.70	62.86	86.73	93.29
	3	1.67	23.99	65.02	87.56	89.82
	4	0.00	24.44	65.37	90.63	89.42
	5	0.00	22.88	70.92	86.65	91.29

Table 8.5. The index of injury for the five replicates at the five test temperatures for the six populations in July 1978.

		Test temperature (°C).				
Population	Replicates	-2	-6	-10	-14	-18
	1	1.05	4.87	90.18	93.73	96.63
	2	1.94	49.57	85.99	90.39	93.41
Br	3	0.68	50.18	88.60	89.67	88.77
	4	3.82	52.02	87.10	95.09	96.72
	5	2.06	49.27	80.11	88.13	-
	1	1.10	20.52	68.04	100	100
	2	0.00	0.00	75.11	97.45	100
Gu	3	1.43	18.25	72.53	97.56	100
	4	1.22	26.94	76.19	95.02	100
	5	0.50	27.69	68.66	90.96	98.64
	1	2.54	46.79	88.51	95.99	100
	2	0.00	33.80	91.99	95.95	95.75
Wy	3	0.00	40.61	90.44	91.51	92.66
	4	0.00	30.70	93.39	97.10	97.16
	5	0.20	42.88	82.05	97.38	98.66
	1	0.00	15.07	54.47	97.26	100
	2	0.00	19.64	62.76	98.70	100
Bu	3	0.16	26.33	63.94	95.80	100
	4	0.34	22.28	63.23	-	100
	5	0.00	17.01	56.15	94.49	100

Table 8.5 (Cont). The index of injury for the five replicates at the five test temperatures for the six populations in July 1978.

Population	Replicates	-2	-6	-10	-14	-18
		Test temperature (°C).				
Ov	1	0.00	27.73	78.38	98.77	100
	2	1.39	21.00	70.81	88.50	95.56
	3	0.70	18.19	73.16	96.30	100
	4	0.12	1.32	80.10	97.59	100
	5	0.19	17.88	79.07	97.52	100
Yb	1	4.51	51.31	82.47	96.79	100
	2	2.27	45.21	88.82	93.51	96.66
	3	2.25	50.88	79.00	94.98	93.00
	4	0.57	55.36	85.79	94.91	92.00
	5	2.52	48.15	87.35	93.51	92.77

Fig 8.2. The index of injury at the five test temperatures (^{0}C) for the six populations for November, 1977.

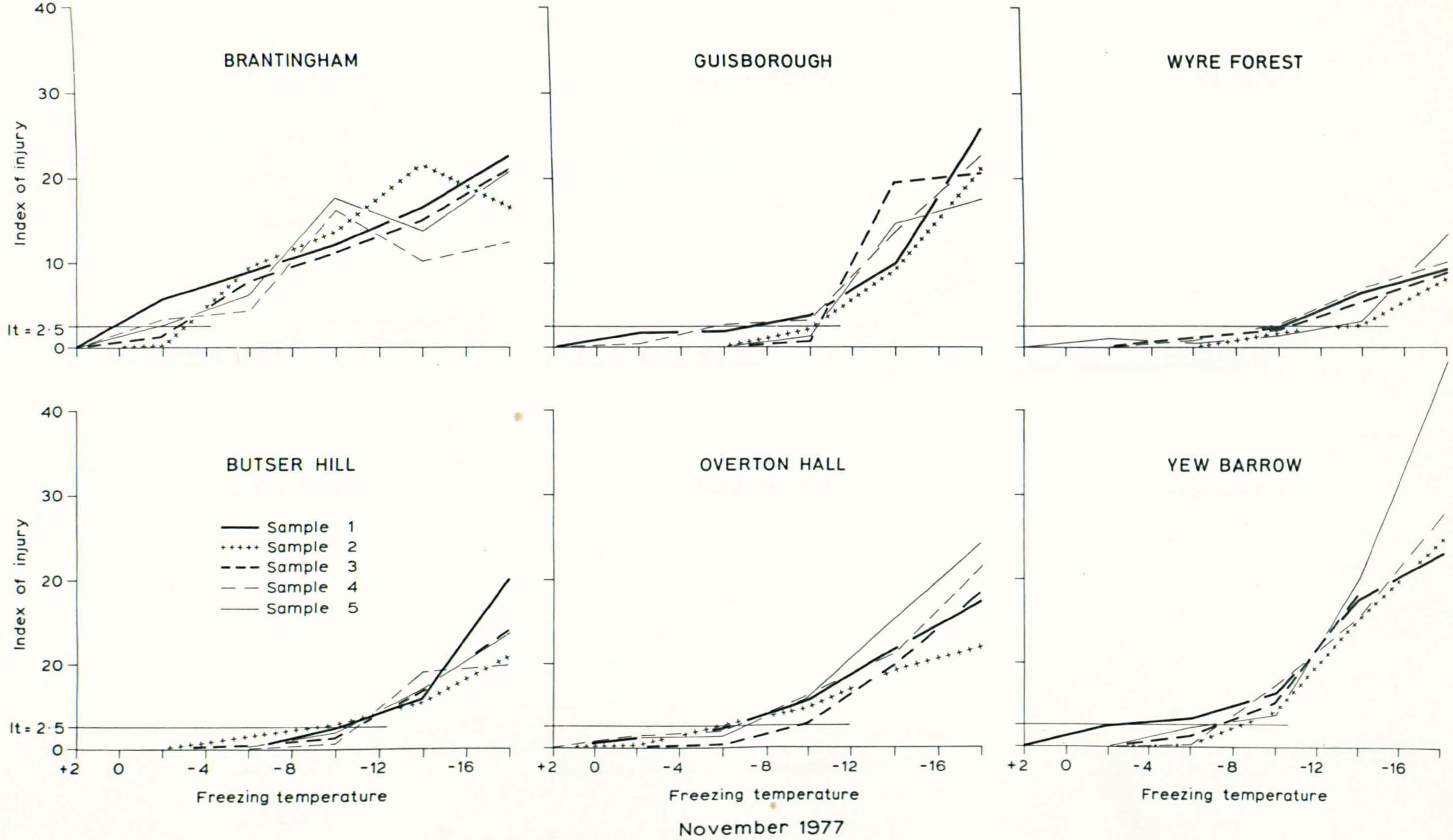


Table 8.5 (Cont). The index of injury for the five replicates at the five test temperatures for the six populations in July 1978.

Population	Replicates	Test temperature (°C). -2	-6	-10	-14	-18
Ov	1	0.00	27.73	78.38	98.77	100
	2	1.39	21.00	70.81	88.50	95.56
	3	0.70	18.19	73.16	96.30	100
	4	0.12	1.32	80.10	97.59	100
	5	0.19	17.88	79.07	97.52	100
Yb	1	4.51	51.31	82.47	96.79	100
	2	2.27	45.21	88.82	93.51	96.66
	3	2.25	50.88	79.00	94.98	93.00
	4	0.57	55.36	85.79	94.91	92.00
	5	2.52	48.15	87.35	93.51	92.77

Fig 8.3. The index of injury at the five test temperatures (°C) for the six populations for January, 1978.

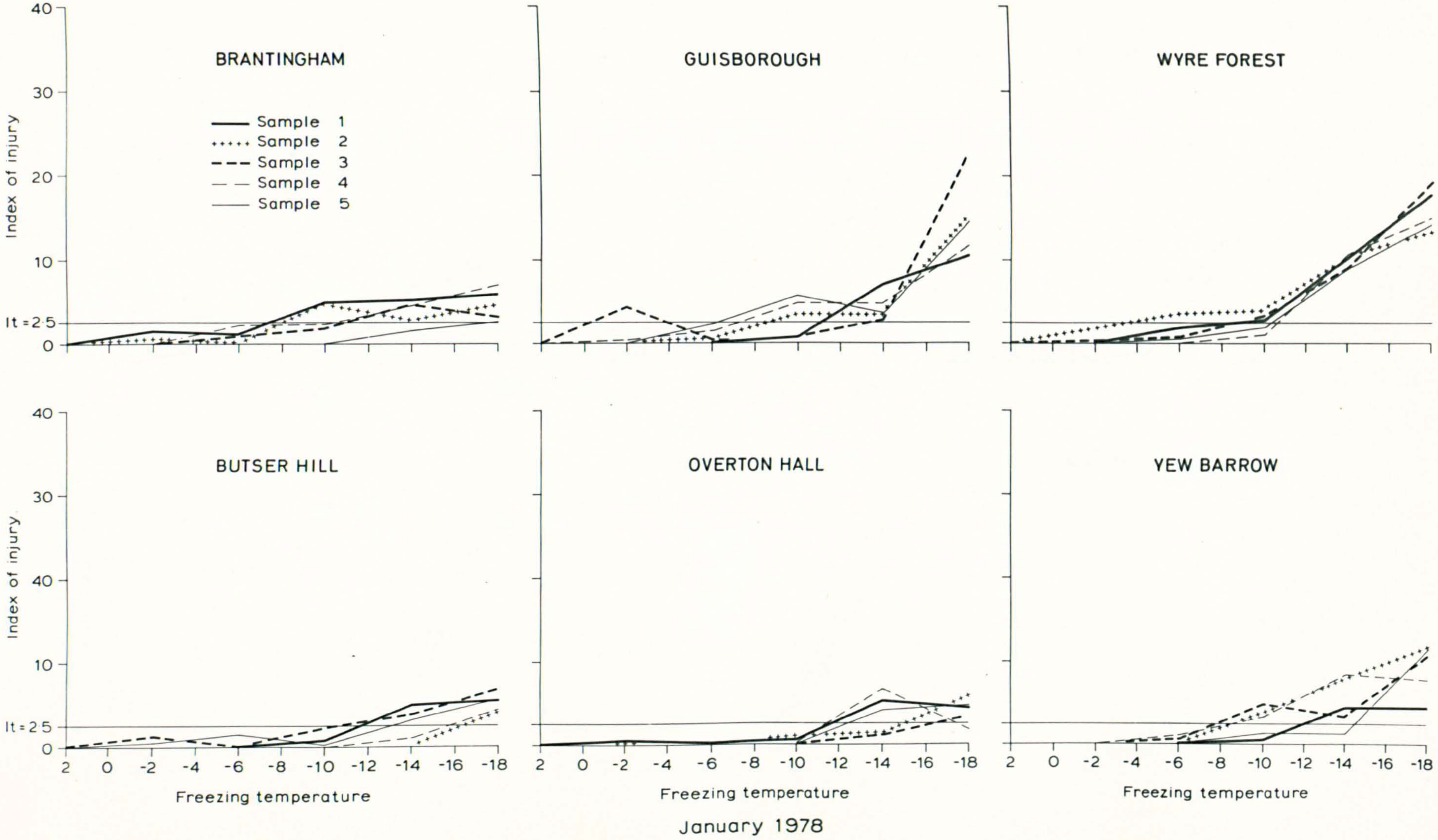
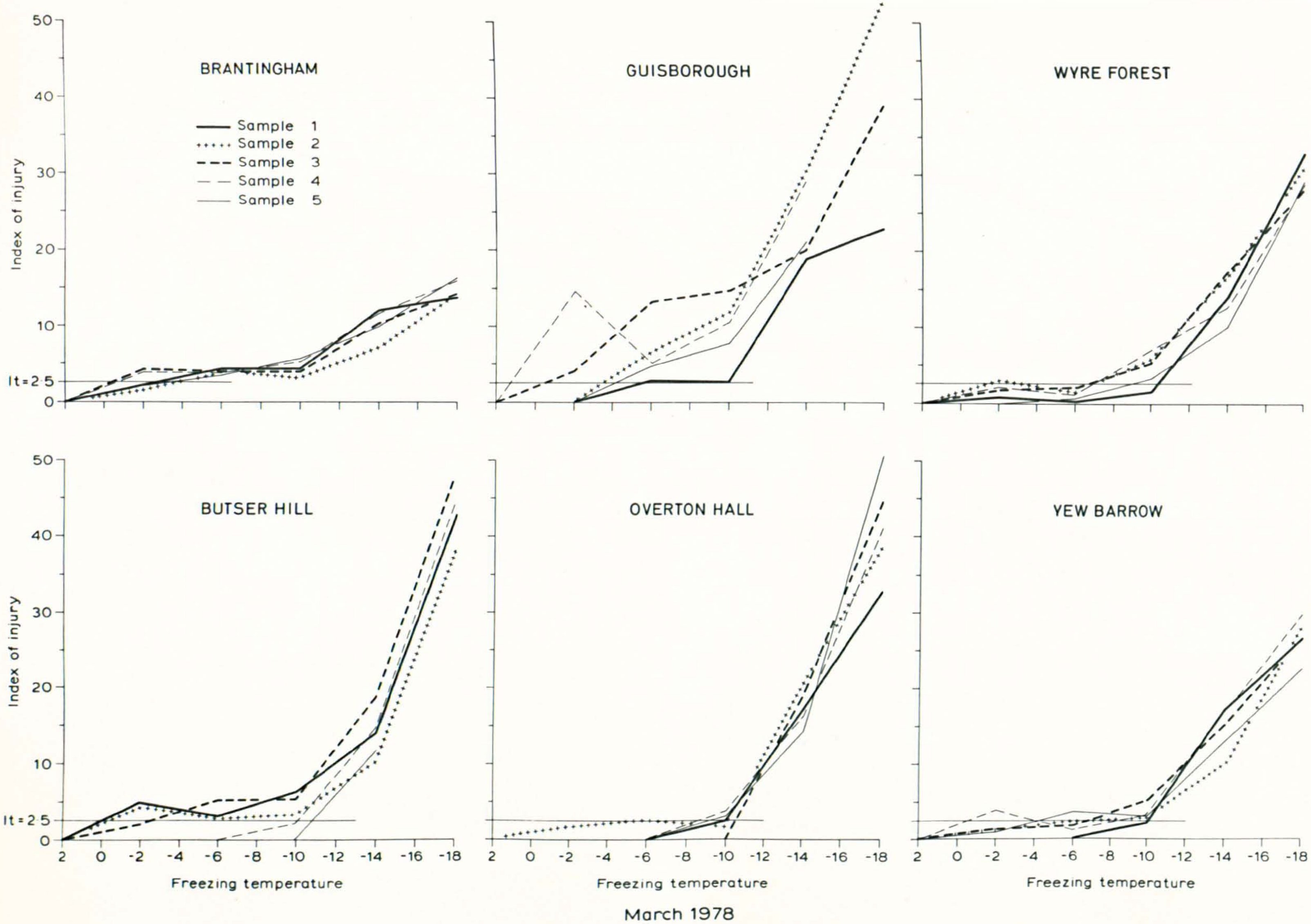
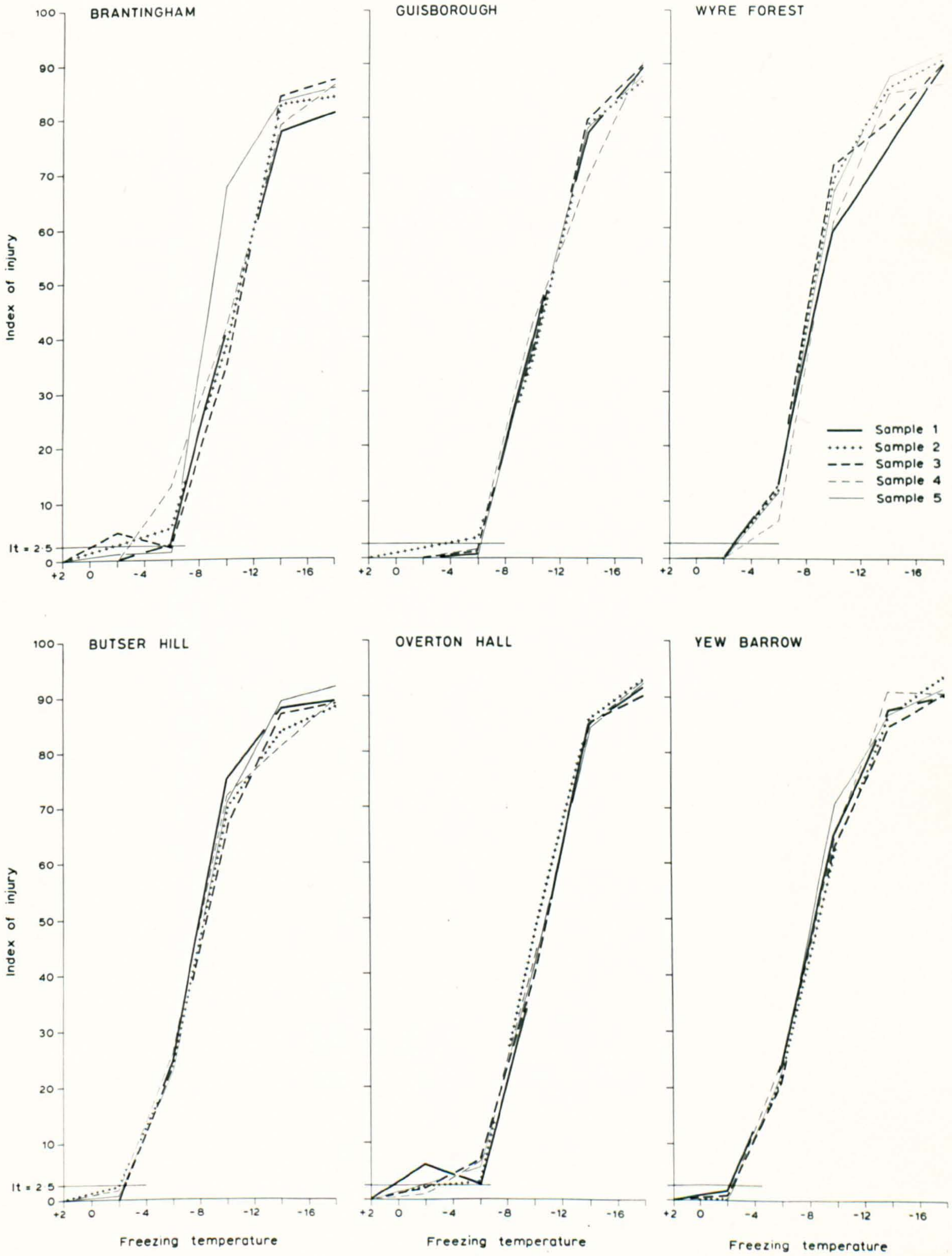


Fig 8.4. The index of injury at the five test temperatures (°C) for the six populations for March, 1978.





May 1978

<u>Fig 8.5.</u> The index of injury at the five test temperatures (^{o}C) for the six populations for May, 1978.

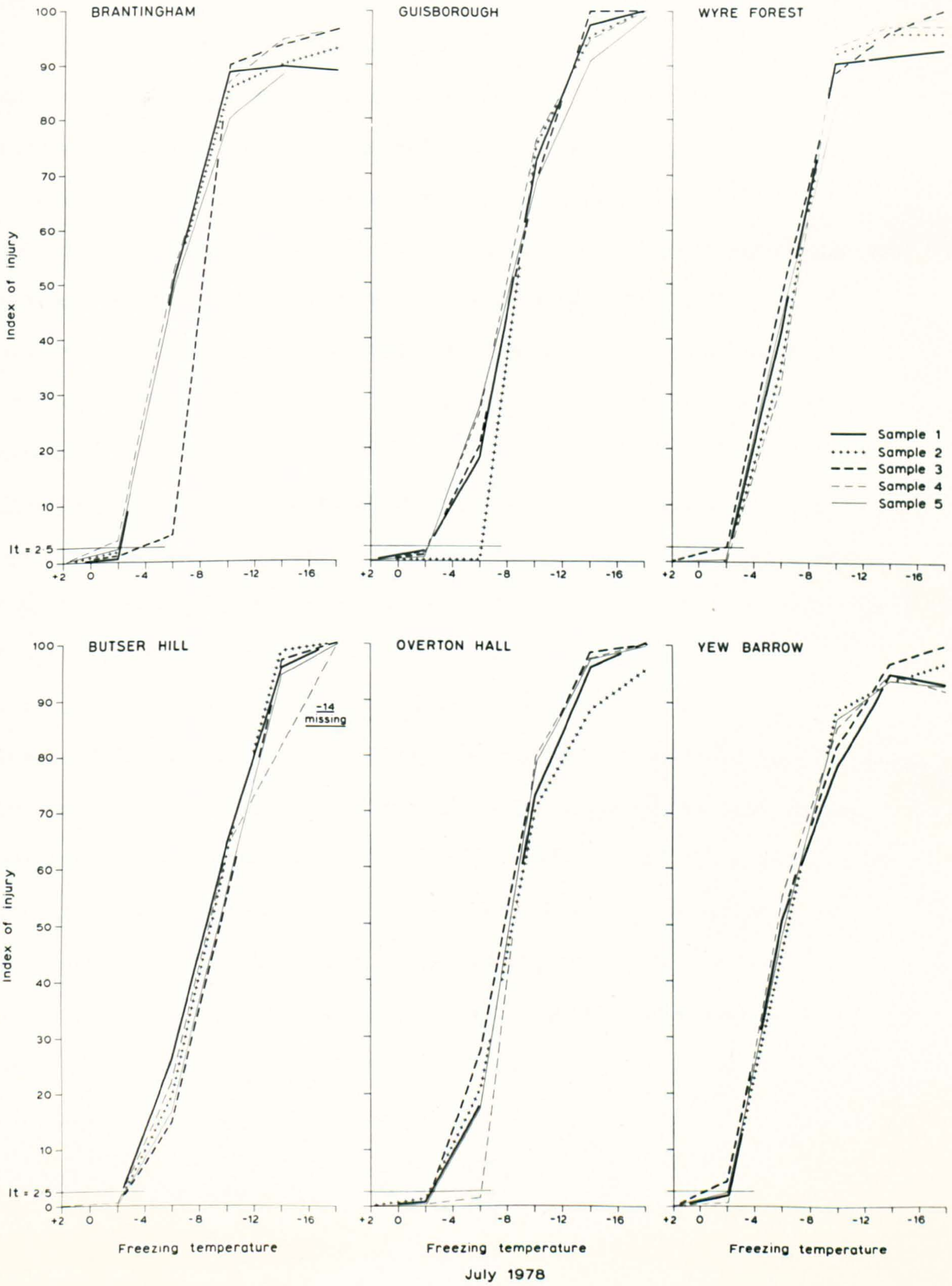


Fig 8.6. The index of injury at the five test temperatures (°C) for the six populations for July, 1978.

except for the Guisborough sample 4 at -2°C, which shows a higher It than at -6°C and -10°C. This is difficult to explain and will therefore be considered to be an artefact and thus be removed from further consideration, as all the other samples show the general trend. In Figs 8.5 and 8.6 the same characteristic curves are seen for all the populations. It can therefore be concluded that a decrease in the test temperature will give an increase of injury in the yew leaf. This of course is not a surprising result in general terms, but it is nevertheless the first time it has been confirmed for this species. Moreover, what seems also to be clear from an examination of these graphs is that the amount of damage in the yew leaf is different for different months, suggesting that the cold hardiness phenomenon in this species shows the general periodicity noted by Kozlowski (1971). To give an indication of what is happening in this respect, the mean of the Index of Injury for -18°C was calculated for all the populations and for all the months; results are summarised in Table 8.6 and plotted in Fig 8.7. This graph shows very clearly that five of the six populations increase their resistance to cold in varying degrees from November 1977 to January 1978, the exception to this trend being the sample from Wyre Forest which, in November 1977, shows the lowest mean injury index and then decreases its resistance in January 1978 to show the highest mean injury index. As January can be considered to be midwinter, the trend of the other five populations is more understandable than the Wyre Forest trend. In March 1978, it can be seen that all the populations are in a process of dehardening, lowering their resistance to the cold, and by May 1978 the resistance of the leaves at -18°C has all but disappeared; by midsummer, July 1978, even less resistance is recorded. It can therefore be concluded that yew leaves generally harden and deharden in a periodic way which coincides with the seasonal changes in temperature.

Table 8.6. Mean It at -18°C for the six populations at the five test months.

Population	Months. November	January	March	May	July
Br	18.69	4.65	14.97	84.93	93.88
Gu	21.63	14.99	37.89	88.73	99.73
Wy	10.20	15.95	30.58	89.66	96.85
Bu	13.81	5.27	43.15	89.39	100
Ov	18.55	4.05	41.48	92.18	99.11
Yb	23.79	9.19	26.93	90.80	94.89

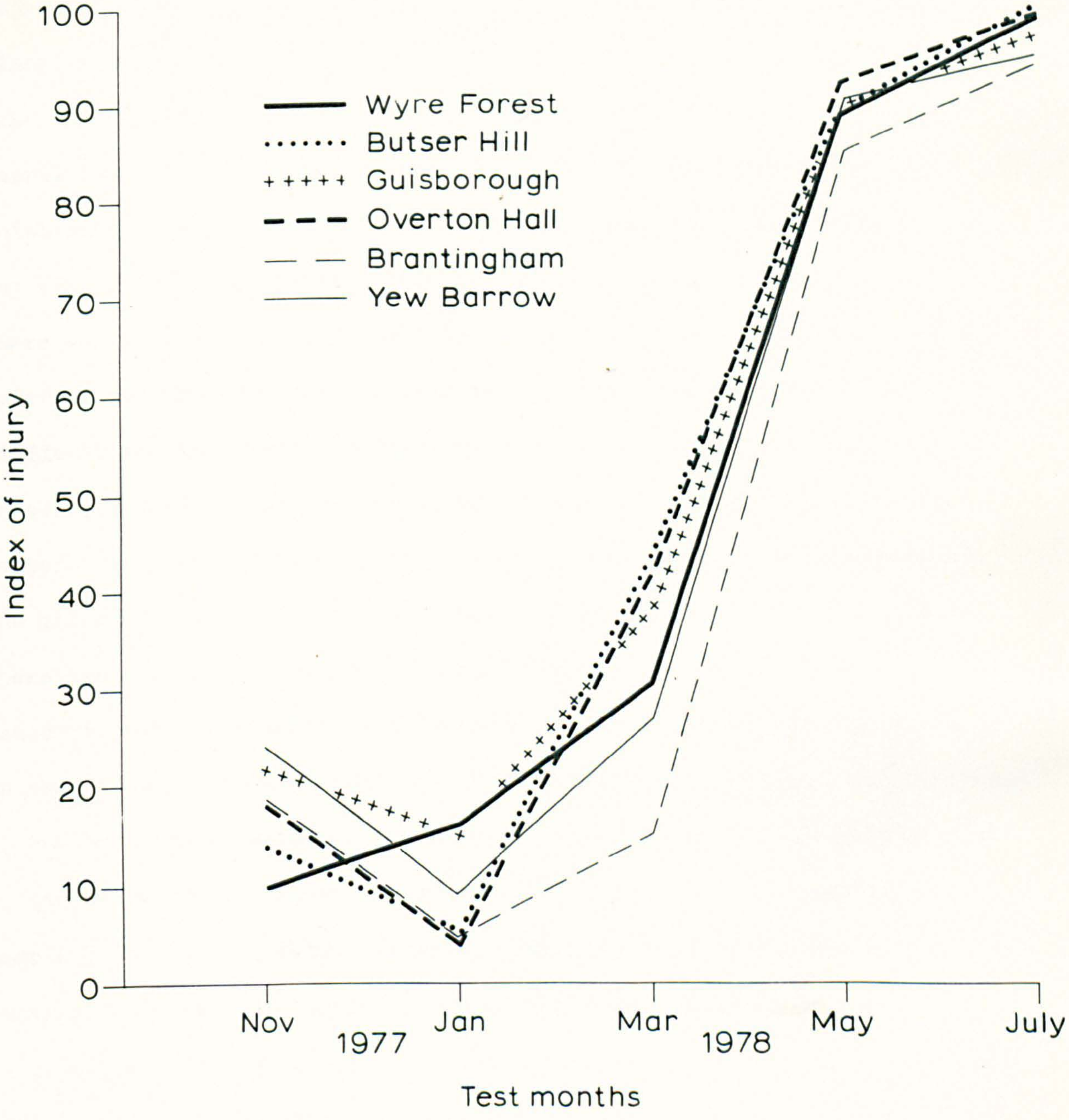


Fig 8.7. The mean index of injury for the six populations and for the five test months at -18°C.

Population variation of killing temperature.

To get an indication of between-population differences, killing temperatures were evaluated by interpolation from Figs 8.2 to 8.6 at It = 2.5. It = 2.5 was chosen as it was a point of early and detectable freezing injury. In the interpolation of It = 2.5, it was found that a small minority of the samples behaved in such a way as to cross the interpolation line twice, the samples in question being Overton Hall (sample 2), Yew Barrow (sample 4) and Wyre Forest (sample 2) in March (Fig 8.4), Guisborough (sample 1) in January (Fig 8.3) and Brantingham (sample 1) in May (Fig 8.5). Interpreting this in the strict sense, it would seem that there was more injury at lower temperatures than that found at intermediate temperatures but even more at the higher temperatures. It is difficult to understand how this could be so, and since the overall trends in all populations was for increased damage with a lowering of test temperature it was decided that in these cases the last intersection of the interpolation line with the sample curve was taken to be the place where the temperature would cause an injury index of 2.5. There are other cases in this study where this fluctuation in damage exists, but the drop in this injury does not cross the interpolation line (see Yew Barrow sample 4, and Brantingham sample 2 in January, Fig 8.3, Butser Hill samples 2 and 3, and Guisborough sample 4 in March, Fig 8.4, and finally Overton Hall sample 3 in May, Fig 8.5). In these cases, although there is an unexplainable drop in injury in the middle test temperatures, this decrease in injury does not fall below 2.5 and therefore the intercept of the interpolation line with the temperature is taken. In one case, i.e. Overton Hall sample 4 in January, there is a drop of injury below the appointed critical level at -18°C, although at -14°C the injury had exceeded 2.5, in this case the -18°C point was again unexplainable and the interpolation was made where the line crossed between -10°C and -14°C. One other problem that occurred in interpolation was when the line between test temperatures did not cross the critical value sharply, as in Wyre Forest sample 2 in November, Yew Barrow sample 2 in March and Overton Hall sample 2 in May. In these cases the average was taken as the critical temperature. All the remaining interpolations were straight forward.

The results of this exercise are shown in Tables 8.7 to 8.11, i.e. for November 1977, January 1978, March 1978, May 1978 and July 1978 respectively. These results were then plotted onto individual population graphs (Figs 8.8a to f); and the standard deviation from the mean killing temperature is shown in Figs 8.9a to f.

Description of Figures.

Fig 8.8a shows the five sample plots of the interpolated killing temperatures for Brantingham through the course of the five test months. Included in the graph is the mean trend of samples from this site, shown by a dotted line. This general trend indicates that Brantingham shows the periodic effect mentioned and described previously. However, it can be seen that there is an unexpected resistance to cold in May which exceeds that of March; this is unexpected as the environmental controls of this phenomenon would not have anticipated such a result. The standard deviation from the mean killing temperature is quite consistent for four of the five test months, shown in Fig 8.9a. It is 1.2 in November, 3.7 in January, 1.9 in March, 1.8 in May and 0.9 in July. However, although the standard deviation from the mean is relatively high in January, all the samples show an increase in resistance. In Fig 8.8b, Guisborough shows the same general trend as Brantingham, i.e. an increase in resistence to January, decreasing to March, and an unexpected further increase in May. However, the cold hardiness in November for this population is much higher than in Brantingham, with a mean killing temperature of -8.8°C in comparison to -1.56°C. The standard deviations of the samples for this population (Fig 8.9b) show that they are all comparable, namely 2.0 in November, 2.6 in January, 2.5 in March, 1.2 in May and 1.6 in July.

The general trend in the Wyre Forest population (Fig 8.8c) shows that the lowest resistance is to be found in November and that this decreases from then onwards. So, as in the two populations above, it seems that Wyre Forest does not reflect the seasonal temperatures between two test months although in this case the months concerned are different to those of the two populations above. When comparing the standard deviations of the test months for Wyre Forest, it can be seen that May and July have very narrow bands of variation from the mean killing temperature, whereas November, January and March have larger deviations in comparison. These are as follows: November 1.4, January 2.4, March 1.4, May 0.3, and July 0.1.

Butser Hill, shown in Fig 8.8d, with standard deviations in Fig 8.9d, shows no aberations in its general trend, and conforms to the seasonal temperature pattern that would be expected. However, when examining the standard deviations, although four of the five test months do not show deviations notably different to any above, in March this figure is very high, standing at 4.7. This suggests that there is an extremely variable dehardening in leaves at the end of the winter, some being much more resistant than others. The other deviations are; November 0.5, January 2.2, May 0.1 and July 0.1. It should be mentioned here that there seems to be a drop in resistance between May and July, but this is only by a difference of 0.2°C; therefore, this is not considered to be a significant trend.

Table 8.7. The results of interpolation at It = 2.5 for the five samples and six populations in November 1977.

			Population			
Sample	Br	Gu	Wy	Bu	Ov	Yb
1	-2.7	-10.4	-10.2	-11.0	-9.8	-7.3
2	-3.0	-10.2	-12.9	- 9.6	-6.0	-8.4
3	+0.2	- 7.4	-10.0	-10.4	-6.5	-2.6
4	-0.5	- 5.6	- 9.4	-11.0	-6.7	-7.4
5	-1.8	-10.4	-12.4	-10.6	-7.2	-6.9
$\bar{x}$	-1.56	- 8.8	-10.98	-10.52	-7.24	-6.52

Table 8.8. The results of interpolation at It = 2.5 for the five samples and the six populations in January 1978.

			Population			
Sample	Br	Gu	Wy	Bu	Ov	Yb
1	-11.0	-13.6	- 8.8	-15.7	-11.3	-8.5
2	- 8.2	- 8.8	- 4.0	-16.2	-15.0	-8.6
3	- 7.4	-11.1	- 8.5	-11.7	-11.7	-12.2
4	-10.4	- 7.4	-10.6	-10.6	-16.4	-7.9
5	-18.0	- 6.2	-10.3	-13.0	-12.4	-14.5
$\bar{x}$	11.00	9.42	8.44	13.44	13.36	10.34

Table 8.9. The results of interpolation at It = 2.5 for the five samples and the six populations in March 1978.

			Population			
Sample	Br	Gu	Wy	Bu	Ov	Yb
1	- 0.4	- 0.4	- 6.4	- 2.4	-10.5	- 6.7
2	- 3.1	- 3.5	- 6.8	- 0.2	-10.2	- 7.4
3	- 2.7	- 5.5	-10.2	- 0.1	- 0.8	-10.1
4	- 0.6	+ 1.3	- 6.8	-10.1	- 8.6	- 8.3
5	- 2.7	- 4.0	- 8.6	-10.6	- 9.1	- 4.1
$\bar{x}$	-1.90	-2.40	-7.76	-4.58	-9.64	-7.32

Table 8.10. The results of interpolation at It = 2.5 for the five samples and the six populations in May 1978.

Sample	Br	Gu	Wy	Bu	Ov	Yb
1	- 6.0	- 6.2	- 2.8	- 2.4	- 2.2	- 2.4
2	- 1.6	- 3.3	- 2.7	- 2.1	- 2.8	- 2.4
3	- 5.4	- 6.2	- 2.8	- 2.4	10.4	- 2.2
4	- 2.8	- 6.1	- 3.5	- 2.2	- 3.1	- 2.4
5	- 6.1	- 6.3	- 2.9	- 2.3	- 1.6	- 2.4
$\bar{x}$	-4.38	-5.62	-2.94	-2.28	-1.86	-2.36

Table 8.11. The results of interpolation for the five samples and the six populations in July 1978.

Sample	Br	Gu	Wy	Bu	Ov	Yb
1	- 3.6	- 2.3	- 2.0	- 2.7	- 2.4	- 0.2
2	- 2.0	- 6.2	- 2.3	- 2.5	- 2.3	- 2.1
3	- 2.2	- 2.2	- 2.3	- 2.3	- 2.4	- 2.1
4	- 0.7	- 2.2	- 2.4	- 2.4	- 6.1	- 2.2
5	- 2.0	- 2.3	- 2.2	- 2.6	- 2.5	- 2.0
$\bar{x}$	- 2.1	-3.04	-2.24	-2.50	-3.14	-1.72

The general trend for Overton Hall, shown in Fig 8.8e, displays the same pattern as that found in Butser Hill, with an increase in resistance from November to January and then a gradual decrease; and again, as in the case of Butser Hill, there is an increase in resistance between May and July, with the difference in this case being approximately 1.0°C. This is also not considered to be substantial. The standard

Fig 8.8a to f. Graphical representation of the interpolation results at It = 2.5 of the five samples and the mean for each test month in the six sampled populations.

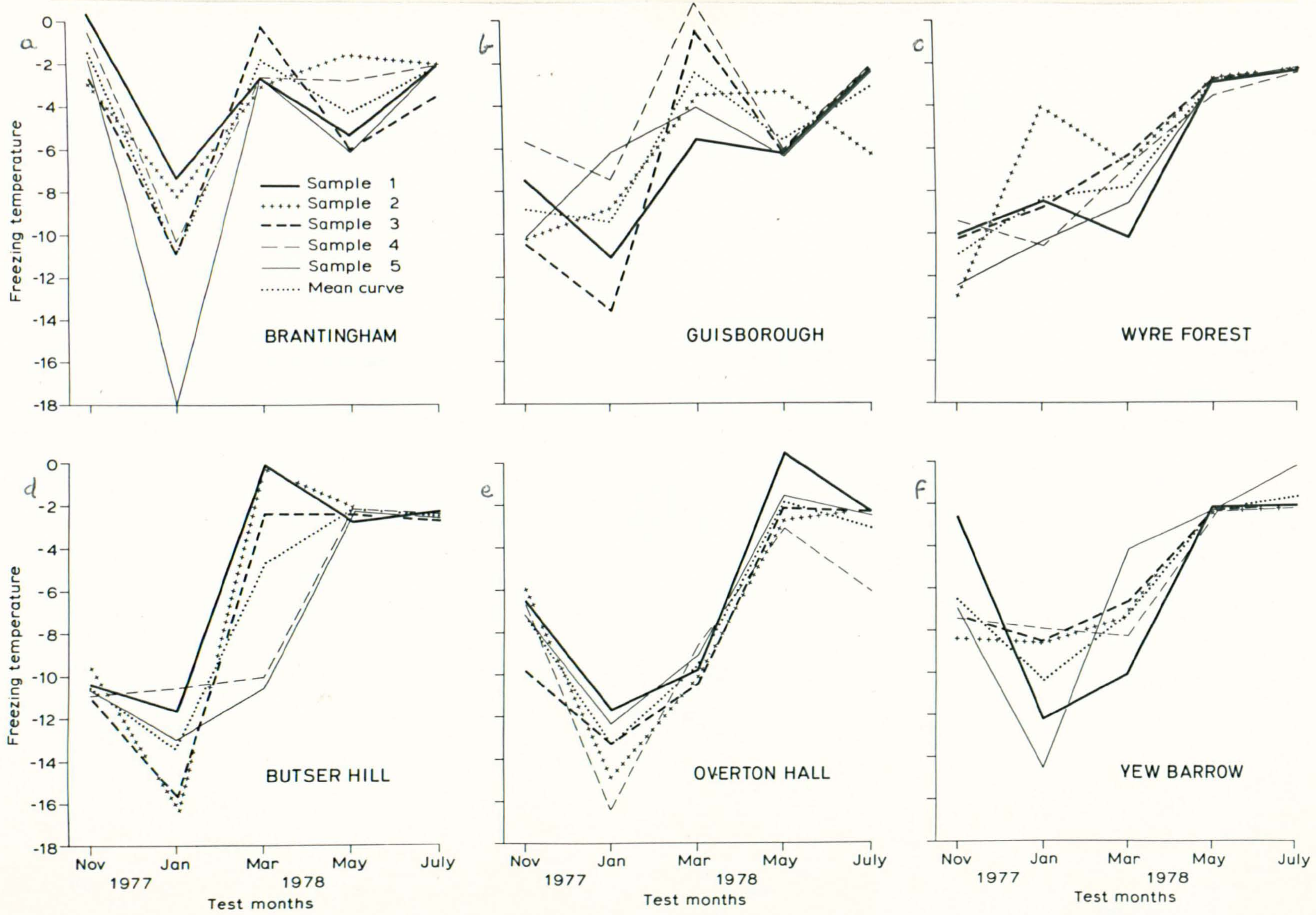
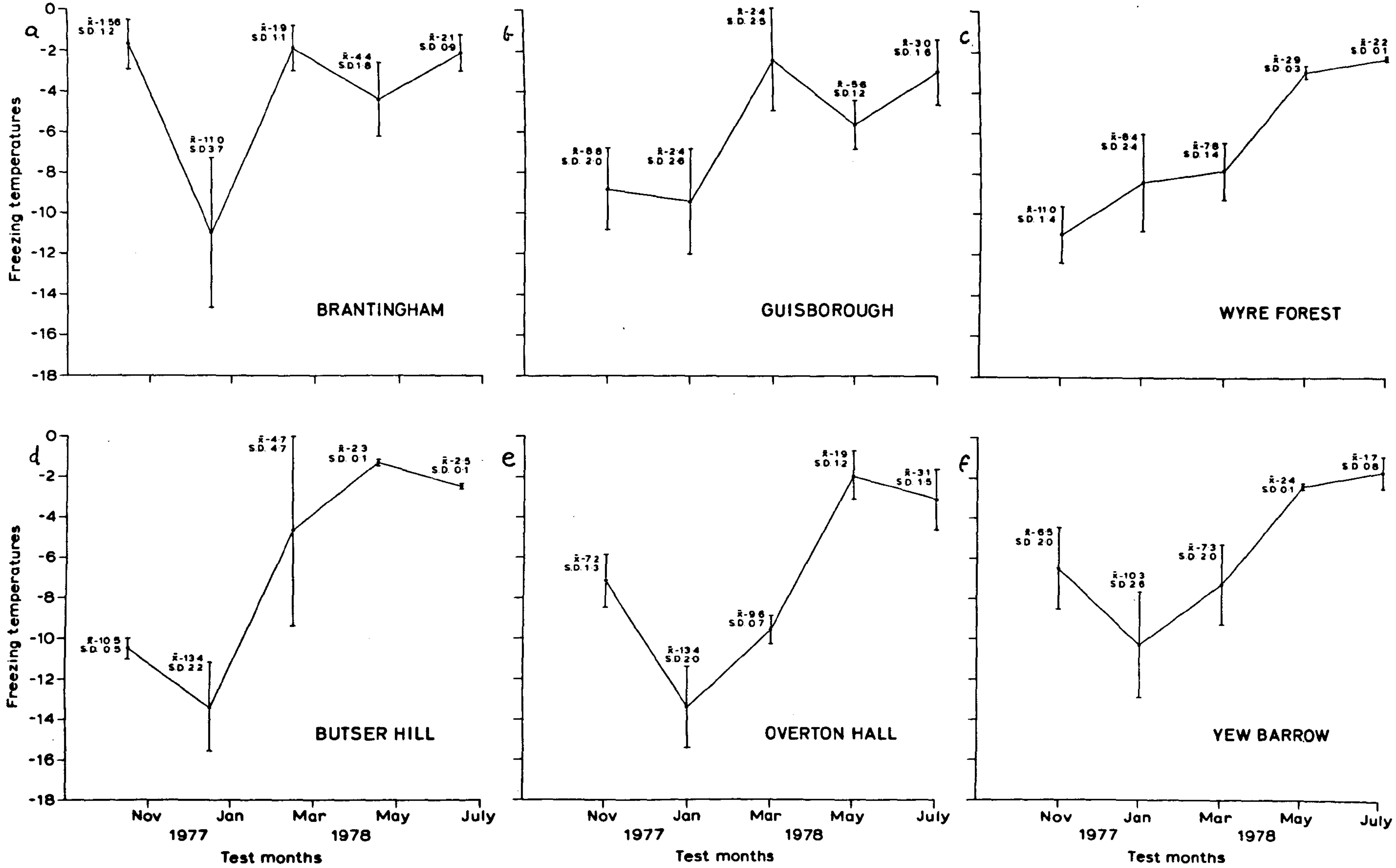


Fig 8.9a to f. The mean of the interpolated results and standard deviation from that mean for the five test months in the six sampled populations.



deviation from the mean killing temperature in each month, shown in Fig 8.8e, does not vary a great deal, the figures being as follows: for November 1.3, for January 2.0, for March 0.7, for May 1.2, and for July 1.5.

Finally, as in all the other population samples, the general trend of seasonal cold hardiness is shown for Yew Barrow (Fig 8.8f), with standard deviations which are comparable to each other in November, January, and March (i.e. 2.0, 2.6, and 2.0 respectively) and with a very small deviation in May, of 0.1, and in July, of 0.8 (Fig 8.9c). It can therefore be concluded that in all populations the mean killing temperature varies seasonally, and that for five out of the six populations, the maximum resistance to cold is found to occur in January, with Wyre Forest being the exception, in which November shows the highest resistance.

In order to obtain some indication of between-population differences within each test month the interpolated results were then subjected to an analysis of variance, and Duncan's multirange test. Both these tests have been discussed previously in chapter 6 and therefore the methods will not be reiterated here.

Results of tests.

An analysis of variance was computed for each month in order to identify significant differences between populations for the killing temperatures at It = 2.5; full details are presented in Tables 8.12 to 8.16. The determined F ratios showed that there were significant differences at the 0.05 level of probability for all but July 1978. It can therefore be concluded that there are significant between-population differences in killing temperature in the months of November 1977,

Table 8.12. The analysis of variance result for November 1977.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between groups	5	295.80	59.17	21.07
Within groups	24	67.39	2.808	
Total	29	363.20	12.53	

Table 8.13. The analysis of variance result for January 1978.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between groups	5	105.00	21.01	2.40
Within groups	24	210.30	8.76	
Total	29	315.30	10.87	

Table 8.14. The analysis of variance result for March 1978.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between groups	5	243.60	48.72	6.45
Within groups	24	181.40	7.56	
Total	29	425.00	14.66	

Table 8.15. The analysis of variance result for May 1978.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between groups	5	53.27	10.65	8.04
Within groups	24	31.82	1.326	
Total	29	85.09	2.934	

Table 8.16. The analysis of variance result for July 1978.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F ratio
Between groups	5	7.63	1.53	1.19
Within groups	24	30.80	1.28	
Total	29	38.43	1.325	

January 1978, March 1978, and May 1978. So as to find out where the population differences lay in these significantly different test months, Duncan's multirange test then was performed. The results are shown in Table 8.17a to d. These results were then transcribed on to Fig 8.10 plotting the sample mean for each population. A description of the results follows.

November 1977. It can be seen that in November 1977, Brantingham is significantly different from the rest of the populations, having a mean killing temperature of -1.56°C. Yew Barrow and Overton Hall are significantly different to Butser Hill and Wyre Forest, with Guisborough being intermediate between them. The mean killing temperature for Yew Barrow is -6.5°C, for Overton Hall it is 7.2°C, for Guisborough it is-8.8°C, for Butser Hill it is -10.5°C, and for Wyre Forest it is -11.0°C. These results suggest that in this particular month leaves from the Brantingham population have an extraordinarily low resistance to freezing as compared with that of other populations and that, in general, leaves from Yew Barrow and Overton Hall will not survive at temperatures lower than -8.8°C, whereas leaves from Butser Hill and Wyre Forest may survive in temperatures as low as -8.8°C, and down to, and possibly lower than -11.0°C. Guisborough's intermediate position between these two sets suggests that some leaves in the population will be more resistant than others, and that they will vary between Yew Barrow's killing temperature range and Wyre Forest's temperature range.

January 1978. In this month, three out of the six populations are significantly different from each other. Wyre Forest is significantly different from Overton Hall and Butser Hill, with Guisborough, Yew Barrow and Brantingham being intermediate of these extremes. The mean killing temperature for Wyre Forest is -8.4°C, for Guisborough it is -9.2°C for Yew Barrow it is -10.3°C, for Brantingham it is -11.0°C, for Overton Hall it is -13.4°C, and for Butser Hill it is -13.4°C. It can therefore be concluded that there is less variation between the populations in this

Table 8.17. Results of the Duncan's multirange test for the four significantly different test months.

(a) November 1977.

Population	$\bar{x}$	$S\bar{x}$	S.R.	S.S.R.		Col.1.	Col.2.	Col.3.	Col.4.	Col.5.
Wyre Forest	-10.98	0.75	3.25	2.44	a	-9.40*				
Butser Hill	-10.52		3.20	2.40	b	-4.46*	-8.96*			
Guisborough	- 8.80		3.12	2.34	c	-3.74*	-4.00*	-7.24*		
Overton Hall	- 7.24		3.04	2.28	d	-2.18	-3.28*	-2.28	-5.68*	
Yew Barrow	- 6.52		2.89	2.17	e	-0.46	-1.72	-1.56	-0.72	-4.96*

Wy Bu Gu Ov Yb Br

Populations that are insignificantly different from each other are shown by underlining.

Table 8.17 (Cont). Results of the Duncan's multirange test for the four significantly different test months.

(b) January 1978.

Population	$\bar{x}$	S$\bar{x}$	S.R.	S.S.R.		Col.1.	Col.2.	Col.3.	Col.4.	Col.5.
Butser Hill	-13.44	1.32	3.25	4.29	a	-5.00*				
Overton Hall	-13.36		3.20	4.22	b	-3.94	-4.92*			
Brantingham	-11.00		3.12	4.12	c	-3.02	-4.02	-2.56		
Yew Barrow	-10.34		3.04	4.01	d	-2.36	-3.10	-1.58	-1.90	
Guisborough	-9.42		2.89	3.81	e	-0.08	-2.44	-0.66	-0.92	-0.98
Wyre Forest	-8.44									

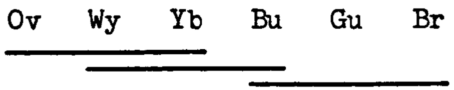
Bu Ov Br Yb Gu Wy

Populations that are insignificantly different from each other are shown by underlining.

Table 8.17 (Cont). Results of the Duncan's multirange test for the four significantly different test months.

(c) March 1978.

Population	$\bar{x}$	$S\bar{x}$	S.R.	S.S.R.		Col.1.	Col.2.	Col.3.	Col.4.	Col.5.
Overton Hall	-9.64	1.23	3.25	4.00	a	-7.74*				
Wyre Forest	-7.76		3.20	3.94	b	-7.24*	-5.86*			
Yew Barrow	-7.32		3.12	3.84	c	-4.96*	-5.36*	-5.42*		
Butser Hill	-4.68		3.04	3.74	d	-2.32	-3.08	-4.92*	-2.78	
Guisborough	-2.40		2.89	3.55	e	-1.88	-0.44	-2.64	-2.28	-0.5
Brantingham	-1.90									



Populations that are insignificantly different from each other are shown by underlining.

Table 8.17 (Cont). Results of the Duncan's multirange test for the four significantly different test months.

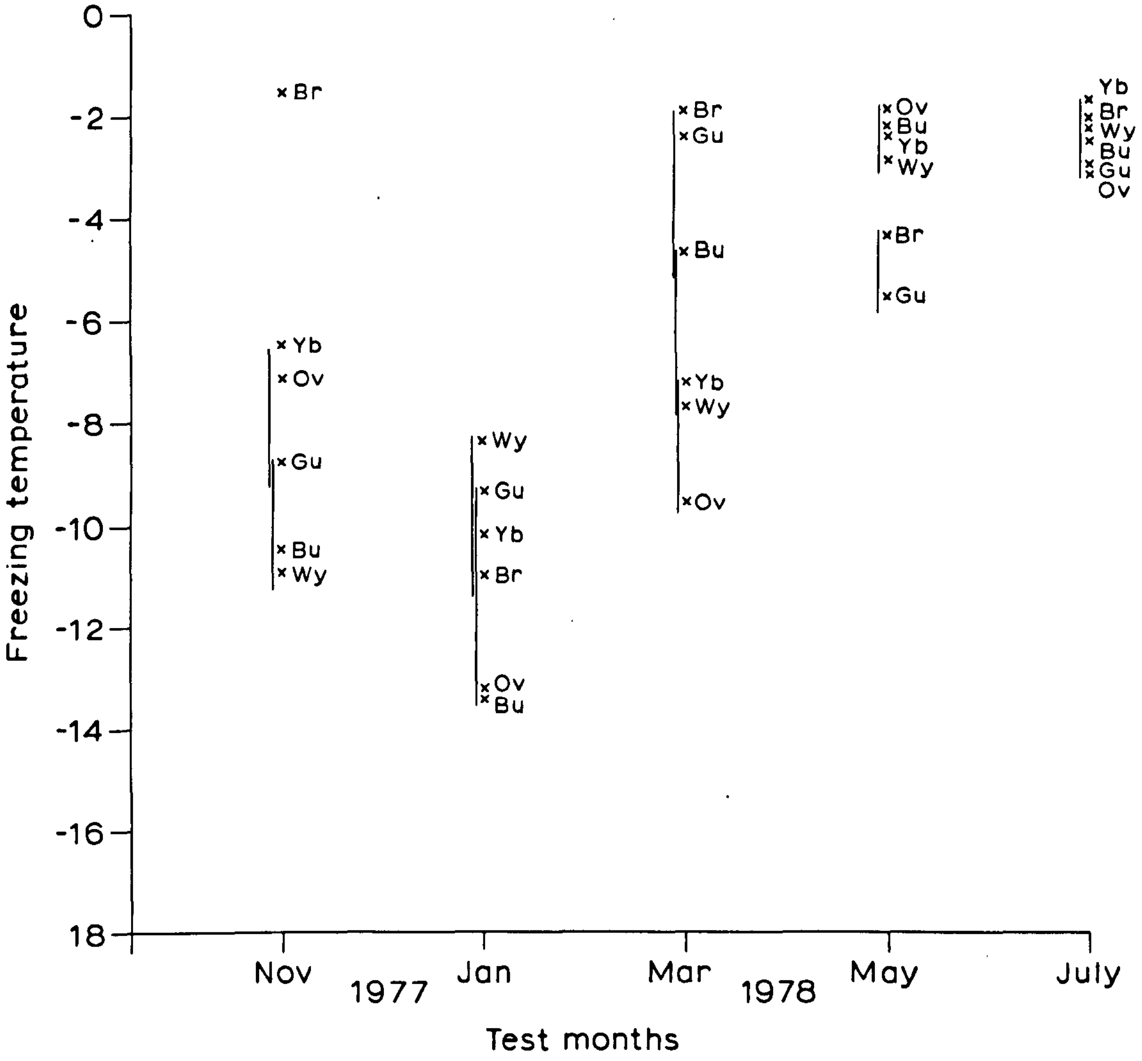
(d) May 1978.

Population	$\bar{x}$	$S\bar{x}$	S.R.	S.S.R.		Col.1.	Col.2.	Col.3.	Col.4.	Col.5.
Guisborough	-5.62	0.51	3.25	1.66	a	-3.76*				
Brantingham	-4.38		3.20	1.63	b	-3.34*	-2.52*			
Wyre Forest	-2.90		3.12	1.59	c	-3.26*	-2.10*	-1.04		
Yew Barrow	-2.36		3.04	1.55	d	-2.72*	-2.02*	-0.62	-0.5	
Butser Hill	-2.28		2.89	1.47	e	-1.42	-1.48*	-0.54	-0.08	-0.42
Overton Hall	-1.86									

Gu Br   Wy Yb Bu Ov

Populations that are insignificantly different from each other are shown by underlining.

Fig 8.10. Graphical representation of the results of the Duncan's multirange test for the six populations in the five test months.



The vertical lines indicate insignificant differences between populations in each test month.

month than there was in November, and that in general the range of killing temperatures between Guisborough and Butser Hill is from -9.4°C to -13.4°C, while the range of killing temperatures between Wyre Forest and Brantingham is -8.4°C to -11.0°C.

March 1978. In this month, the picture is a little more complex, with there being significant differences between Overton Hall and Butser Hill, with Wyre Forest and Yew Barrow being intermediate; and significant differences between Overton Hall, Wyre Forest and Yew Barrow, and Guisborough and Brantingham, with Butser Hill being intermediate between them. The mean killing temperatures for the populations in this month are Brantingham -1.90°C, Guisborough -2.40°C, Butser Hill -4.68°C, Yew Barrow -7.32°C, Wyre Forest -7.76°C, and Overton Hall -9.64°C. In comparison to January's results, here variation increases again with the range of killing temperatures for the Brantingham to Butser Hill set being -1.9°C to 4.68°C, the range of the Butser Hill to Wyre Forest set being -4.68°C to -7.76°C, and the range of the Yew Barrow to Overton Hall set being -7.32°C to -9.64°C.

May 1978. In this month, there is a clear distinction between populations, with the Guisborough and Brantingham means not being significantly different from each other, and other populations making a separate group. The mean killing temperature range of the former group is-5.62°C to -4.38°C, and the latter from -1.86°C for Overton Hall, to 2.90°C for Wyre Forest, with Yew Barrow and Butser Hill in between, having means of -2.36°C and -2.28°C respectively.

In the final month (July, 1978) it has been shown that there are no significant differences between the populations, with a mean killing temperature range of -1.72°C to -3.14°C.

Discussion and conclusions.

The aim of this part of the study has been to identify cold hardiness and its periodicity, in the yew, as well as the examination of variation between leaf samples taken from different regions of the country. The working hypotheses have been that the yew tree will show the cold hardiness phenomenon in all the sites of study and that during the winter months the resistance to cold will be higher in the more northern populations than in those of the south. The method used has been to examine the differential conductivity measurements of leaf samples from six different sites for five months of the seasonal year, from the beginning of winter in November 1977, to midwinter in January 1978, to the end of winter in March 1978, to midspring in May 1978, and finally to summer in July 1978. The conductivity measurements of each sample were analysed by inserting the results into the Index of Injury equation formulated by Flint et al., (1967). These results were both tabulated and graphically illustrated and it was found in all populations that a decrease in test temperature increased the It damage in the individual samples. From these graphs, the means of the damage occurring at the lowest temperature, -18°C, were calculated and plotted on a further graph. This showed that the damage at this temperature for the five months tested differed, and for five out of the six populations tested the least injury occurred in midwinter, i.e. in January, the exception being Wyre Forest, which showed least injury in November 1977. The other populations showed more resistance to cold in January 1978 and from then on all the populations without exception showed a gradual dehardening, i.e. a reduction of hardiness towards a peak of least resistance in July 1978. These results confirmed that, as in the case of other trees in which this phenomenon has been studied, the yew tree shows a periodic hardening of its leaves which coincides with the seasonal reduction in temperatures.

To get an indication of the between-population variation in freezing temperature, which causes damage to the leaves, a constant Index of Injury was identified, and the temperature that caused that amount of damage to individual leaf samples was interpolated from the graphs. The Index of Injury chosen for this analysis was It = 2.5, as at this value all population samples from all months could be compared, with the lowest It found at the lowest test temperature. The interpolated temperatures were thus called the killing temperature for the particular sample. The killing temperatures for each population were then compared with the killing temperatures for the other populations in each particular month. This was achieved by employing the analysis of variance and F test, which showed that there were significant differences between populations for four out of the five months tested, namely November 1977, January 1978, March 1978 and May 1978.

The working hypotheses further suggested that this variation would show the more northerly populations as having a higher resistance to winter temperatures than their more southerly counterparts, and indeed that the populations will show a gradual increase of resistance from the south to the north in a clinal fashion in each of the test months. This was tested for each month by comparing the population means, using the Duncan's multirange test. The results from this test showed that for November 1977 the hardiest leaf samples were found to originate in the south and the midlands, i.e. in Butser Hill from Sussex, and in Wyre Forest from Worcestershire, with killing temperature means of -10.52°C and -10.98°C respectively. The leaf samples from Yew Barrow in Cumbria, and Overton Hall in Derbyshire, were significantly different from these two populations, having a lower resistance to the cold, there mean killing temperatures being -6.52°C and -7.24°C respectively. The two northeastern populations, namely Guisborough and Brantingham, were significantly different from each other, with the former being intermediate between the four populations mentioned above, with a variable range of killing temperatures of its leaf samples (mean, -8.80°C) which makes it insignificantly different from both sets of populations. Brantingham is significantly different from all other populations, having the least resistance to freezing temperatures in this month, with a mean killing temperature of -1.56°C. It can therefore be concluded that the reversal of the working hypothesis seems to be the case in this test month, with the two most southerly populations having the highest resistance to freezing. It is also of interest to note that Brantingham shows extremely low resistance to freezing temperatures; indeed it could be suggested that this population is in danger of frost damage. It should also be pointed out that the other northeastern population, namely Guisborough, is much hardier than Brantingham, suggesting that it is fitter in this month, in the respect of cold hardiness, than its 'neighbour'.

In January 1978, the analysis shows that the picture has changed, with Wÿre Forest being the least resistant to cold, and Overton Hall and Butser Hill being the most resistant, the range of mean killing temperatures falling between -8.44°C for Wyre Forest to -13.44°C for Butser Hill, with the other three populations being intermediate between these means. It is interesting to note that the most southerly population, namely Butser Hill, is still amongst the most hardy of all the populations, and that Brantingham now has comparable resistance to any of the other populations in the sample set.

In March 1978, all populations start to deharden from their maximum resistance in January, the notable exception being Wyre Forest, its maximum resistance being in November. However, it does deharden in the same manner as the other populations in this month. Significant differences of killing temperature have again been demonstrated for March 1978, but the order of the populations has again changed. In this case, the two populations with the least resistance are the two northeastern populations, Brantingham and Guisborough having mean killing temperatures of -1.90°C and -2.40°C respectively; and Overton Hall shows most resistance, with a mean killing temperature of -9.64°C. Note should be made here of the position of Butser Hill, as it is no longer amongst the most resistant of populations; instead, it shows large variability, being intermediate between the northeastern sample populations and those at Yew Barrow and Wyre Forest, which have mean killing temperatures of -7.32°C and-7.76°C respectively. This suggests that the dehardening process for this population is variable i.e. while some leaves have lost a considerable amount of their hardiness, others still retain a large measure of it. It can further be suggested that the rate of hardening in the Brantingham population was extremely rapid in comparison with the other sample populations between the months of November and January; it can be seen from the results of the month of March that the dehardening process was as swift, and that in this month as in November it can be suggested that this population is in danger of frost damage. However, in this month it is not alone (as it was in November), as its regional 'neighbour' Guisborough, has a comparable low resistance and therefore must also face the same danger.

The results from May 1978 show a very small band of variation between the six populations, with four continuing the dehardening process and being insignificantly different from each other, namely Overton Hall, Butser Hill, Yew Barrow, and Wyre Forest, all of which lie within the mean killing temperature range of 1.86°C to -2.90°C. Notably, the two northeastern populations show some strange behaviour, being significantly different from the other populations by being relatively more resistant, seemingly increasing their resistance to freezing temperatures from March to May. This feature cannot be logically explained, as the environmental controls on hardening and dehardening could never have forecast this result. However, the July results show that these two populations have fallen into line with the other populations by mid-summer, when the dehardening process for all populations is complete, with all being insignificantly different to each other. The mean killing temperature range for July is from -1.72°C to -3.14°C.

In summary therefore it can be said that all populations show seasonal hardening and dehardening with the exceptions of Wyre Forest from November to January, and Brantingham and Guisborough from March to May. The working hypothesis seems to be rejected on both counts. First, in none of the months that show significant differences between the populations can it be argued that there is a gradual north-to-south trend; therefore the pattern of variation cannot be said to be clinal, at least in any obvious and maintained sense, and it must be concluded that there is a partially random pattern operating, and even though significantly different groups can be determined within each month. The populations at Yew Barrow and Overton Hall are the only ones that behave consistently in the sense that they are placed within the same groups throughout the test period (Fig 8.9). Secondly, it cannot be said that the more northern populations are hardier than their southern counterparts. Indeed, in November and January, Butser Hill, the most southerly population, is found to be more hardy than its more northerly counterparts. The positions of Brantingham in November, and Brantingham and Guisborough in March, suggest that they may both be in danger of frost damage, at the beginning of winter in the case of Brantingham, and at the end of winter in the case of both populations. This supposition is further examined below.

In order to get an indication as to the minimum regional temperatures for particular months and to compare them with the killing temperatures as defined above, temperature means were taken from selected climatological stations as meteorlogical Averages of temperature for the United Kingdom, 1941-70 . The relative positions of the stations used with respect to the populations sampled are shown in Fig 8.11. In the case of Butser Hill, the mean of three stations was taken, i.e. Leckford, Southsea, and Bognor Regis; for Wyre Forest, two means were taken, Oaken and Birmingham; for Overton Hall, Belper and Buxton; for Yew Barrow, Ambleside and Morecambe; for Brantingham, Kingston upon Hull and Cleethorpes; and for Guisborough, Redcar. These stations were selected on the basis of their being the nearest stations to the sampled populations within each region.

The average monthly minimum temperature and the absolute monthly minimum temperature were extrapolated from the meteorological office data for the above mentioned stations for each of the test months, i.e. November, January, March, May, and July. These data are shown in Table 8.18 to 8.22, along with the means for the climate stations, which are used as a comparison with the killing temperatures. Table 8.23 shows these results, along with the mean killing temperatures, as extrapolated from Tables 8.7 to 8.11.

Butser Hill. In November the average killing temperature (AKT) was found to be -10.52°C, in the same month the average monthly minimum temperature (AMMT) is -1.13°C and the extreme monthly minimum temperature (EMMT) is -3.70°C. In January the AKT was -13.44°C while the AMMT is -4.93°C and the EMMT is -12.03°C. In March the AKT was found to be -4.68°C with the AMMT being -2.50°C and the EMMT being -6.47°C. In May the AKT was -2.28°C the AMMT is +2.73°C and the EMMT is -0.73°C. Finally, in July the AKT was -2.50°C the AMMT is +8.60°C and the EMMT is +6.10°C. It will be noticed that in each case the AKT is lower than the AMMT, thus suggesting that the population is cold hardy throughout the season and is in no danger from

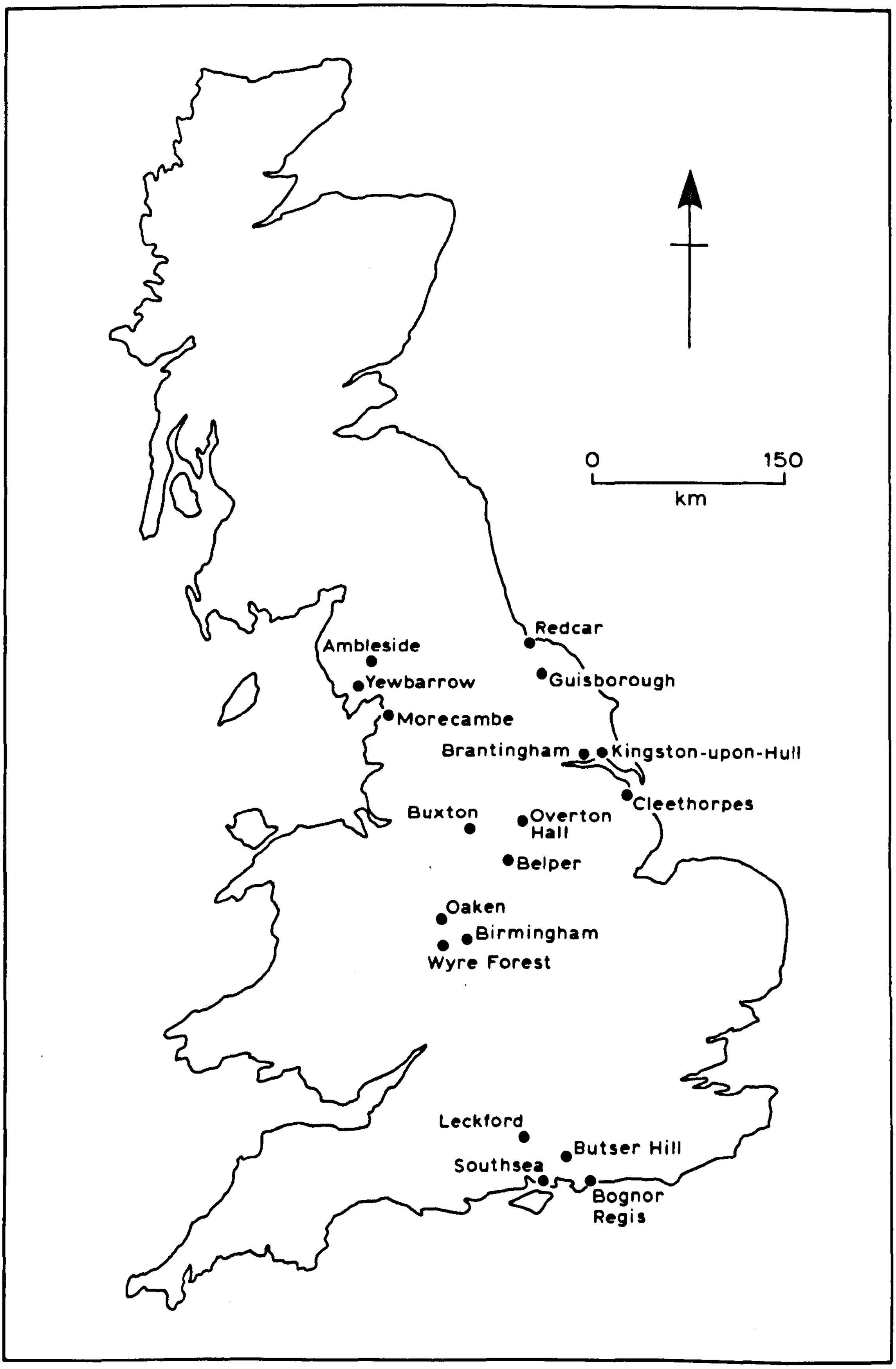


Fig 8.11. The climatological stations near to the sampled populations.

(from the meteorological office publication, 1971).

Table 8.18. The average monthly minimum and absolute monthly minimum temperature of the selected climate stations for November.

Climate Station	Average Monthly minimum temperature	Absolute Monthly minimum temperature	Collective Mean for region	
Bognor Regis	-0.8	-3.9		
Southsea	0.2	-2.2		
Leckford	-2.8	-5.0	-1·13	-3·70
Oaken	-3.5	-6.7		
Birmingham	-1.1	-4.4	-2.3	-5.55
Buxton	-3.7	-7.8		
Belper	-3.6	-8.3	-3.65	-8.05
Ambleside	-4.3	-8.3		
Morecambe	-1.2	-4.4	-2.75	-6.35
Redcar	-1.7	-5.6	-1.7	-5.6
Kingston upon Hull	-1.5	-4.4		
Cleethorpes	-1.5	-5.6	-1.5	-5.0

Table 8.19. The average monthly minimum and absolute monthly minimum of the selected climate stations for January.

Climate Station	Average Monthly minimum temperature	Absolute Monthly minimum temperature	Collective Mean for region	
Bognor Regis	-4.4	-11.1		
Southsea	-3.7	-11.1		
Leckford	-6.7	-13.9	-4.93	-12.03
Oaken	-7.8	-17.8		
Birmingham	-5.0	-10.6	-6.4	-14.2
Buxton	-8.2	-14.4		
Belper	-7.4	-16.7	-7.8	-15.55
Ambleside	-8.1	-15.6		
Morecambe	-5.1	-13.3	-6.6	-14.45
Redcar	-5.1	-15.0	-5.1	-15.0
Kingston upon Hull	-4.4	-11.1		
Cleethorpes	-4.2	-9.4	-4.3	-10.25

Table 8.20. **The average monthly minimum and absolute monthly minimum of the selected climate stations for March.**

Climate Station	Average Monthly minimum temperature	Absolute Monthly minimum temperature	Collective Mean for region	
Bognor Regis	-2.0	-6.1		
Southsea	-1.5	-5.0		
Leckford	-4.0	-8.3	-2.5	-6.47
Oaken	-5.0	-13.9		
Birmingham	-2.7	-7.4	-3.85	-10.65
Buxton	-5.8	-16.7		
Belder	-5.1	-13.3	-5.45	-15.0
Ambleside	-5.5	-14.4		
Morecambe	-2.4	-7.8	-3.95	-11.10
Redcar	-3.2	-11.1	-3.2	-11.1
Kingston upon Hull	-2.8	-10.0		
Cleethorpes	-2.9	-10.0	-2.85	-10.00

Table 8.21. The average monthly minimum and absolute minimum temperature of the selected climate stations for May.

Climate Station	Average Monthly minimum temperature	Absolute Monthly minimum temperature	Collective Mean for review	
Bognor Regis	3.1	-0.6		
Southsea	4.1	0.6		
Leckford	1.0	-2.2	2.73	-0.73
Oaken	0.2	-3.9		
Birmingham	2.3	-1.1	1.25	-2.5
Buxton	-0.4	-4.4		
Belder	-0.1	-5.0	-0.25	-4.7
Ambleside	-0.4	-2.8		
Morecambe	2.7	0.0	1.15	-1.4
Redcar	1.8	-1.1	1.8	-1.1
Kingston upon Hull	1.8	-1.7		
Cleethorpes	2.5	-0.6	2.15	-1.15

Table 8.22. The average monthly minimum and absolute monthly minimum of the selected climate stations for July.

Climate station	Average Monthly minimum temperature	Absolute Monthly minimum temperature	Collective Mean for region	
Bognor Regis	9.0	6.7		
Southsea	10.3	8.3		
Leckford	6.5	3.3	8.6	6.1
Oaken	5.8	2.8		
Birmingham	8.2	5.9	7.0	4.35
Buxton	5.9	2.2		
Belper	5.6	2.8	5.75	2.5
Ambleside	5.1	2.2		
Morecambe	8.8	4.4	6.95	3.3
Redcar	7.6	4.4	7.6	4.4
Kingston upon Hull	7.7	4.4		
Cleethorpes	7.9	6.1	7.8	5.25

Table 8.23. The collective regional average monthly and absolute monthly temperatures and the average killing temperature for the test months.

Population	Test months	Average population killing temperature	Regional average monthly minimum temperature	Regional extreme monthly minimum temperature
Butser Hill	November	-10.52	-1.13	-3.70
	January	-13.44	-4.93	-12.03
	March	- 4.68	-2.5	- 6.47
	May	- 2.28	2.73	- 0.73
	July	- 2.50	8.60	6.10
Wyre Forest	November	-10.98	-2.30	-5.55
	January	- 8.44	-6.40	-14.20
	March	- 7.76	-3.85	-10.65
	May	- 2.94	1.25	- 2.50
	July	- 2.24	7.00	4.35
Overton Hall	November	- 7.24	-3.65	- 8.05
	January	-13.36	-7.80	-15.55
	March	- 9.64	-5.45	-15.00
	May	- 1.86	-0.25	- 4.70
	July	- 3.14	5.75	2.50

Table 8.23 (Cont). The collective regional average monthly and absolute monthly temperatures and the average killing temperature for the test months.

Population	Test months	Average population killing temperature	Regional average monthly minimum temperature	Regional extreme monthly minimum temperature
Yew Barrow	November	-6.52	-2.75	-6.35
	January	-10.34	-6.60	-14.45
	March	- 7.32	-3.95	-11.10
	May	- 2.36	1.15	- 1.40
	July	- 1.72	6.95	3.30
Brantingham	November	- 1.56	-1.50	- 5.0
	January	-11.00	-4.30	-10.25
	March	-1. 90	-2.85	-10.00
	May	- 4.38	2.15	- 1.15
	July	- 2.10	7.80	5.25
Guisborough	November	- 8.80	-1.70	- 5.60
	January	- 9.42	-5.10	-15.00
	March	- 2.40	-3.20	-11.10
	May	- 5.62	1.80	- 1.10
	July	- 3.04	7.60	4.40

frost damage. However, when comparing the AKT with EMMT it will be noticed that in March the AKT is higher than the EMMT, although in all the other months the contrary is true. This could suggest two conclusions, either that in an extreme climatological situation the leaves in this population will be damaged by spring frost, or that in an extremely cold March the leaves will adapt to the extremes and that in the year being tested the temperatures were not as extreme as they could be.

Wyre Forest. For this population, in November the AKT was -10.98°C while the AMMT was -2.30°C and the EMMT was -5.55°C. In January, the AKT was -8.44°C, and AMMT was -6.40°C and the EMMT was -14.20°C. In March, the AKT was -7.76°C the AMMT was -3.85°C and the EMMT was -10.65°C. In May, the AKT was -2.94°C, the AMMT was +1.25°C and the EMMT was -2.50°C. Finally, in July, the AKT was -2.24°C the AMMT was +7.00°C and the EMMT was +4.35°C. The same conclusions can be drawn from these results as in the case of Butser Hill, i.e. that in each case the AKT is lower than the AMMT, thus suggesting that the leaves will survive average temperatures throughout the season. However, in January and March the EMMT is lower than the AKT.

Overton Hall. In November, for this population, the AKT was -7.24°C the AMMT was -3.65°C and the EMMT was -8.05°C. In January, the AKT was -13.36°C, the AMMT was -7.80°C and the EMMT was -15.55°C. In March, the AKT was -9.64°C, the AMMT was -5.45°C and the EMMT was -15.00°C. In May, the AKT was -1.86°C, the AMMT was -0.25°C and the EMMT was -4.70°C. Finally, for July, the AKT was -3.14°C, the AMMT was +5.75°C and the EMMT was +2.50°C. In the case of this population, it can be seen again that in each test month the AKT is lower than the AMMT, and that for the months November, January and March the EMMT is lower than the AKT.

Yew Barrow. In November, the AKT was -6.52°C, the AMMT was -2.75°C and the EMMT was -6.35°C. In January, the AKT was -10.34°C, the AMMT was -6.60°C and the EMMT was -14.45°C. In March, the AKT was -7.32°C, the AMMT was -3.95°C and the EMMT was -11.10°C. In May, the AKT was -2.36°C, the AMMT was +1.15°C and the EMMT was -1.40°C. In July, the AKT was -1.72°C, the AMMT was +6.95°C and the EMMT was +3.30°C. In this population, again, all the AKT measures are lower than the AMMT values, while in January and March the EMMT values are lower than the AKT.

Brantingham. In November, the AKT was -1.56°C, the AMMT was -1.50°C and the EMMT was -5.00°C. In January, the AKT was -11.00°C, the AMMT was -4.30°C and the EMMT was -10.25°C. In March, the AKT was -1.90°C, the AMMT was -2.85°C and the EMMT was -10.00°C. In May, the AKT was -4.38°C, the AMMT was +2.15°C and the EMMT was -1.15°C. In July, the AKT was -2.10°C, the AMMT was +7.80°C and the EMMT was +5.25°C. In this population, for the first time it can be seen that for one month, that of March, the AMMT is lower than the AKT, suggesting that the leaves are in danger of frost damage at this time of the year. Also it can be seen that for the months of November and March, the EMMT is lower than the AKT.

Guisborough. In November, the AKT was -8.80°C, the AMMT was -1.70°C and the EMMT was -5.60°C. In January, the AKT was -9.42°C, the AMMT was -5.10°C and the EMMT was -15.00°C. In March, the AKT was -2.40°C, the AMMT was -3.20°C and the EMMT was -11.10°C. In May, the AKT was -5.62°C, the AMMT was +1.80°C and the EMMT was -1.10°C. In July, the AKT was -3.04°C, the AMMT was +7.60°C and the EMMT was +4.40°C. As in Brantingham, this population is found to have a lower AMMT for the month of March than its AKT, suggesting again a danger of frost damage. Also in January and March, the EMMT is lower than the AKT.

From these results, it can firstly be said that in all but two populations, i.e. Brantingham and Guisborough, all the AKT's are lower than the AMMT's, therefore suggesting that in the general temperature conditions of the respective regions the yew leaf is capable of withstanding cold conditions throughout the year. This bears out the conclusions drawn from the last section. It was also suggested in the last section that

Brantingham might be in danger of frost damage in both November and March; however, this is not shown clearly to be the case for November, as it can be seen that the AKT is 0.06°C lower than the AMMT. In this case, therefore, it can be concluded that the leaves from this population can withstand the average minimum regional temperatures without damage, although the AKT is perilously close to the AMMT. The March values, however, show that there is definite danger of frost damage for the leaves in this region as the AMMT is approximately one degree lower than the AKT, being -2.85°C and -1.90°C respectively. It was also suggested in the last section that in the case of the Guisborough population the leaves would be in danger of frost damage in March. This is found to be the case, as the AMMT is lower than the AKT for this month, being -3.20°C and -2.40°C respectively. These temperatures suggest that these two north-eastern populations may very well be in danger of frost damage in March, and this could help to explain why the yew is relatively rare in this region.

It has also been noted that no population escapes the danger of frost damage when comparing the AKT with the EMMT. To test whether an extremely cold winter will in fact affect all the populations as suggested by these figures a controlled experiment should be undertaken artificially, hardening the leaves before attempting the cold hardiness experiment, or indeed taking advantage of an unusually cold winter. This should help in the understanding of the yew leaf in extreme temperature conditions, but all that can be said at the moment is that there might be a danger of frost damage to all the populations in severe temperature conditions.

Finally, it should be pointed out that when the leaf is completely dehardened i.e. in July, the leaf can still withstand below freezing temperatures as shown in Table 8.23. The AKT for Butser Hill is -2.50°C, for Wyre Forest it is -2.24°C, for Overton Hall -3.14°C, for Yew Barrow -1.72°C, for Brantingham -2.10°C, and for Guisborough -3.04°C.

CHAPTER 9.

Conclusions.

My main interest in biogeography has been the study and understanding of variation in organisms in general, and the study of intraspecific variation in particular; I also wanted to apply this interest to a native tree species in the British Isles. My attention was drawn to the yew tree (Taxus baccata) for two reasons. First, it had what seemed to be an unusual 'probable native distribution' in Britain, as mapped by Perring and Walters (1962), with a broad arc from the South Downs towards the northwest of England; and secondly, it became increasingly clear, as I searched the literature, that there was no published information on intraspecific variation within this species in this country. Moreover, I eventually discovered that surprisingly little scientifically-based work had been undertaken at all on this, one of our three native conifers. This dissertation marks the beginning of an attempt to redress the balance in our lack of knowledge.

Initially, I chose to compare characteristics of native yew populations from various parts of the country in order to see if within-species variation existed. As no work along these lines had ever been attempted on the yew tree in Britain previously, the study areas were selected mainly for reasons of practicality. I decided that due to extensive travelling involved in the research programme, it would be more practical to restrict my work to English sites, and not go further afield. But before entering into the field programme proper, it was clearly necessary to identify any similar work which had been undertaken in other parts of the species range outside of Britain. I therefore went to the European literature. Only one examination of intraspecific variation in the yew was found, this looking at the anatomical variation of the leaf of the species, in the Caucasus and Crimea, by Kulikov & Ruguzov (1973). It is clear, accordingly, that the work presented in this dissertation is not only an advance in our knowledge of the characteristics of this species in this country but further, it is a new and extended approach to the study of variation in *Taxus baccata* in general, which has future applications throughout its entire range. The study of intraspecific variation is of course an immense discipline, and the amount of information that can be collected in a time-restricted programme clearly can only represent a beginning in the overall understanding of problems raised. In view of this, it is hoped that my work will mark the foundation of an ongoing project to understand much more about this fascinating species.

In published research relating to other tree species, some workers have examined patterns of variation in the field, while others have identified genotypic variation by collecting seeds from different seed sources and growing them in a common garden; still others have attempted to use both techniques, to examining both the genotypic and plastic variation within a species. At the outset of this project, the intention was to employ both techniques. But although there were no methodological problems arising from the use of the first technique, it was discovered that a common garden experiment was impossible to accomplish within the time available, due to the long germination period of the yew seed. However, it was quickly determined that a preliminary investigation of seed source variation in respect of seed weight, germination percentage, and seedling vigour was possible instead. Moreover, as the field and laboratory examination of between-region and between-population variation in the morphological characteristics of the adult yew was completed within the first year of the project, and the germination of seed was expected to take approximately one year, it was deemed appropriate to extend the work further so as to consider another aspect of possible variation, namely cold hardiness.

The examination of cold hardiness in the yew is particularly interesting in that it had previously been suggested that the tree's northern limit (in Britain and elsewhere) might be due to its intolerance to winter cold (Godwin, 1956); it becomes increasingly rare towards the northeast of England. Therefore a controlled experiment was undertaken on the yew leaf. It should be pointed out here that although the main direction of this part of the research programme was to investigate between-population differences in this phenomenon, it had never been established previously that the yew shows hardiness at all, in the same manner as suggested in other trees, so the most fundamental questions were also being investigated. In other words I sought to discover whether cold hardiness existed in the yew, and whether this phenomenon displayed periodicity, both in general terms and in terms of variation between populations.

Accordingly, the three pieces of work undertaken in this dissertation were; first the intraspecific variation of morphological characteristics; secondly seed source variation; and thirdly cold hardiness variation.

Intraspecific variation in morphological characteristics.

In this part of the research programme, thirteen variables were measured for each tree, as follows: the number of leaves on last season's shoot (NLY); the length of the same shoot (LYG); the angle of the leaf (AL); the length and breadth of the same leaf (LL and LB respectively); the length of the petiole (LP); the breadth of the transverse section of the leaf (DL); the number of buds on the same shoot (NBY); the length and breadth of the resting bud (BL and BB respectively); the height of the tree (HT); the circumference of the tree bole (DT); and the number of trunks per tree (NB). The populations chosen were: Ravensdale (Ra) and Overton Hall (Ov) in Derbyshire; Yew Barrow (Yb) and Scout Scar (Ss) in Cumbria; Brantingham (Br) and

Guisborough (Gu) in the northeast; and Butser Hill (Bu) and Chichester Road (Ch) in the south.

Using the multivariate technique called Principal Components Analysis, results from the study of variation in the morphological characteristics of adult yew trees, as described in Chapter 4, identified between-population variation, but no distinctive between-region variation could be seen. Initially, the analysis suggested that only the first four components of variation were statistically meaningful, and for convenience of discussion these components were given names based on the weightings of the original thirteen measured variables along each component. The given names were shoot vigour, leaf dimensions, tree dimensions, and leaf angle, respectively.

Along the shoot vigour axis, i.e. component I, the southern pure yew wood at Butser Hill showed the highest shoot vigour of any of the populations. This was also confirmed by analysis of the population mean coordinates, the placing of individual trees in a scatter diagram and in a further examination of the eight clusters identified by Ward's method (Chapter 5). However, when examining the individual tree scatter diagrams and the clusters, it was also noted that the separation of the populations along this component was not absolutely discrete, as some individuals were found to resemble individuals from other populations more closely than those in the same population. This was clearly seen to be the case in respect of the three northern regions in this analysis, i.e. Cumbria, Derbyshire, and the northeast of England. Therefore, the conclusion was reached that although shoot vigour variation did exist to some extent, especially when comparing the southern pure yew wood, Butser Hill, to the northern populations, the within-site variation of the latter groups were greater than the variation between-sites.

When studying the patterns of variation identified along the leaf dimension axis, component II, there seemed to be a north-south clinal trend for the population mean coordinates, with the northeastern populations having the highest value, followed by the Derbyshire populations, then the Cumbrian sites and finally the southern pure yew wood of Butser Hill, which had the lowest values. This conclusion was not clearly confirmed by the study of the scatter diagrams or the cluster analyses, as these indicated that two populations, namely Yew Barrow from Cumbria and Overton Hall from Derbyshire, were particularly variable for this characteristic; and therefore the regions themselves were not clearly defined in a statistical sense. Thus I have described the trend along this component as being a weak cline.

It was clear from the study of variation along the third component, that of tree dimensions, that in all three analyses there were no differences between regions; consequently and referring back to the component II data, it follows that high shoot vigour does not indicate the presence of taller trees, or trees with larger bole circumferences. This result may be confirmed by simple observation, as much of the growth vigour of the tree goes to produce a spreading habit (see frontispiece). But two populations seemed to be distinctive in general terms, in respect to the tree dimension study. First, Brantingham showed consistently low tree dimensions as compared to other populations; and the southern population of Chichester Road, had trees that were consistently larger than other populations.

Along the fourth and final component studied, it was found that the leaf angle tended to increase as the leaf length decreased; however, this component was considered to be of little importance to the overall study, as there was even less variation to be seen along it than could be found in component III. No clear between-region or between-population variation could be identified.

One may conclude from this study of between-region variation of morphological characteristics of Taxus baccata that there are no clear distinctions to be found along the four components studied. It can however be said that Butser Hill, the southern pure yew wood, shows a more consistently high shoot vigour than other populations, and that the northeastern populations of Brantingham and Guisborough and the southern population, Butser Hill, show consistently high and low values for leaf dimensions respectively although, when taking the remaining populations into account, the latter trend can only be described as a weak cline. Finally, there seems to be a tendency for larger tree dimensions in the south and lower dimensions in the northeast, as indicated by Chichester Road and Brantingham respectively.

Seed source variation: seed weight, germination percentage, seedling vigour.

As noted in Chapter 6, it is clear that there are no general rules which link these variables, as far as trees already studied are concerned. Thus it is not always the case that the heavier the seed, the higher the percentage of germination, or the greater the seedling vigour. These three variables were examined with this knowledge in mind, but with the main intention of discovering whether any between-region or between-population differences in the individual variables could be found. All the regions selected for the previous morphological study were represented; however, in this section of the research, one more region and population was included, namely Coughton Hall in the Midlands. Since my previous work had indicated at least the possibility of a south-north trend in certain characteristics (shoot vigour and leaf dimensions), it was thought that the inclusion of a population from the Midlands might provide a useful check for any possible similar trends in seed source variation.

In this part of the research programme, the variables were examined separately, by univariate analysis: the analysis of variance was employed to identify any significant differences between populations, and

Duncan's multirange test identified where any such differences lay.

For seed weight, it was determined that there were statistically-significant differences between populations, with the six populations forming two groups of three. Within each group there were further statistically-significant differences. Thus in a "heavier" group, Butser Hill had the heaviest seed weights and Yew Barrow had the lightest seed weights but Coughton Hall had a mixture of seeds, some of which were as light and others as heavy as in the other two populations. In the "lighter" group, a similar pattern occurred, with Warter having the heaviest seeds in the group and Overton Hall the lightest, and with Guisborough having seeds that were in part as light and as heavy as the two other populations. The conclusion drawn from these results was that there does indeed seem to be a clinal pattern from south to north, but that within the north there is no particularly distinctive pattern.

Although there was little in the literature on Taxus baccata that could be used for comparison with the work on seed weight presented in this dissertation, one interesting general but relevant comment may be made. It was found by Szczesny (1952) that 1000 -seed weight of yew seed collected in Poland ranged from 43 to 59 gm, whereas Detz & Kemperman (1968) have shown that similar weights of yew seed collected from Holland were 77 gm. Although only 180 seeds were weighed in this study, an extrapolation indicates that the 1000 -seed weight equivalent would be 56.5 gm. This result suggested that seed from Britain is intermediate in weight between the heavier seeds from Holland, and the somewhat lighter seeds from Poland.

In examining germination percentages, there was a surprising outcome, namely that the most southerly site (and that with the heaviest seed), Butser Hill, had the lowest percentage of germination of all populations. But it is clear overall that this variable does not display any national clinal trend. Means of germination percentages shows an order of, from highest to lowest, Yew Barrow, Warter, Coughton Hall, Overton

Hall, Guisborough, and Butser Hill. It is concluded that the pattern for this variable can only be described as being random.

The examination of seedling vigour was based on the dry weights of seedlings after two months of growth. In this, no statistically-distinct population groupings were found overall, although Coughton Hall and Overton Hall were heavier and significantly different in themselves from the lightest, namely Warter. However, the other three populations, Butser Hill, Yew Barrow, and Guisborough, whose seedling vigour was intermediate between these extremes, displayed no statistically-significant differences with the other three populations. It is suggested that the pattern of variation for this variable on a national scale can only be described as being geographically random.

Finally, I attempted to correlate the three variables, and concluded that there were no statistically-significant relationships between them.

Variation in cold hardiness.

As the existence and periodicity of cold hardiness had not been demonstrated in the yew before, the determination of these features in themselves were of importance to this section of the research; and it was of interest to see if there were regional differences in these phenomena in respect to the yew leaf. However, the main hypothesis being tested was that yew leaves would be more cold hardy in the north than in the south, since they would have to withstand harsher climates in northern regions.

This study was undertaken in experimentally-controlled conditions. By using the conductivity method outlined by Flint et al., (1967), damage in six populations at five preselected test temperatures (-2°C, -6°C, -10°C, -14°C, -18°C) and at five test months (November '77, January '78, March '78, May '78, and July '78) was identified. The six populations selected for the experiment were: Butser Hill, Sussex; Wyre Forest, Worcestershire; Yew Barrow, Cumbria; Overton Hall, Derbyshire; Brantingham and Guisborough, northeast England. An index of injury (It) was then calculated for each sample for each test temperature and for each test month, as specified in Chapter 8, and these indices were then plotted graphically: by interpolation, the temperature that caused an index of injury of 2.5 then was identified. These data were subsequently analysed by analysis of variance procedures, and Duncan's multirange test.

An initial result was that the yew leaf does indeed become cold hardy, and when studying the damage caused by the lowest test temperature, i.e. -18°C, the leaf also showed periodicity for the phenomenon. Secondly, the statistical tests showed that, in respect to resistance to cold, the grouping of populations varied from test month to test month.

In November 1977, Wyre Forest and Butser Hill, the most cold hardy populations in this test month, were significantly different to Overton Hall and Yew Barrow, with Guisborough being intermediate between these two groups; moreover Brantingham, the least cold hardy population in this month, was significantly different from all of these.

In January 1978, Butser Hill and Overton Hall, the most cold hardy populations in this test month were found to be significantly different to Wyre Forest, with Brantingham, Yew Barrow, and Guisborough being intermediate between these extremes.

In March 1978, Overton Hall, the most cold hardy population in this test month, was significantly different to Butser Hill, with Wyre Forest and Yew Barrow being intermediate between these two populations. In a second grouping, Overton Hall, Wyre Forest, and Yew Barrow were more cold hardy and significantly different to Guisborough and Brantingham, with Butser Hill being intermediate.

Of the two remaining test months May 1978 showed some significant differences between populations, whereas July 1978 did not. In May 1978, Guisborough and Brantingham were found to be more cold hardy and significantly different from the other four populations, namely, Butser Hill, Wyre Forest, Overton Hall, and Yew Barrow.

From these results, it was therefore concluded that in none of the statistically-significant test months can it be argued that there is a gradual south-north or north-south trend. This can be seen by looking at the order of the significant differences noted above for each test month. In November 1977, it was seen that the two most southerly sites, Wyre Forest and Butser Hill, were the most cold hardy, while Overton Hall, Derbyshire and Yew Barrow, Cumbria were less cold hardy. However, the two northeastern sites, Guisborough (the most northerly site of all), and Brantingham showed very different hardiness here, with Guisborough being intermediate between the two groups mentioned above and Brantingham being the least cold hardy of all. In January 1978, the populations had changed places in terms of their relative cold hardiness, with Butser Hill and Overton Hall being the most cold hardy, and Wyre Forest the least hardy, while Brantingham, Yew Barrow, and Guisborough were intermediate. In March 1978, Overton Hall is the most cold hardy of the tested populations, with Butser Hill being significantly less cold hardy, and Wyre Forest and Yew Barrow being intermediate between these two populations; the two northeastern populations, Guisborough and Brantingham are the least cold hardy in this test month. Finally, in May 1978, Guisborough and Brantingham are more cold hardy than the other four populations, with the latter populations showing no significant differences at all.

It can therefore be concluded that the pattern of variation within the test months cannot be said to be simply clinal in temporal terms, since the order of the populations varies from month to month. It is therefore suggested that a partially random pattern of cold hardiness is operating, even though significant groupings can be determined within each month. It was also concluded from these results that the northern populations were not hardier in general than their southern counterparts, especially in November and January. However, in May 1978, the northeastern populations were clearly more cold hardy than those elsewhere.

It should also be mentioned that two populations were found to be consistently within the same statistical group in each of the five test months, namely, Overton Hall and Yew Barrow, suggesting that these two populations are adapted to the cold to the same extent throughout the year.

In order to get an indication as to the survival potential of the various populations within the test months, a further study was completed which compared the average monthly mean temperatures (AMMT) and the absolute (extreme) monthly mean temperatures (EMMT) from selected climatological stations within each population, with the average killing temperatures (AKT) at index of injury 2.5. It was found that in all but two populations, i.e. Brantingham and Guisborough, the AKT's are lower than the AMMT's, suggesting that in the general temperature conditions of the respective regions the yew leaf is capable of withstanding cold conditions throughout the year. In the case of the two exceptions, it was determined that for November, Brantingham's AKT was only 0.06°C below the AMMT; and in March, both Brantingham and Guisborough seem to be in danger of frost damage, as their respective AKT's are both higher than the AMMT's. These results suggest that the northeastern populations may very well be in danger of frost damage at this period of the year, and this in itself might help to explain why yew trees are relatively rare in this region.

Finally, it is important to note that within the confines of this work it has been established that the highest shoot vigour, the heaviest seeds, and the most cold hardy leaves in midwinter can be found in the Butser Hill population, suggesting that this population, in the south of England, is perhaps better adapted to environmental conditions than are the trees that make up the northern sites.

Suggestions for the continuation of work on Taxus baccata L.

It should be emphasised that the work completed herein only scratches the surface of the study of variability, in respect of the yew tree. As some considerable variation within England was found with respect to morphological characteristics and for the preliminary seed source data, this might suggest that intraspecific variation throughout its range could be quite substantial.

It has previously been mentioned that this species has a wide geographic range, stretching from Britain, France, Germany and southern Scandinavia to the Carpathian Mountains, and southeast to Iran. The British distribution has been mapped by Perring & Walters (1962), although their interpretation has been challenged by R. Bunce (pers. comm.), who suggests that there are more populations to be found than are displayed therein. It is suggested that work on patterns of morphological variation of the yew should be expanded first in England. The initial task here would be to reanalyse the distribution points of natural yew stands in the country, and then by using one variable from each of the components in the analysis in this dissertation, for example, length of shoot, leaf length, height of tree and angle of leaf, a more comprehensive provenance test could be performed, taking in more populations from the south and the midlands. This would give a better overall impression of latitudinal trends in variation. It is also suggested that by using the same four variables this work should be expanded to become an international project, so giving an impression of trends in the latitudinal and longitudinal direction throughout its range; in this analysis, it is suggested that an altitudinal transect should also be included, as these three geographic parameters have been found to be important controls of variables in other tree species. The same should be attempted to seed weight data, but in respect of this it is further suggested that the length and breadth of the seed should be included as variables to be measured. Germination may be compared in a controlled experiment, using the same conditions as in this work for comparison.

From my experiment which compared the seedling vigour of the different seed sources some seedlings were saved. It is hoped that these will be planted out in a common garden on a long term basis so that variation can be examined under the same environmental conditions, in order to see if there are any genetic differences between individuals from the different regions of England studied.

Cold hardiness has been clearly identified in respect of the yew leaf in this work. It has been previously pointed out that in other woody species different organs can have different cold tolerance levels. So it is suggested that, by using the same populations as above, shoots, apical buds and other parts of the tree should be tested for this phenomenon using the same freezing techniques as herein to enable direct comparison with the leaf data. In a direct extension of the leaf cold hardiness study, it would be of further interest to look at the cold hardiness variation of the leaves in an altitudinal direction, possibly within one region, for example in Cumbria, to see whether trees at a higher elevation have a higher cold tolerance than those lower down. Finally, this work should be extended to include material throughout its range but to do this cooperation from other research centres would be needed as testing the naturally hardened material must be done swiftly; the standardisation of equipment would also be an additional problem to be resolved.

APPENDIX 1.

Raw data for the variation in morphological characteristics study.

Population: Butser Hill Collection date: 8. 4.77.

Individual No. 1.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	49	3.6	45	1.3	0.2	2.5	4.0	3	5.2	4.2			
East	28	3.9	71	2.2	0.25	2.6	5.5	2	5.4	4.2			
South	25	2.8	47	1.8	0.2	3.0	5.2	1	3.7	2.8			
West	33	3.8	90	1.5	0.2	2.5	4.2	1	6.3	3.7			
Mean	33.75	3.53	63.25	1.70	0.21	2.65	4.73	1.75	5.15	3.73	10.0	3.33	2

Individual No. 2.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	28	2.4	85	1.3	0.25	2.5	5.2	1	5.0	3.8			
East	42	4.3	45	1.4	0.2	3.0	4.5	6	7.0	4.6			
South	54	5.8	37	1.5	0.2	2.9	4.7	8	6.9	5.3			
West	32	2.7	67	1.1	0.2	2.5	4.2	0	5.2	4.0			
Mean	39.00	3.80	58.50	1.33	0.21	2.73	4.65	3.75	6.03	4.43	9.4	2.15	3

Butser Hill (Cont).

Individual No. 3.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	50	5.2	48	2.1	0.2	2.5	5.0	4	6.3	4.6			
East	43	5.1	51	2.0	0.25	3.2	5.1	3	6.0	4.7			
South	32	3.1	51	1.6	0.2	2.5	5.0	0	5.0	4.4			
West	47	6.1	86	2.0	0.2	3.3	4.5	3	6.5	4.5			
Mean	43.00	4.88	59.00	1.93	0.21	2.88	4.90	2.50	5.95	4.55	4.9	1.36	2

Individual No. 4.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	53	7.9	35	1.8	0.2	2.7	4.9	9	7.0	4.5			
East	56	7.7	46	1.6	0.2	2.6	4.1	11	7.2	4.6			
South	68	13.9	40	2.0	0.2	2.8	4.5	12	10.0	6.0			
West	70	11.2	22	1.8	0.2	2.5	4.4	14	8.4	5.6			
Mean	61.75	10.18	35.75	1.80	0.20	2.65	4.48	11.50	8.15	5.18	6.6	3.12	3

Butser Hill (Cont).

Individual No. 5.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	52	9.1	63	1.7	0.2	2.8	4.8	4	6.6	4.6			
East	39	5.1	40	2.6	0.25	3.9	5.5	3	5.5	4.5			
South	38	4.9	61	2.3	0.2	2.6	4.7	3	5.7	4.2			
West	29	3.0	70	2.0	0.2	2.5	4.8	2	5.5	4.0			
Mean	39.50	5.53	58.50	2.15	0.21	2.95	4.95	3.00	5.83	4.33	6.0	3.07	3

Individual No. 6.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	29	3.8	58	2.0	0.2	1.5	4.9	1	3.0	2.3			
East	40	4.4	46	2.3	0.2	3.0	4.8	4	6.5	4.1			
South	35	4.5	47	2.3	0.2	2.5	4.8	7	6.4	4.2			
West	21	3.4	37	2.0	0.25	2.6	5.0	1	5.1	3.3			
Mean	31.25	4.03	47.00	2.15	0.21	2.40	4.88	3.25	5.25	3.48	11.2	1.95	3

Butser Hill (Cont).

Individual No. 7.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	1.9	44	1.4	0.2	2.9	4.4	0	4.1	3.2			
East	29	3.9	42	2.1	0.25	3.3	5.5	1	5.6	3.1			
South	51	5.9	59	1.9	0.25	3.0	5.0	6	8.0	4.5			
West	47	11.2	32	2.2	0.25	3.4	5.2	4	11.0	5.6			
Mean	37.50	5.73	44.25	1.90	0.24	3.15	5.03	2.75	7.18	4.10	7.6	3.58	3

Individual No. 8.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	57	5.8	42	2.1	0.2	2.4	4.8	5	6.5	4.8			
East	36	3.1	52	1.7	0.2	2.4	4.7	2	5.5	3.9			
South	34	2.9	49	1.8	0.2	2.8	4.4	2	4.3	4.1			
West	60	5.1	55	2.1	0.2	2.3	4.9	6	6.0	4.8			
Mean	46.75	4.23	49.50	1.93	0.20	2.48	4.70	3.75	5.58	4.40	4.3	1.60	1

Butser Hill (Cont).

Individual No. 9.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	63	5.4	34	1.1	0.2	2.9	4.0	4	6.6	5.0			
East	54	4.4	29	1.2	0.2	2.8	4.0	6	6.0	4.4			
South	39	6.0	39	1.9	0.2	3.0	4.7	4	5.6	3.9			
West	67	7.7	71	1.4	0.2	3.0	4.4	7	7.5	4.8			
Mean	55.75	5.88	43.25	1.40	0.20	2.93	4.28	5.25	6.43	4.53	6.0	3.20	6

Individual No. 10.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	33	4.4	39	2.3	0.2	3.4	4.6	1	5.5	3.3			
East	25	2.6	35	1.6	0.2	2.7	4.5	1	4.4	3.7			
South	29	2.9	39	1.5	0.2	2.3	4.2	1	5.8	4.5			
West	28	3.0	54	1.8	0.2	3.6	4.3	0	5.8	3.4			
Mean	28.75	3.23	41.75	1.80	0.20	3.00	4.40	0.75	5.38	3.73	5.5	2.68	9

Butser Hill (Cont).

Individual No. 11.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	38	5.1	28	2.1	0.25	3.0	5.5	4	6.5	4.2			
East	52	6.2	41	1.6	0.2	3.1	4.9	2	7.6	4.7			
South	56	7.7	37	2.1	0.2	3.0	5.3	6	8.5	4.5			
West	37	3.2	18	1.8	0.2	3.1	4.8	3	6.1	4.2			
Mean	45.75	5.55	31.00	1.90	0.21	3.05	5.13	3.75	7.18	4.40	4.9	2.23	3

Individual No. 12.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	1.9	58	1.9	0.2	2.2	4.8	0	4.4	3.0			
East	38	3.9	47	1.9	0.2	3.5	4.8	5	6.4	4.5			
South	46	6.6	26	2.2	0.2	3.7	5.1	5	6.7	5.4			
West	58	7.7	43	2.2	0.2	3.4	4.5	8	7.0	6.3			
Mean	40.00	5.03	43.50	2.05	0.20	3.20	4.80	4.50	6.13	4.80	7.6	2.77	2

Butser Hill (Cont).

Individual No. 13.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	29	3.2	51	1.9	0.2	2.5	4.6	0	4.7	3.5			
East	52	5.6	50	1.9	0.2	2.9	4.4	4	5.6	4.2			
South	29	3.4	52	1.4	0.2	1.5	4.2	0	3.6	3.0			
West	36	4.3	50	1.9	0.2	2.4	4.7	2	4.8	3.3			
Mean	36.50	4.13	50.75	1.78	0.20	2.33	4.48	1.50	4.68	3.50	7.4	2.75	1

Individual No. 14.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	53	6.9	43	1.9	0.2	3.1	4.4	4	6.7	4.1			
East	34	2.9	60	1.1	0.15	2.0	3.6	1	3.8	2.9			
South	44	4.9	50	1.5	0.2	3.0	4.3	8	6.8	4.5			
West	28	3.1	71	1.4	0.2	2.5	4.1	1	4.5	3.4			
Mean	39.75	4.45	56.00	1.48	0.19	2.65	4.10	3.50	5.45	3.73	6.2	3.60	2

Butser Hill (Cont).

Individual No. 15.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	38	5.1	27	2.0	0.2	2.9	4.8	4	7.3	4.8			
East	27	3.4	38	1.7	0.2	2.6	4.6	1	5.7	4.7			
South	21	2.3	56	1.9	0.25	2.4	4.9	0	5.0	3.3			
West	16	1.8	42	1.8	0.2	3.0	4.5	0	4.4	3.3			
Mean	25.50	3.15	40.75	1.85	0.21	2.73	4.70	1.25	5.60	4.03	6.3	3.22	4

Individual No. 16.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	17	1.4	73	1.4	0.2	2.6	5.0	0	2.7	2.4			
East	20	2.3	42	1.7	0.2	2.0	4.8	1	4.2	3.0			
South	25	2.9	61	1.6	0.25	2.5	5.4	2	4.5	3.4			
West	19	2.6	58	1.6	0.3	2.7	6.0	2	3.4	2.9			
Mean	20.25	2.30	58.50	1.58	0.24	2.45	5.30	1.25	3.70	2.93	10.0	2.02	1

Butser Hill (Cont).

Individual No. 17.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	1.8	70	1.5	0.2	2.8	4.4	3	4.9	3.3			
East	34	3.0	40	1.7	0.2	3.4	4.5	7	5.8	4.5			
South	13	1.4	52	1.6	0.2	2.8	5.0	0	3.0	2.7			
West	26	3.3	63	1.8	0.2	3.1	4.5	1	4.0	3.1			
Mean	23.25	2.38	56.25	1.65	0.20	3.03	4.60	2.75	4.43	3.40	8.5	3.86	6

Individual No. 18.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	70	13.0	55	2.2	0.25	3.2	5.5	5	9.5	5.2			
East	42	7.2	29	2.6	0.25	3.2	5.4	5	7.3	4.7			
South	32	3.2	66	2.1	0.25	2.8	5.3	1	5.0	3.6			
West	11	0.8	26	0.7	0.2	2.0	3.8	0	2.0	1.8			
Mean	38.75	6.05	44.00	1.90	0.24	2.80	5.00	2.75	5.95	3.83	9.8	2.99	2

Butser Hill (Cont).

Individual No. 19.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	37	4.8	58	1.9	0.25	4.0	4.6	4	6.2	4.2			
East	36	5.0	46	2.5	0.3	3.2	5.5	1	5.0	3.4			
South	54	7.4	30	2.2	0.25	3.4	5.4	5	6.3	4.4			
West													
Mean	42.33	5.73	44.67	2.20	0.27	3.53	5.17	3.33	5.83	4.00	11.5	3.31	5

Individual No. 20.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	43	3.0	57	1.1	0.2	2.7	4.0	4	4.8	4.3			
East	17	1.6	48	1.1	0.2	2.1	4.5	0	4.0	2.8			
South	50	4.6	33	1.3	0.2	2.5	4.3	4	6.4	4.1			
West	15	1.3	34	0.9	0.2	2.0	4.1	0	3.3	1.6			
Mean	31.25	2.63	43.00	1.10	0.20	2.33	4.23	2.00	4.63	3.20	6.4	0.69	1

Butser Hill (Cont).

Individual No. 21.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	30	3.5	60	1.9	0.25	3.0	5.3	2	5.5	4.2			
East	39	4.9	45	1.9	0.25	3.0	5.1	1	6.8	4.4			
South	37	4.1	67	1.8	0.2	2.3	5.3	1	6.5	4.8			
West	31	3.5	36	1.9	0.25	2.6	5.1	0	4.3	3.4			
Mean	34.25	4.00	52.00	1.88	0.24	2.73	5.20	1.00	5.78	4.20	5.2	0.64	1

Individual No. 22.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	28	3.1	49	1.3	0.2	1.9	4.3	0	3.4	3.7			
East	59	8.4	50	1.9	0.2	2.5	4.6	6	7.4	4.6			
South	33	4.3	61	1.5	0.2	2.0	4.6	2	4.4	3.2			
West	28	4.0	40	1.8	0.25	2.4	5.0	1	5.3	3.4			
Mean	37.00	4.95	50.00	1.63	0.21	2.20	4.63	2.25	5.13	3.73	4.8	0.97	3

Butser Hill (Cont).

Individual No. 23.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	29	3.3	56	1.6	0.2	2.2	4.8	0	3.9	3.0			
East	48	4.6	51	1.3	0.2	2.0	4.8	4	4.2	3.0			
South	66	9.3	46	2.1	0.25	2.3	5.5	6	5.5	3.8			
West	34	4.6	52	1.4	0.2	2.1	4.6	0	5.1	3.6			
Mean	44.25	5.45	51.25	1.60	0.21	2.15	4.93	2.50	4.68	3.35	6.8	2.71	5

Individual No. 24.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	17	1.6	48	1.5	0.2	1.8	4.5	0	3.0	1.6			
East	55	7.5	47	1.8	0.25	2.1	5.0	3	8.4	4.3			
South	54	6.7	54	1.8	0.2	2.0	4.8	0	5.5	3.8			
West	28	2.7	28	1.8	0.2	2.5	4.8	1	5.3	3.8			
Mean	38.50	4.63	44.25	1.73	0.21	2.10	4.78	1.00	5.55	3.38	6.4	0.59	1

Butser Hill (Cont).

Individual No. 25.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	2.6	55	1.8	0.2	2.8	4.4	1	6.0	3.7			
East	54	6.2	23	2.0	0.2	3.0	4.3	5	6.0	4.1			
South	43	5.0	33	2.1	0.2	3.4	4.8	3	6.5	4.5			
West	35	3.9	53	1.7	0.2	2.6	4.4	1	5.8	3.6			
Mean	38.75	4.43	41.00	1.90	0.20	2.95	4.48	2.50	6.08	3.98	10.5	3.05	3

Individual No. 26.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	41	4.9	49	1.6	0.2	2.2	4.0	0	5.0	3.9			
East	46	5.0	42	1.8	0.2	2.0	4.4	2	6.0	4.3			
South	34	3.3	37	1.4	0.2	1.5	4.1	2	5.4	3.7			
West	35	3.4	59	1.2	0.2	2.5	3.9	1	5.2	3.8			
Mean	39.00	4.15	46.75	1.50	0.20	2.05	4.10	1.25	5.40	3.93	7.5	2.15	10

Butser Hill (Cont).

Individual No. 27.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	27	3.8	59	2.1	0.25	2.5	4.7	0	4.0	3.1			
East	30	4.3	48	1.6	0.2	1.6	4.3	0	5.6	4.2			
South	38	5.7	60	1.7	0.2	3.0	4.5	1	7.0	4.2			
West	29	4.2	61	1.9	0.2	1.9	4.9	1	5.2	3.0			
Mean	31.00	4.50	57.00	1.83	0.21	2.25	4.60	0.50	5.45	3.63	7.5	3.35	12

Individual No. 28.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	45	6.2	45	1.7	0.2	2.1	4.1	0	4.9	4.0			
East	51	5.9	51	1.7	0.25	2.0	4.7	5	6.0	4.5			
South	26	3.2	61	1.5	0.2	1.7	4.0	2	5.3	3.9			
West	21	2.6	50	1.9	0.2	2.0	3.5	0	3.5	2.9			
Mean	35.75	4.48	51.75	1.70	0.21	1.95	4.08	1.75	4.93	3.83	7.5	3.35	14

Butser Hill (Cont).

Individual No. 29.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	35	5.3	55	1.5	0.2	2.4	4.1	1	6.4	3.5			
East	53	6.9	43	1.9	0.2	2.7	3.8	3	7.4	4.6			
South	35	4.1	60	1.4	0.2	2.0	4.2	0	6.0	3.7			
West	15	2.3	49	1.8	0.2	2.4	4.7	0	1.2	2.4			
Mean	34.50	4.65	51.75	1.65	0.20	2.38	4.20	1.00	5.25	3.55	4.7	0.65	3

Individual No. 30.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	45	8.3	55	1.8	0.2	2.8	4.1	6	7.3	4.3			
East	21	2.7	37	1.6	0.2	2.9	4.2	0	6.0	3.4			
South	23	2.4	55	1.5	0.25	2.2	4.9	0	5.0	3.1			
West	94	17.0	45	2.3	0.25	2.5	5.5	9	5.2	3.7			
Mean	45.75	7.60	48.00	1.80	0.23	2.60	4.68	3.75	5.88	3.63	6.0	0.81	2

Population: Chichester Road   Collection date: 21.4.77.

Individual No. 1.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	31	4.0	57	2.0	0.2	1.9	5.1	0	4.6	4.1			
East	28	3.9	72	1.5	0.2	2.0	5.0	1	5.5	4.5			
South	22	2.7	50	2.1	0.25	1.9	5.3	1	3.5	2.3			
West	28	3.7	55	2.0	0.3	2.5	5.8	3	5.3	4.5			
Mean	27.25	3.58	58.50	1.90	0.24	2.08	5.30	1.25	4.73	3.85	14.8	1.61	1

Individual No. 2.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	31	4.7	66	1.9	0.3	2.0	5.8	1	6.3	4.8			
East	35	5.5	65	1.8	0.3	1.8	5.8	0	5.1	3.7			
South	27	4.3	45	2.0	0.25	1.9	5.4	0	3.0	2.4			
West	24	3.2	51	1.7	0.2	2.0	5.1	0	3.3	1.9			
Mean	29.25	4.43	56.75	1.85	0.26	1.93	5.53	0.25	4.43	3.20	14.2	1.89	1

Chichester Road (Cont).

Individual No. 3.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	49	7.6	46	2.7	0.3	2.9	5.9	0	4.3	3.0			
East	23	3.2	57	2.3	0.3	2.6	6.5	0	3.3	3.2			
South	48	6.9	35	2.3	0.25	2.9	5.9	2	5.8	4.7			
West	45	6.7	44	3.0	0.3	3.2	6.6	1	5.5	3.3			
Mean	41.25	6.10	45.50	2.58	0.29	2.90	6.23	0.75	4.73	3.55	20.0	3.35	1

Individual No. 4.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	2.4	52	1.6	0.25	1.9	5.0	0	2.4	2.0			
East	13	2.0	67	1.8	0.3	2.0	5.5	0	4.5	2.9			
South	22	2.7	62	1.6	0.3	2.1	5.7	0	4.0	2.7			
West	17	1.7	92	2.0	0.2	1.6	4.2	0	2.1	1.9			
Mean	17.50	2.20	68.25	1.75	0.26	1.90	5.10	0.00	3.25	2.38	15.4	1.87	1

Chichester Road (Cont).

Individual No. 5.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	2.9	58	2.1	0.2	2.0	5.1	0	DEAD				
East	21	4.0	72	2.6	0.3	2.4	6.1	0	DEAD				
South	34	6.1	57	2.2	0.25	1.8	5.3	2	6.4	3.4			
West	20	1.9	62	1.4	0.2	2.2	6.3	0	2.5	1.7			
Mean	24.50	3.73	62.25	2.08	0.24	2.10	5.70	0.50	4.45	2.55	10.2	2.23	1

Individual No. 6.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	22	2.5	49	2.2	0.2	2.5	4.6	1	4.2	3.2			
East	15	1.9	37	2.7	0.25	2.6	5.4	2	2.5	1.5			
South	13	1.6	31	2.2	0.2	2.5	4.5	0	2.3	1.6			
West	30	3.9	30	2.7	0.25	2.8	5.3	0	3.9	2.7			
Mean	20.00	2.48	36.75	2.45	0.23	2.60	4.95	0.75	3.23	2.25	19.0	1.93	1

Chichester Road (Cont).

Individual No. 7.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	43	7.5	46	2.0	0.25	3.2	5.3	4	4.3	4.5			
East	26	4.2	62	1.9	0.3	1.5	6.0	0	5.1	4.0			
South	23	3.4	63	1.7	0.3	2.1	6.1	0	5.5	3.7			
West	19	2.6	110	2.0	0.3	2.2	5.7	0	3.8	3.0			
Mean	27.75	4.43	70.25	1.90	0.29	2.25	5.78	1.00	4.68	3.80	13.6	2.10	1

Individual No. 8.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	31	5.2	48	2.4	0.25	2.0	5.3	2	6.0	4.2			
East	20	3.1	63	1.9	0.2	2.1	4.9	1	4.4	3.4			
South	40	6.9	22	2.7	0.2	3.2	5.0	3	6.1	4.0			
West	26	4.6	45	2.3	0.25	2.8	5.0	0	2.2	2.1			
Mean	29.25	4.95	44.50	2.33	0.23	2.53	5.05	1.50	4.68	3.43	10.4	1.57	1

Chichester Road (Cont).

Individual No. 9.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	3.5	42	2.3	0.25	2.1	5.5	2	6.5	3.9			
East	41	6.5	55	1.7	0.25	2.6	5.8	2	7.0	4.5			
South	19	2.1	49	1.3	0.2	2.1	4.9	0	3.5	2.4			
West	15	2.2	42	1.4	0.2	2.0	4.9	0	2.5	2.2			
Mean	23.25	3.58	47.00	1.68	0.23	2.20	5.28	1.00	4.88	3.25	10.8	1.44	1

Individual No. 10.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	25	3.1	65	2.0	0.25	3.0	4.8	2	3.9	2.8			
East	19	2.3	51	1.4	0.2	2.4	4.4	3	3.9	2.5			
South	17	1.9	42	1.2	0.2	2.0	4.7	0	2.9	2.2			
West	33	4.5	43	2.0	0.25	2.8	5.6	0	4.3	3.5			
Mean	23.50	2.95	50.25	1.65	0.23	2.55	4.88	1.25	3.75	2.75	16.0	2.27	1

Chichester Road (Cont).

Individual No. 11.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	15	1.7	43	1.2	0.2	2.2	4.2	0	DEAD				
East	17	2.3	46	1.6	0.2	2.1	4.9	0	3.7	2.7			
South	32	3.3	41	1.7	0.2	2.6	4.2	0	5.9	3.9			
West	17	1.4	33	1.1	0.2	2.1	4.1	0	DEAD				
Mean	20.25	2.18	40.75	1.40	0.20	2.25	4.35	0.00	4.80	3.30	15.2	3.27	1

Individual No. 12.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	24	2.3	55	1.6	0.2	1.6	4.7	0	4.5	3.4			
East	25	3.0	50	2.4	0.25	2.0	5.6	0	2.5	1.9			
South	1.5	1.4	61	2.0	0.2	2.3	4.8	0	2.5	1.1			
West	38	4.0	52	1.6	0.2	2.0	3.7	2	5.5	3.0			
Mean	22.13	2.68	54.50	1.90	0.21	1.98	4.70	0.50	3.75	2.35	14.4	2.09	1

Chichester Road (Cont).

Individual No. 13.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	28	4.6	94	2.5	0.25	2.4	5.5	0	2.4	1.8			
East	25	4.0	47	2.2	0.25	2.0	5.1	0	3.5	2.8			
South	14	1.3	60	1.2	0.2	1.4	3.7	0	3.0	1.9			
West	21	3.4	70	2.4	0.2	2.0	4.8	0	3.0	1.8			
Mean	22.00	3.33	67.75	2.08	0.23	1.95	4.78	0.00	2.98	2.08	13.6	1.87	1

Individual No. 14.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	25	3.5	51	2.5	0.25	2.0	5.5	2	4.0	2.6			
East	11	1.4	51	1.2	0.2	2.0	4.5	0	DEAD				
South	16	3.0	50	3.2	0.3	2.0	6.2	0	4.4	2.6			
West	14	1.7	70	2.1	0.2	1.5	5.3	0	3.5	1.7			
Mean	16.50	2.40	55.50	2.25	0.24	1.88	5.38	0.50	3.97	2.30	11.2	2.49	1

Chichester Road (Cont).

Individual No. 15.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	17	2.8	49	1.7	0.25	1.6	5.9	0	2.4	1.8			
East	18	3.2	39	2.2	0.2	2.1	5.5	0	1.7	1.4			
South	25	4.7	45	2.6	0.3	1.6	6.5	0	4.0	2.5			
West	22	3.7	54	1.8	0.3	2.5	6.5	0	3.3	1.9			
Mean	20.50	3.60	46.75	2.08	0.26	1.95	6.10	0.00	2.85	1.90	12.0	1.83	1

Individual No. 16.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	2.9	81	1.9	0.25	2.0	5.9	0	7.0	4.5			
East	18	1.9	60	1.9	0.2	2.3	4.9	0	1.0	1.4			
South	27	3.0	64	2.0	0.2	1.5	4.9	1	2.0	2.0			
West	18	2.1	49	1.5	0.2	1.8	4.9	0	3.5	2.9			
Mean	20.75	2.48	63.50	1.83	0.21	1.90	5.15	0.25	3.38	2.70	16.8	3.48	1

Chichester Road (Cont).

Individual No. 17.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	11	1.0	47	2.3	0.25	2.0	5.0	0	2.2	2.0			
East	28	3.4	70	2.3	0.3	2.0	6.8	1	4.9	2.9			
South	26	4.9	53	2.8	0.3	2.3	6.0	3	5.8	3.7			
West	31	4.5	55	2.4	0.3	2.0	6.9	0	3.3	2.9			
Mean	24.00	3.45	56.25	2.45	0.29	2.08	6.18	1.00	4.05	2.88	15.2	3.13	1

Individual No. 18.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	19	2.6	55	1.8	0.2	1.9	4.8	0	4.3	3.0			
East	16	2.1	52	1.5	0.2	2.1	5.0	1	5.7	3.1			
South	18	2.0	47	2.0	0.2	1.9	5.1	1	DEAD				
West	15	1.5	56	1.8	0.2	2.4	4.8	0	2.5	1.9			
Mean	17.00	2.05	52.50	1.78	0.20	2.08	4.93	0.25	4.17	2.67	15.6	2.45	1

Chichester Road (Cont).

Individual No. 19.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	25	3.1	28	2.1	0.2	2.5	4.2	1	3.9	2.4			
East	36	4.8	49	1.8	0.2	2.7	4.8	0	2.8	1.7			
South	27	3.7	67	2.0	0.25	2.0	5.8	2	4.0	2.5			
West	25	3.2	43	1.8	0.25	2.7	5.2	0	DEAD				
Mean	28.25	3.70	46.75	1.93	0.23	2.48	5.00	0.75	3.57	2.20	13.4	1.48	1

Individual No. 20.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	3.2	35	2.7	0.2	3.0	4.3	0	3.0	2.4			
East	33	3.9	73	2.1	0.2	1.9	4.7	0	3.5	3.7			
South	31	6.1	73	2.2	0.25	2.2	5.4	4	8.0	4.5			
West	24	3.3	73	2.2	0.2	1.7	4.8	1	3.3	1.7			
Mean	27.75	4.13	63.50	2.30	0.21	2.20	4.80	1.25	4.45	3.08	12.0	2.16	1

Chichester Road (Cont).

Individual No. 21.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	29	3.7	78	2.6	0.25	2.3	5.9	0	7.8	3.6			
East	24	3.2	79	2.5	0.2	1.8	5.1	1	4.3	3.3			
South	35	4.5	66	2.6	0.2	2.8	5.0	0	4.0	2.9			
West	37	5.2	59	3.1	0.25	2.5	5.6	2	7.6	4.4			
Mean	31.25	4.15	70.50	2.70	0.23	2.35	5.40	0.75	5.93	3.55	14.0	3.66	3

Individual No. 22.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	3.0	35	2.0	0.25	2.1	5.8	1	6.5	4.4			
East	24	2.4	45	1.8	0.25	2.1	5.8	0	2.7	2.2			
South	15	1.7	49	1.6	0.25	1.6	5.7	0	2.2	1.5			
West	17	2.2	45	2.3	0.3	2.2	7.0	1	5.0	3.0			
Mean	19.00	2.33	43.50	1.93	0.26	2.00	6.08	0.50	4.10	2.78	12.4	2.91	1

Chichester Road (Cont).

Individual No. 23.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	3.8	53	2.4	0.25	2.3	5.6	0	7.2	3.6			
East	20	3.7	64	2.0	0.2	2.0	5.1	0	2.9	1.5			
South	14	2.5	50	2.6	0.25	2.4	5.6	0	2.4	1.7			
West	23	4.6	64	2.4	0.25	2.3	5.5	2	5.5	2.6			
Mean	19.25	3.65	57.75	2.35	0.24	2.25	5.45	0.50	4.50	2.35	15.0	1.24	1

Individual No. 24.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	21	4.7	77	2.5	0.3	2.2	6.4	0	DEAD				
East	14	2.4	52	1.9	0.3	2.6	6.2	0	6.9	3.9			
South	17	2.7	59	2.0	0.2	2.3	5.0	0	4.4	2.3			
West	22	4.0	52	2.5	0.3	2.5	6.8	3	6.5	3.0			
Mean	18.50	3.45	60.00	2.23	0.28	2.40	6.10	0.75	5.93	3.07	16.2	1.40	1

Chichester Road (Cont).

Individual No. 25.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	22	2.4	31	1.6	0.2	2.5	4.3	0	4.4	2.8			
East	9	0.7	29	1.3	0.2	1.4	4.0	1	2.4	2.2			
South	14	1.0	28	1.3	0.15	1.8	3.6	1	2.0	1.6			
West	21	3.2	35	2.1	0.2	2.8	4.7	1	DEAD				
Mean	16.50	1.83	30.75	1.58	0.19	2.13	4.15	0.75	2.93	2.20	16.0	2.01	1

Individual No. 26.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	17	1.2	49	1.2	0.2	1.5	4.6	1	2.7	2.3			
East	17	1.6	15	1.6	0.2	1.8	4.9	5	3.3	2.9			
South	15	1.0	49	1.3	0.2	2.1	5.0	0	3.4	2.0			
West	26	2.3	22	1.4	0.2	1.8	4.7	1	4.1	3.5			
Mean	18.75	1.53	33.75	1.38	0.20	1.80	4.80	1.75	3.38	2.68	13.4	3.20	1

Chichester Road (Cont).

Individual No. 27.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	22	2.6	52	1.6	0.15	2.1	4.2	0	DEAD				
East	15	1.7	97	1.7	0.2	2.5	4.5	0	6.3	3.8			
South	16	2.1	51	2.3	0.2	1.7	4.8	2	4.2	2.3			
West	27	3.0	65	1.4	0.2	2.0	4.5	2	5.2	3.2			
Mean	20.00	2.35	66.25	1.75	0.19	2.08	4.50	1.00	5.23	3.10	14.8	2.32	1

Individual No. 28.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	36	4.1	80	1.7	0.25	2.0	5.4	1	4.2	2.9			
East	43	6.5	57	2.4	0.3	2.2	6.5	1	5.5	3.5			
South	33	4.4	54	2.1	0.3	2.3	6.4	0	5.3	3.8			
West	38	4.8	58	1.9	0.2	2.0	5.4	2	6.5	4.5			
Mean	37.50	4.95	62.25	2.03	0.26	2.13	5.93	1.00	5.38	3.68	15.0	1.76	1

Chichester Road (Cont).

Individual No. 29.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	28	4.7	67	2.5	0.25	2.0	5.8	1	4.6	3.8			
East	24	3.6	67	2.3	0.25	2.1	5.4	0	3.7	1.9			
South	21	3.5	37	2.5	0.3	2.8	5.9	1	5.4	3.8			
West	27	4.6	30	1.9	0.25	2.0	5.4	1	6.0	3.6			
Mean	25.00	4.10	50.25	2.30	0.26	2.23	5.63	0.75	4.93	3.28	13.8	2.26	1

Individual No. 30.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	24	2.9	42	1.6	0.2	1.8	3.9	0	3.6	2.5			
East	20	1.8	46	1.8	0.2	1.6	4.3	0	2.0	2.0			
South	38	5.6	54	2.3	0.25	2.0	5.2	3	5.0	2.8			
West	25	3.1	52	2.1	0.2	1.8	4.5	1	3.6	2.7			
Mean	26.75	3.35	48.50	1.95	0.21	1.80	4.48	1.00	3.55	2.50	17.8	4.25	2

Population: Overton Hall **Collection date 23.3.77.**

Individual No. 1.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	22	3.6	43	2.1	0.25	2.8	5.6	1	3.7	2.4			
East	24	4.7	49	2.3	0.3	2.5	6.6	1	5.6	3.7			
South	37	7.5	35	2.1	0.25	2.5	5.6	5	5.6	3.2			
West	18	3.0	47	2.1	0.3	2.5	5.6	1	4.1	2.5			
Mean	25.25	4.70	43.50	2.15	0.28	2.58	5.85	2.00	4.75	2.95	13.4	0.96	1

Individual No. 2.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	3.4	43	1.8	0.2	2.8	5.0	2	3.4	2.5			
East	21	3.7	66	2.0	0.3	2.6	6.2	0	3.0	2.7			
South	28	5.5	82	2.0	0.3	2.4	6.5	1	4.0	2.6			
West	25	5.2	50	2.0	0.25	2.5	5.7	0	5.2	2.8			
Mean	24.25	4.45	60.25	1.95	0.26	2.58	5.85	0.75	3.90	2.65	7.4	0.88	1

Overton Hall (Cont).

Individual No. 3.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	45	5.8	41	2.2	0.25	3.3	5.0	1	4.8	3.2			
East	13	1.7	37	1.7	0.2	2.0	4.5	0	1.4	1.7			
South	35	4.2	46	1.8	0.2	2.8	4.6	1	3.9	3.0			
West	25	4.1	42	2.2	0.3	2.5	6.2	1	3.5	2.8			
Mean	29.50	3.95	41.50	1.98	0.24	2.65	5.08	0.75	3.40	2.68	15.0	1.88	1

Individual No. 4.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	32	4.0	42	1.9	0.2	3.2	4.5	1	4.9	3.3			
East	37	5.8	45	1.8	0.3	2.1	6.4	1	4.5	3.4			
South	20	2.0	34	1.5	0.2	2.0	4.9	0	3.0	2.2			
West	23	2.9	35	1.7	0.2	2.5	4.3	0	3.5	2.5			
Mean	28.00	3.68	39.00	1.73	0.23	2.45	5.03	0.25	3.98	2.85	11.6	1.34	1

Overton Hall (Cont).

Individual No. 5.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	37	6.2	55	2.2	0.25	3.1	5.2	2	3.5	3.0			
East	22	3.8	56	2.0	0.25	2.9	5.5	2	4.9	3.7			
South	16	2.3	51	1.9	0.25	3.1	5.5	1	3.5	2.4			
West	41	7.0	56	2.1	0.25	3.6	5.2	2	4.6	3.5			
Mean	29.00	4.83	54.50	2.05	0.25	3.18	5.35	1.75	4.13	2.90	9.4	1.35	1

Individual No. 6.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	45	5.5	41	1.7	0.25	2.7	4.9	4	3.9	3.2			
East	21	3.2	68	1.8	0.25	2.6	5.3	1	3.0	2.5			
South	27	3.5	32	1.8	0.2	2.9	4.5	3	3.3	2.7			
West	36	4.1	55	1.5	0.2	3.2	4.5	2	3.4	2.8			
Mean	32.25	4.08	49.00	1.70	0.23	2.85	4.80	2.50	3.40	2.80	13.4	1.56	1

Overton Hall (Cont).

Individual No. 7.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	32	4.8	60	2.0	0.2	2.9	4.1	4	5.5	3.4			
East	26	3.5	40	1.8	0.2	3.1	4.3	2	5.0	3.5			
South	26	4.1	31	2.0	0.2	3.0	4.8	2	4.5	3.5			
West	48	7.3	37	1.8	0.25	2.4	5.2	1	6.4	4.0			
Mean	33.00	4.93	42.00	1.90	0.21	2.85	4.60	2.25	5.35	3.60	10.5	1.11	1

Individual No. 8.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	29	3.1	51	1.7	0.2	2.3	4.7	1	3.8	2.6			
East	33	3.6	50	1.8	0.2	3.1	4.5	3	4.6	3.5			
South	40	4.8	19	1.5	0.2	3.4	4.6	5	4.3	3.3			
West	24	2.4	55	1.5	0.2	3.0	5.0	2	3.6	3.1			
Mean	31.50	3.48	43.75	1.63	0.20	2.95	4.70	2.75	4.08	3.13	9.4	2.74	3

Overton Hill (Cont).

Individual No. 9.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	2.2	30	1.9	0.2	2.7	4.7	0	2.8	2.3			
East	14	1.6	42	1.9	0.2	3.2	5.0	1	4.5	3.8			
South	21	2.2	36	2.0	0.25	3.4	5.2	1	4.0	2.8			
West	32	3.9	37	2.2	0.2	3.6	5.0	2	4.6	3.5			
Mean	21.25	2.48	36.25	2.00	0.21	3.23	4.98	1.00	3.98	3.10	10.8	2.75	2

Individual No. 10.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	1.7	55	2.0	0.2	2.7	4.3	0	2.4	2.0			
East	21	3.0	41	1.6	0.2	2.4	4.6	0	4.8	3.7			
South	29	4.0	29	2.1	0.2	3.6	4.6	2	5.0	3.4			
West	35	4.0	31	1.7	0.2	3.9	4.0	3	4.9	3.4			
Mean	25.75	3.18	39.00	1.85	0.20	3.15	4.38	1.25	4.28	3.13	10.6	1.54	1

Overton Hall (Cont).

Individual No. 11.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	21	3.6	66	2.1	0.2	3.7	4.8	1	4.6	3.8			
East	18	3.3	43	1.9	0.25	3.0	5.0	0	5.0	3.5			
South	22	3.9	54	2.3	0.3	2.9	6.0	1	6.5	3.8			
West	23	3.8	47	2.8	0.25	4.0	5.1	0	4.3	4.5			
Mean	21.00	3.65	52.50	2.28	0.25	3.40	5.23	0.50	5.10	3.90	10.0	1.93	1

Individual No. 12.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	3.8	59	2.3	0.3	2.5	5.7	2	3.5	2.7			
East	27	3.1	37	1.8	0.2	3.3	4.1	2	3.4	2.8			
South	25	2.9	55	2.4	0.2	3.2	4.5	1	3.6	2.9			
West	27	3.8	50	2.2	0.25	3.0	5.2	2	3.7	3.1			
Mean	25.50	3.40	50.25	2.18	0.24	3.00	4.88	1.75	3.55	2.88	8.2	1.58	1

Overton Hall (Cont).

Individual No. 13.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	57	7.9	39	2.3	0.26	2.6	5.0	3	6.0	3.3			
East	40	5.6	38	2.2	0.25	1.8	5.0	2	3.8	3.0			
South	39	5.8	60	1.7	0.25	2.0	5.3	2	4.4	2.8			
West	43	6.0	59	2.2	0.25	2.4	4.9	2	3.3	3.0			
Mean	44.75	6.33	49.00	2.10	0.25	2.20	5.05	2.25	4.38	3.03	5.8	1.30	2

Individual No. 14.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	21	3.3	64	2.3	0.2	3.2	4.1	0	3.5	2.4			
East	25	4.0	54	2.5	0.2	3.4	4.4	1	3.5	2.4			
South	25	4.4	46	2.7	0.25	3.1	4.9	2	4.9	3.1			
West	27	4.3	55	2.7	0.2	3.6	4.5	1	3.7	2.6			
Mean	24.50	4.00	54.75	2.55	0.21	3.33	4.48	1.00	3.90	2.63	5.8	0.73	1

Overton Hall (Cont).

Individual No. 15.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	4.3	27	2.4	0.25	3.2	5.5	1	4.7	3.0			
East	17	3.1	60	2.4	0.25	2.6	5.4	1	4.0	3.1			
South	16	3.3	42	2.5	0.3	2.0	5.9	1	3.8	3.2			
West	26	5.5	42	2.0	0.2	2.6	5.0	2	5.0	3.5			
Mean	19.75	4.05	42.75	2.33	0.25	2.60	5.45	1.25	4.38	3.20	5.0	0.54	1

Individual No. 16.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	26	4.2	40	2.5	0.2	2.7	4.9	1	4.3	3.0			
East	51	8.6	57	2.2	0.25	3.4	5.7	2	7.2	3.5			
South	26	3.4	42	1.9	0.2	2.7	4.6	0	4.1	3.1			
West	33	4.3	37	2.4	0.2	3.7	4.5	3	5.0	3.3			
Mean	34.00	5.13	44.00	2.25	0.21	3.13	4.93	1.50	5.15	3.23	10.8	3.30	1

Overton Hall (Cont).

Individual No. 17.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	39	6.0	62	2.5	0.25	2.6	5.4	0	3.4	3.8			
East	29	3.6	43	2.5	0.2	3.0	4.5	1	3.0	2.6			
South	25	3.7	37	1.7	0.2	3.0	4.6	0	3.1	2.5			
West	39	5.4	44	4.3	0.3	3.0	6.2	1	2.2	2.8			
Mean	33.00	4.68	46.50	2.75	0.24	2.90	5.18	0.50	2.93	2.93	8.0	0.68	1

Individual No. 18.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	28	3.8	59	1.6	0.25	2.6	5.8	3	4.8	3.0			
East	18	2.1	32	1.7	0.2	2.5	4.4	1	2.8	2.2			
South	24	3.0	29	1.8	0.2	3.0	4.4	1	2.9	2.3			
West	26	3.1	21	1.6	0.2	3.0	4.0	1	2.3	2.6			
Mean	24.00	3.00	35.25	1.68	0.21	2.78	4.65	1.50	3.20	2.53	8.6	0.81	1

Overton Hall (Cont).

Individual No. 19.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	27	4.3	53	2.1	0.25	3.7	5.9	4	4.4	4.0			
East	15	2.0	57	1.9	0.25	2.4	5.0	1	2.4	2.5			
South	41	5.7	47	1.9	0.25	4.1	5.3	6	4.3	3.2			
West	34	4.7	39	2.1	0.3	3.4	5.4	3	3.6	3.1			
Mean	29.25	4.18	49.00	2.00	0.26	3.40	5.40	3.50	3.68	3.20	14.6	1.16	1

Individual No. 20.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	24	3.1	58	2.2	0.2	2.5	4.9	2	3.8	2.6			
East	23	3.0	42	2.0	0.2	2.4	4.5	0	3.2	2.5			
South	22	2.8	58	2.0	0.2	3.0	4.2	1	2.9	2.6			
West	22	3.2	53	2.2	0.2	2.6	5.0	0	2.2	2.1			
Mean	22.75	3.03	52.75	2.10	0.20	2.63	4.65	0.75	3.03	2.45	11.8	1.22	1

Overton Hall (Cont).

Individual No. 21.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	39	6.1	60	2.0	0.3	2.9	5.9	1	5.0	3.3			
East	27	4.1	49	2.2	0.25	3.0	5.4	2	4.7	3.4			
South	37	6.3	21	2.5	0.2	3.6	5.0	4	6.0	3.6			
West	18	2.4	60	2.9	0.25	3.4	5.2	2	4.0	2.7			
Mean	30.25	4.73	47.50	2.40	0.25	3.23	5.38	2.25	4.93	3.25	9.6	1.52	1

Individual No. 22.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	24	4.0	56	2.1	0.2	2.4	4.7	1	2.8	2.6			
East	22	4.0	43	2.5	0.25	2.1	5.0	1	2.8	2.0			
South	45	9.7	40	3.2	0.3	3.1	6.3	4	5.4	3.5			
West	29	5.1	50	2.4	0.25	3.0	5.0	1	4.5	3.5			
Mean	30.00	5.70	47.25	2.55	0.25	2.65	5.25	1.75	3.88	2.90	14.2	2.01	1

Overton Hall (Cont).

Individual No. 23.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	3.0	58	2.3	0.25	2.5	7.5	0	3.4	2.1			
East	26	4.5	70	2.2	0.25	2.4	5.4	1	2.9	2.4			
South	36	6.8	55	2.4	0.25	2.6	5.2	2	4.2	3.0			
West	24	3.9	40	2.4	0.25	2.8	5.1	0	3.0	2.4			
Mean	26.00	4.55	55.75	2.33	0.25	2.58	5.80	0.75	3.38	2.48	5.0	0.80	1

Individual No. 24.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	38	5.1	49	2.3	0.2	3.8	4.5	4	5.5	3.6			
East	33	6.2	43	2.9	0.2	2.9	4.5	4	7.0	4.0			
South	21	5.2	53	3.1	0.25	2.9	5.5	2	4.9	3.5			
West	27	4.9	54	2.3	0.25	2.0	5.1	0	4.0	2.2			
Mean	29.75	5.35	49.75	2.65	0.23	2.90	4.90	2.50	5.35	3.33	11.6	1.26	1

Overton Hall (Cont).

Individual No. 25.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	22	3.8	47	2.7	0.25	2.9	6.0	1	4.5	3.5			
East	30	5.2	57	2.4	0.25	2.6	5.6	2	4.8	3.3			
South	27	4.5	70	2.4	0.25	3.0	5.0	1	4.5	3.6			
West	33	3.8	54	2.5	0.25	2.7	5.8	2	3.4	3.5			
Mean	28.00	4.33	57.00	2.50	0.25	2.80	5.60	1.50	4.30	3.48	6.2	0.57	2

Individual No. 26.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	27	3.0	84	1.5	0.2	2.1	4.9	0	3.5	2.7			
East	40	6.7	65	1.5	0.25	1.9	5.4	2	5.7	4.2			
South	48	7.9	55	1.7	0.25	2.5	5.3	4	6.5	4.0			
West	22	3.0	54	1.4	0.3	1.7	5.6	0	4.4	3.4			
Mean	34.25	5.15	64.50	1.53	0.25	2.05	5.30	1.50	5.03	3.58	9.8	1.60	2

Overton Hall (Cont).

Individual No. 29.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	33	2.9	49	1.8	0.2	2.7	4.4	0	4.2	3.2			
East	24	2.4	66	2.0	0.2	3.5	4.6	1	3.4	3.0			
South	28	2.6	59	1.8	0.25	3.5	4.6	0	3.5	3.0			
West	28	2.6	28	1.8	0.2	2.6	4.4	1	4.0	2.9			
Mean	28.25	2.63	56.50	1.85	0.21	3.08	4.50	0.50	3.78	3.03	11.6	2.33	1

Individual No. 30.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	35	4.2	44	1.4	0.2	2.5	4.5	4	5.1	3.7			
East	27	4.4	48	1.6	0.2	2.2	4.4	1	3.8	2.9			
South	35	4.0	50	1.4	0.2	2.5	4.3	4	5.0	3.5			
West	52	5.7	54	1.2	0.2	2.6	4.0	3	5.0	4.0			
Mean	37.25	4.58	49.00	1.40	0.20	2.45	4.30	3.00	4.73	3.53	14.4	2.24	1

Population: Ravensdale

Collection date 23.3.77.

Individual No. 1.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	21	2.5	56	1.9	0.2	2.6	4.7	0	2.7	2.1			
East	19	3.3	58	2.3	0.25	2.6	5.4	2	3.8	2.4			
South	15	1.5	57	1.6	0.2	2.5	4.5	4	2.0	1.5			
West	27	3.3	66	1.9	0.2	2.6	4.7	1	4.5	2.8			
Mean	20.50	2.65	59.25	1.93	0.21	2.58	4.83	1.75	3.25	2.20	11.0	1.45	1

Individual No. 2.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	21	2.2	66	1.9	0.25	2.6	5.1	1	2.5	1.8			
East	21	2.7	63	2.2	0.2	2.5	4.7	1	3.3	2.2			
South	18	2.6	35	2.1	0.2	2.1	5.1	0	2.9	2.0			
West	18	2.1	50	2.1	0.2	2.3	4.1	0	2.5	1.9			
Mean	19.50	2.40	53.50	2.08	0.21	2.38	4.75	0.50	2.80	1.98	9.3	1.50	1

Ravensdale (Cont).

Individual No. 3.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	17	1.5	81	2.0	0.3	2.5	5.3	2	2.5	1.9			
East	48	6.3	66	1.9	0.25	3.0	5.0	6	4.8	3.4			
South	23	2.5	47	1.7	0.25	2.2	4.6	0	2.5	1.5			
West	19	2.8	65	2.2	0.3	2.2	5.6	0	3.0	2.8			
Mean	26.75	3.28	64.75	1.95	0.28	2.48	5.13	2.00	3.20	2.40	10.5	2.35	2

Individual No. 4.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	60	9.2	41	2.0	0.25	3.1	4.9	4	4.8	3.3			
East	29	4.3	52	2.1	0.25	2.8	5.3	0	2.7	2.1			
South	51	5.8	55	1.9	0.2	3.8	4.7	3	5.2	3.5			
West	34	5.2	38	2.2	0.25	3.1	5.2	1	4.3	3.1			
Mean	43.50	6.13	46.50	2.05	0.24	3.20	5.03	2.00	4.23	3.00	5.6	0.76	1

Ravensdale (Cont).

Individual No. 5.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	31	4.6	46	2.5	0.3	3.0	5.4	3	4.5	4.2			
East	19	3.5	58	2.2	0.3	3.0	5.3	1	2.8	2.6			
South	30	3.2	36	2.1	0.2	3.6	4.6	2	5.6	3.5			
West	42	5.7	46	2.4	0.25	3.4	4.7	3	4.5	3.1			
Mean	30.50	4.25	46.50	2.30	0.26	3.25	5.00	2.25	4.35	3.35	9.3	2.01	2

Individual No. 6.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	46	9.4	60	2.7	0.3	3.6	6.9	3	4.0	2.8			
East	33	4.4	52	2.2	0.2	4.4	4.7	5	4.0	3.2			
South	41	5.4	66	2.4	0.2	3.3	4.7	8	4.7	3.2			
West	28	6.1	58	2.5	0.3	3.5	5.5	2	4.3	3.4			
Mean	37.00	6.33	59.00	2.45	0.25	3.70	5.45	4.50	4.23	3.15	12.6	1.52	2

Ravensdale (Cont).

Individual No. 7.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	1.9	73	2.1	0.25	3.9	5.2	1	3.2	2.3			
East	23	2.4	48	1.5	0.2	3.0	4.0	1	3.8	2.3			
South	26	4.1	58	1.6	0.3	2.4	5.8	2	2.5	2.0			
West	29	6.5	73	2.0	0.3	2.9	6.5	4	4.2	2.2			
Mean	24.00	3.73	63.00	1.80	0.26	3.05	4.38	2.00	3.43	2.20	11.2	0.85	1

Individual No. 8.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	2.5	49	1.9	0.25	3.0	4.8	1	3.7	2.6			
East	35	4.1	55	2.6	0.3	3.9	5.8	2	5.0	3.5			
South	47	7.9	57	2.6	0.3	3.5	5.8	4	5.9	4.1			
West	38	5.5	81	2.6	0.3	3.5	6.1	3	3.6	3.7			
Mean	35.75	5.00	60.50	2.43	0.29	3.48	5.63	2.50	4.55	3.48	11.0	1.05	1

Ravensdale (Cont).

Individual No. 9.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	21	3.8	46	3.0	0.3	3.5	5.5	2	3.8	2.5			
East	16	2.9	45	3.0	0.3	3.6	5.3	2	4.5	2.9			
South	31	6.0	37	2.1	0.25	3.8	4.6	2	4.4	3.4			
West	36	6.0	74	2.6	0.3	3.9	5.9	4	4.5	4.0			
Mean	26.00	4.68	50.50	2.68	0.29	3.70	5.33	2.50	4.30	3.20	8.2	1.11	2

Individual No. 10.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	16	2.3	29	2.5	0.25	2.8	5.5	1	3.5	2.1			
East	24	4.1	67	2.8	0.3	2.9	6.2	1	5.0	2.7			
South	21	4.5	48	2.5	0.3	2.7	6.1	1	5.3	2.7			
West	18	3.1	61	2.5	0.3	3.2	5.5	1	3.9	2.7			
Mean	19.75	3.50	51.25	2.58	0.29	2.90	5.83	1.00	4.43	2.55	10.2	1.06	2

Ravensdale (Cont).

Individual No. 11.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	2.5	65	2.1	0.2	3.1	5.0	2	2.9	1.8			
East	18	3.2	25	2.4	0.3	3.4	5.7	0	5.0	2.3			
South	34	5.7	45	2.1	0.25	3.4	5.3	0	6.0	3.5			
West	35	6.1	47	2.4	0.25	3.4	5.2	0	5.2	3.5			
Mean	26.75	4.38	45.50	2.25	0.25	3.33	5.30	0.50	4.78	2.78	9.1	2.40	2

Individual No. 12.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	45	6.3	66	1.9	0.25	3.3	4.9	4	4.0	3.1			
East	7	0.8	77	0.9	0.2	1.4	4.4	0	DEAD				
South	21	1.9	48	1.5	0.2	3.4	3.9	1	3.2	2.5			
West	12	1.2	66	1.3	0.2	2.5	4.9	1	1.9	1.6			
Mean	21.25	2.55	64.25	1.40	0.21	2.65	4.53	1.50	3.03	2.40	8.6	1.47	2

Ravensdale (Cont).

Individual No. 13.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	2.0	70	1.8	0.25	3.1	5.0	2	2.9	1.6			
East	21	2.7	48	1.9	0.2	2.7	4.6	1	2.5	2.1			
South	18	1.6	59	2.1	0.2	2.5	5.0	2	3.8	2.1			
West	50	10.6	53	2.4	0.3	4.0	5.6	7	4.6	3.3			
Mean	26.75	4.23	57.50	2.05	0.24	3.08	5.05	3.00	3.45	2.28	10.5	1.70	2

Individual No. 14.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	26	3.3	80	1.7	0.2	3.0	4.4	0	2.0	1.8			
East	22	2.9	55	1.2	0.2	2.1	4.6	1	4.1	2.9			
South	51	7.5	41	1.6	0.2	3.1	4.5	6	4.4	3.5			
West	25	3.0	51	1.3	0.2	2.4	4.4	1	3.0	2.7			
Mean	31.00	4.18	56.75	1.45	0.20	2.65	4.48	2.00	3.38	2.73	14.4	3.75	4

Ravensdale (Cont).

Individual No. 15.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	1.7	50	1.0	0.2	2.0	3.8	0	2.8	2.3			
East	30	4.1	66	2.0	0.25	2.5	5.2	0	3.4	2.2			
South	33	4.0	52	2.0	0.25	2.5	5.1	1	3.2	2.2			
West	30	4.0	49	2.2	0.25	2.6	5.0	1	3.4	2.3			
Mean	28.25	3.45	54.25	1.80	0.24	2.40	4.78	0.50	3.20	2.25	14.1	1.77	2

Individual No. 16.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	22	3.6	51	2.0	0.25	2.0	5.2	0	2.0	2.2			
East	11	1.2	75	1.3	0.25	2.5	4.6	0	3.0	2.3			
South	17	2.0	70	1.6	0.25	2.0	5.0	0	3.9	2.6			
West	28	4.4	59	2.0	0.3	2.3	6.0	1	4.5	2.7			
Mean	19.50	2.80	63.75	1.73	0.26	2.20	5.20	0.25	3.35	2.45	13.0	3.32	3

Ravensdale (Cont).

Individual No. 17.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	13	1.2	58	1.9	0.2	2.5	4.6	0	1.9	1.4			
East	30	4.5	55	1.9	0.3	2.5	6.0	1	3.5	2.6			
South	21	2.4	58	1.6	0.25	2.0	5.2	0	2.0	1.4			
West	30	4.7	70	1.7	0.25	2.5	5.7	1	4.4	3.0			
Mean	23.50	3.20	60.25	1.78	0.25	2.38	5.38	0.50	2.95	2.10	9.5	1.06	2

Individual No. 18.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	19	2.7	53	2.2	0.25	2.8	5.2	0	2.0	2.0			
East	30	3.6	71	2.1	0.25	2.5	5.5	2	2.7	2.4			
South	24	4.0	71	2.2	0.3	3.1	5.3	1	4.0	2.3			
West	13	1.7	49	1.6	0.25	2.1	4.9	0	1.6	1.7			
Mean	21.50	3.00	61.00	2.03	0.26	2.63	5.23	0.75	2.58	2.10	9.0	1.01	1

Ravensdale (Cont).

Individual No. 19.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	21	3.0	39	2.7	0.3	3.3	5.8	0	2.8	2.2			
East	20	3.4	49	2.7	0.3	3.8	5.5	2	2.8	2.5			
South	18	3.2	46	3.5	0.3	3.5	6.3	1	1.7	1.8			
West	30	5.6	41	2.6	0.3	4.2	5.7	1	3.3	2.9			
Mean	22.25	3.80	43.75	2.88	0.30	3.70	5.83	1.00	2.65	2.35	10.8	2.91	3

Individual No. 20.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	3.4	59	1.9	0.25	2.5	5.4	2	4.3	2.7			
East	41	7.2	58	2.0	0.3	3.6	6.4	3	4.9	3.5			
South	18	3.3	64	1.8	0.3	3.1	5.5	0	3.8	2.5			
West	21	3.4	52	1.9	0.3	3.0	5.7	0	3.9	2.7			
Mean	25.75	4.33	58.25	1.90	0.29	3.05	5.75	1.25	4.23	2.85	13.5	1.79	2

Ravensdale (Cont).

Individual No. 21.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	14	2.0	55	2.3	0.25	2.6	5.0	1	2.5	1.7			
East	17	2.1	58	2.1	0.25	3.3	5.0	1	1.8	1.8			
South	19	3.3	54	2.5	0.25	2.9	5.3	1	2.7	2.4			
West	14	2.4	52	2.3	0.25	2.6	5.5	2	3.0	2.0			
Mean	16.00	2.45	54.75	2.30	0.25	2.85	5.20	1.25	2.50	1.98	9.9	1.76	2

Individual No. 22.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	22	3.7	73	2.0	0.25	2.5	5.5	1	4.0	2.3			
East	28	5.5	93	1.7	0.25	1.7	5.3	1	4.7	2.8			
South	20	3.9	55	1.9	0.25	2.5	5.4	0	3.5	2.2			
West	25	4.7	49	1.8	0.25	2.4	5.4	0	3.5	2.4			
Mean	23.75	4.45	67.50	1.85	0.25	2.28	5.40	0.50	3.93	2.43	10.3	1.86	2

Ravensdale (Cont).

Individual No. 23.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	26	5.4	61	2.1	0.3	3.5	6.0	2	4.4	3.5			
East	20	4.1	66	2.5	0.3	3.3	6.1	0	4.4	3.1			
South	29	4.5	60	1.8	0.3	3.2	5.8	1	4.2	2.7			
West	28	5.3	51	1.9	0.3	3.8	6.1	1	5.0	3.2			
Mean	25.75	4.83	54.50	2.08	0.30	3.45	6.00	1.00	4.50	3.13	10.4	1.60	2

Individual No. 24.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	25	4.6	90	2.2	0.3	2.6	6.8	1	3.0	2.4			
East	23	3.5	77	1.8	0.3	2.8	5.7	0	4.5	3.0			
South	34	5.9	47	2.0	0.3	3.0	4.7	2	5.6	3.2			
West	12	1.5	50	1.0	0.2	2.6	4.2	0	3.2	2.6			
Mean	23.50	3.88	66.00	1.75	0.28	2.75	5.35	0.75	4.08	2.80	10.0	2.12	2

Ravensdale (Cont).

Individual No. 25.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	15	1.9	59	1.5	0.3	1.9	6.1	0	2.4	1.9			
East	15	2.3	71	1.5	0.3	1.8	5.8	0	3.5	2.0			
South	19	3.3	57	1.8	0.3	1.9	6.0	1	4.0	2.9			
West	20	3.4	73	1.6	0.3	2.0	6.9	0	3.2	2.2			
Mean	17.25	2.73	65.00	1.60	0.30	1.90	6.20	0.25	3.28	2.25	10.1	0.87	1

Population: Scout Scar. Collection date: 4.5.77.

Individual No. 1.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	2.8	46	2.1	0.2	2.2	4.8	0	4.2	3.3			
East	35	5.8	57	2.4	0.2	2.6	5.0	2	3.6	2.8			
South	24	3.3	43	1.8	0.2	2.5	4.8	1	5.6	3.5			
West	48	5.3	35	1.6	0.2	2.6	4.5	5	5.5	4.2			
Mean	32.50	4.30	45.25	1.98	0.20	2.48	4.78	2.00	4.73	3.45	10.4	2.45	1

Individual No. 2.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	27	4.2	52	2.3	0.2	3.1	5.0	1	6.0	4.0			
East	25	2.8	47	2.0	0.2	2.8	4.7	1	2.5	2.2			
South	21	4.2	54	2.1	0.3	2.7	6.3	2	7.5	4.5			
West	20	3.7	49	2.4	0.3	3.0	5.8	1	5.8	4.0			
Mean	23.25	3.73	50.50	2.20	0.25	2.90	5.45	1.25	5.45	3.68	10.6	3.30	4

Scout Scar (Cont).

Individual No. 3.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	12	1.8	53	1.8	0.2	2.7	4.9	0	2.0	2.3			
East	9	1.0	50	1.6	0.2	3.0	4.5	0	2.5	2.1			
South	10	1.5	48	1.7	0.2	2.1	4.9	0	2.5	2.2			
West	12	1.7	60	1.3	0.25	1.9	5.2	0	2.5	2.2			
Mean	10.75	1.50	52.75	1.60	0.21	2.43	4.88	0.00	2.38	2.20	9.2	1.40	1

Individual No. 4.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	29	4.4	52	1.7	0.25	3.0	5.3	1	-	-			
East	24	2.6	46	1.4	0.2	2.8	4.0	0	7.3	4.0			
South	29	4.6	22	1.5	0.2	2.5	4.3	1	-	-			
West	19	2.9	55	1.8	0.3	2.7	6.1	1	4.5	3.4			
Mean	25.25	3.63	43.75	1.60	0.24	2.75	4.93	0.75	$\overset{++}{5}$.90	3.70	8.8	2.06	5

Scout Scar (Cont).

Individual No. 5.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North													
East	14	1.5	60	1.5	0.2	2.5	4.1	0	4.5	3.6			
South	18	2.1	61	2.0	0.2	2.4	4.5	0	5.5	3.4			
West	19	2.0	69	1.1	0.2	2.1	3.8	0	4.6	3.9			
Mean	17.00	1.87	63.33	1.53	0.20	2.33	4.13	0.00	4.87	3.63	6.2	0.97	2

Individual No. 6.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	53	8.0	30	2.6	0.25	3.0	5.1	3	5.3	3.6			
East	15	2.0	71	2.3	0.2	2.0	5.0	0	1.4	1.5			
South	22	2.4	7	2.1	0.2	2.3	4.2	2	2.5	2.0			
West	40	5.4	33	2.0	0.2	2.6	4.4	2	6.2	4.0			
Mean	32.50	4.45	35.25	2.25	0.21	2.48	4.68	1.75	3.85	2.78	8.8	1.26	1

Scout Scar (Cont).

Individual No. 7.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	45	5.6	49	1.8	0.2	3.7	4.5	5	8.9	5.5			
East	18	1.9	56	1.4	0.2	2.5	4.0	1	2.0	1.5			
South	37	3.5	61	1.6	0.2	3.3	4.7	4	4.5	3.3			
West	13	1.5	49	1.2	0.2	3.2	3.9	3	5.5	3.8			
Mean	28.25	3.13	53.75	1.50	0.20	3.18	4.28	3.25	5.23	3.53	7.7	1.34	3

Individual No. 8.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	25	1.9	33	1.7	0.2	2.5	4.4	1	4.5	3.5			
East	20	2.5	42	1.7	0.2	2.3	4.5	2	4.4	3.0			
South	22	2.2	43	1.4	0.2	2.8	3.8	0	5.2	3.8			
West	17	1.9	47	1.6	0.2	1.6	4.5	1	3.7	2.8			
Mean	21.00	2.13	41.25	1.60	0.20	2.30	4.30	1.00	4.45	3.28	8.6	1.11	1

Scout Scar (Cont).

Individual No. 9.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	11	1.3	50	1.3	0.2	3.4	4.6	0	4.5	3.2			
East	15	1.8	29	2.2	0.25	2.3	5.9	0	2.6	2.0			
South	21	2.2	46	1.7	0.25	2.2	5.3	2	3.8	2.8			
West	33	4.0	37	1.7	0.2	2.4	4.9	1	5.7	3.8			
Mean	20.00	2.33	40.50	1.73	0.23	2.58	5.18	0.75	4.15	2.95	8.3	1.15	1

Individual No. 10.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	13	1.5	42	1.5	0.2	2.4	4.8	0	5.4	3.5			
East	25	3.1	45	1.8	0.25	2.5	5.0	3	5.5	3.1			
South	26	3.8	49	1.5	0.2	2.5	4.5	2	-	-			
West	11	1.1	54	1.2	0.2	2.0	4.8	0	DEAD				
Mean	18.75	2.38	47.50	1.50	0.21	2.35	4.78	1.25	++ 5.45	3.30	12.8	1.46	1

Scout Scar (Cont).

Individual No. 11.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	22	3.7	41	2.1	0.3	2.8	5.8	0	3.0	2.0			
East	14	2.1	45	1.3	0.2	1.7	4.8	0	2.4	2.0			
South	24	5.3	42	2.6	0.3	3.0	5.9	3	-	-			
West	37	8.1	46	2.3	0.25	3.3	5.5	5	8.0	4.5			
Mean	24.25	4.80	43.50	2.08	0.26	2.70	5.50	2.00	+++ 4.47	2.83	13.0	1.45	1

Individual No. 12.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	16	2.4	68	2.0	0.25	2.5	5.4	0	2.5	2.2			
East	16	2.3	56	2.2	0.25	2.2	5.5	0	2.3	2.0			
South	26	3.7	68	2.3	0.25	2.5	5.5	0	2.5	2.0			
West	18	2.9	64	2.3	0.25	2.6	5.0	0	5.0	3.2			
Mean	19.00	2.83	64.00	2.20	0.25	2.45	5.35	0.00	3.08	2.35	17.5	2.37	1

Scout Scar (Cont).

Individual No. 13.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	16	2.5	48	2.5	0.2	2.7	4.9	0	-	-			
East	14	1.9	88	2.1	0.2	3.0	4.3	0	DEAD				
South	14	2.8	60	2.2	0.2	2.5	4.7	0	3.5	2.7			
West	25	5.4	48	3.2	0.25	3.3	5.5	1	-	-			
Mean	17.25	3.15	61.00	2.50	0.21	2.88	4.85	0.25	+ 3.50	2.70	11.4	2.19	1

Individual No. 14.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	28	3.5	42	2.0	0.2	2.4	4.8	0	-	-			
East	23	2.8	51	1.9	0.25	2.0	5.4	1	-	-			
South	14	1.7	58	1.8	0.25	2.4	5.4	1	-	-			
West	22	2.2	58	2.0	0.25	2.5	5.4	3	7.0	4.6			
Mean	21.75	2.55	52.25	1.93	0.24	2.33	5.25	1.25	+ 7.00	4.60	11.4	1.69	1

Scout Scar (Cont).

Individual No. 15.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	47	8.8	31	2.7	0.25	3.2	5.6	0	DEAD				
East	42	5.8	61	2.0	0.25	2.7	5.2	0	DEAD				
South	31	3.7	47	2.2	0.25	2.8	5.6	2	5.6	3.8			
West	42	4.6	36	1.8	0.2	2.6	4.4	1	6.0	4.1			
Mean	40.50	5.73	43.75	2.18	0.24	2.83	5.20	0.75	5.80	3.95	12.2	2.22	1

Individual No. 16.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	2.1	57	1.3	0.2	2.6	4.3	1	-	-			
East	29	3.6	51	1.1	0.25	3.0	5.1	0	9.5	6.2			
South	16	2.4	50	1.5	0.2	2.9	4.5	0	-	-			
West	22	3.0	48	1.8	0.25	2.8	5.1	0	4.5	3.9			
Mean	21.25	2.78	51.50	1.43	0.23	2.83	4.75	0.25	++ 7.00	5.05	9.5	1.24	1

Scout Scar (Cont).

Individual No. 17.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	2.4	49	1.1	0.2	2.2	4.7	0	5.7	3.7			
East	22	3.1	36	1.4	0.25	2.3	5.5	1	DEAD				
South	29	4.4	40	2.2	0.3	2.9	5.6	0	4.3	3.7			
West	32	6.0	36	2.0	0.3	2.6	6.2	1	2.5	1.45			
Mean	25.75	3.98	40.25	1.68	0.26	2.50	5.50	0.50	+++ 4.17	2.95	7.5	0.80	1

Individual No. 18.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	2.4	42	2.0	0.2	2.5	4.5	0	2.9	2.8			
East	19	2.9	52	1.6	0.2	2.3	4.3	1	5.2	3.6			
South	23	3.5	55	2.4	0.2	2.5	5.1	3	5.3	4.6			
West	14	1.9	40	1.7	0.2	2.1	4.4	0	2.5	1.9			
Mean	18.50	2.68	47.25	1.93	0.20	2.35	4.58	1.00	+ 2.50	1.90	9.4	1.51	1

Scout Scar (Cont).

Individual No. 19.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	35	4.5	43	1.7	0.2	2.5	4.5	1	-	-			
East	37	6.0	45	1.7	0.2	2.9	4.8	4	-	-			
South	30	4.0	35	2.0	0.25	2.3	4.9	0	-	-			
West	16	1.7	32	1.7	0.2	2.1	4.8	0	2.6	2.0			
Mean	29.50	4.05	38.75	1.78	0.21	2.45	4.75	1.25	$\overset{+}{2.60}$	2.00	14.6	2.36	1

Individual No. 20.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	37	5.4	31	1.8	0.2	3.4	4.0	4	4.9	1.6			
East	35	5.1	42	1.7	0.2	3.8	3.7	5	5.8	4.1			
South	25	3.4	31	1.6	0.2	3.0	3.7	1	3.0	4.3			
West	24	3.2	50	1.4	0.2	2.1	3.6	2	4.0	2.8			
Mean	30.25	4.28	38.50	1.63	0.20	3.08	3.75	3.00	4.43	3.21	7.8	1.84	3

Scout Scar (Cont).

Individual No. 21.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	28	5.5	51	2.3	0.3	2.7	5.7	0	4.4	2.8			
East	26	4.3	59	2.6	0.2	2.5	4.7	1	4.0	2.5			
South	21	3.8	35	2.4	0.2	2.1	5.0	1	3.5	2.3			
West	24	3.8	50	2.8	0.2	3.4	5.3	1	4.1	3.5			
Mean	24.75	4.35	48.75	2.53	0.23	2.68	5.18	0.75	4.00	2.78	11.4	1.89	1

Individual No. 22.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	8	0.8	40	1.3	0.15	2.5	3.7	0	DEAD				
East	19	3.1	65	2.7	0.2	2.4	4.6	0	3.3	1.6			
South	25	4.0	56	2.3	0.25	3.4	5.2	1	-	-			
West	22	2.8	66	1.9	0.2	2.2	4.6	0	2.5	1.6			
Mean	18.50	2.68	56.75	2.05	0.20	2.63	4.53	0.25	++ 2.90	1.60	10.6	2.11	1

Scout Scar (Cont).

Individual No. 23.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	26	4.4	31	2.3	0.25	2.5	5.5	1	6.0	2.4			
East	36	6.1	63	1.9	0.25	2.5	5.6	1	3.8	3.7			
South	24	4.6	29	2.0	0.2	2.7	4.8	1	4.4	3.2			
West	29	5.4	36	2.4	0.2	2.2	5.9	2	3.4	2.5			
Mean	28.75	5.13	39.75	2.15	0.23	2.48	5.45	1.25	4.40	2.95	13.0	1.97	1

Individual No. 24.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	27	3.2	50	2.3	0.2	2.5	4.6	3	6.4	4.0			
East	13	1.5	20	2.5	0.2	2.5	4.6	0	1.5	1.9			
South	22	2.2	25	2.3	0.2	2.6	4.2	0	2.5	2.0			
West	25	3.4	41	2.5	0.25	2.6	5.1	1	-	-			
Mean	21.75	2.58	34.00	2.40	0.21	2.55	4.63	1.00	+++ 3.47	2.63	11.4	1.92	1

Scout Scar (Cont).

Individual No. 25.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	28	3.5	59	1.7	0.25	2.8	5.4	2	-	-			
East	33	5.6	30	2.3	0.25	2.7	5.8	3	-	-			
South	20	2.8	53	2.0	0.25	2.4	5.2	0	2.7	2.0			
West	15	1.8	51	1.5	0.25	1.9	4.8	2	1.8	1.8			
Mean	24.00	3.43	48.25	1.88	0.25	2.45	5.30	1.75	++ 2.25	1.90	10.6	1.61	1

Individual No. 26.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	3.5	24	2.0	0.25	2.5	5.5	3	5.5	3.7			
East	32	5.1	40	2.2	0.3	2.7	5.7	3	6.0	4.5			
South	32	5.0	46	2.3	0.3	3.1	5.8	3	6.4	4.3			
West	28	3.6	38	2.0	0.25	3.0	5.4	4	6.3	3.7			
Mean	28.75	4.30	37.00	2.13	0.28	2.83	5.60	3.25	6.05	4.05	16.2	2.93	2

Scout Scar (Cont).

Individual No. 27.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	47	9.6	42	1.8	0.25	3.2	5.3	2	6.9	5.4			
East	42	8.6	73	2.0	0.25	2.6	5.4	4	-	-			
South	43	8.4	37	1.7	0.2	3.1	4.9	2	-	-			
West	25	4.7	43	1.6	0.25	2.6	5.1	2	5.4	4.5			
Mean	39.25	7.83	48.75	1.78	0.24	2.88	5.18	2.50	++ 6.15	4.95	12.0	2.05	1

Individual No. 28.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	48	5.9	47	1.8	0.25	3.0	5.3	4	3.8	4.3			
East	32	4.5	53	1.8	0.25	2.4	5.2	1	DEAD				
South	44	5.4	39	1.5	0.2	2.5	4.7	2	2.8	2.8			
West	30	4.3	61	1.9	0.25	2.5	5.5	2	7.0	2.5			
Mean	38.50	5.03	50.00	1.75	0.24	2.60	5.18	2.25	+++ 4.50	3.20	11.4	0.51	1

Scout Scar (Cont).

Individual No. 29.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	13	2.1	26	1.9	0.25	1.9	5.4	1	-	-			
East	19	2.1	55	1.3	0.2	2.0	4.8	2	4.4	3.0			
South	21	2.6	66	1.4	0.2	3.0	4.8	0	-	-			
West	37	6.0	55	1.9	0.25	3.0	4.8	6	-	-			
Mean	22.50	3.20	50.50	1.63	0.23	2.48	4.95	2.25	+ 4.40	3.00	11.6	1.75	1

Individual No. 30.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	52	8.3	56	1.6	0.2	2.4	4.6	8	7.7	5.2			
East	31	5.2	41	1.9	0.25	2.5	5.3	3	7.3	4.5			
South	21	3.2	70	1.9	0.25	2.1	5.5	2	5.0	3.5			
West	33	3.9	41	1.1	0.2	2.0	4.0	1	6.3	4.2			
Mean	34.25	5.15	52.00	1.63	0.23	2.25	4.85	3.50	6.58	4.35	9.0	2.33	2

Population: Yew Barrow. Collection date: 4.5.77.

Individual No. 1.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	3.6	68	2.7	0.25	2.8	5.2	0	3.6	2.5			
East	20	3.1	46	3.0	0.25	2.9	4.9	2	3.8	2.7			
South	20	3.6	42	2.6	0.2	3.0	4.9	1	4.5	3.0			
West	35	5.4	47	2.6	0.2	3.4	4.9	5	5.0	3.5			
Mean	24.50	3.93	50.75	2.73	0.23	3.03	4.98	2.00	4.23	2.93	15.2	2.33	4

Individual No. 2.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	15	1.3	61	1.6	0.2	1.9	4.5	2	2.0	1.8			
East	22	2.3	52	1.9	0.25	2.4	5.1	0	-	-			
South	19	2.4	51	1.9	0.3	2.0	5.9	1	-	-			
West	27	3.8	38	2.0	0.3	2.5	5.8	2	-	-			
Mean	20.75	2.45	50.50	1.85	0.26	2.20	5.33	1.25	+ 2.00	1.80	11.8	1.90	2

Yew Barrow (Cont).

Individual No. 3.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	3.2	49	2.8	0.2	3.0	5.0	1	3.0	2.3			
East	34	4.7	68	1.7	0.2	2.7	4.9	2	4.5	3.5			
South	38	7.1	45	2.9	0.3	3.3	6.4	2	-	-			
West	20	3.4	37	2.4	0.25	3.0	5.4	1	2.5	2.1			
Mean	28.00	4.60	49.75	2.45	0.24	3.00	5.43	1.50	$\overset{+++}{3.33}$	2.63	13.6	2.04	1

Individual No. 4.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	22	4.1	53	3.2	0.3	2.5	5.5	2	2.4	1.8			
East	17	2.1	71	2.1	0.3	2.4	6.0	1	2.7	2.2			
South	27	4.7	75	2.7	0.3	2.4	5.9	3	4.5	3.9			
West	22	3.7	66	2.8	0.3	2.6	5.9	0	2.0	3.0			
Mean	22.00	3.65	66.25	2.70	0.30	2.48	5.83	1.50	3.40	2.73	14.0	2.44	3

Yew Barrow (Cont).

Individual No. 5.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	2.8	51	1.9	0.25	2.7	5.5	1	-	-			
East	31	5.8	67	2.0	0.2	2.9	4.9	1	-	-			
South	19	3.0	47	1.9	0.2	2.5	4.8	1	3.7	2.6			
West	12	1.2	48	1.8	0.2	2.6	4.5	0	DEAD				
Mean	21.25	3.20	53.25	1.90	0.21	2.68	4.93	0.75	$\overset{+}{3.70}$	2.60	14.0	1.75	2

Individual No. 6.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	13	2.0	71	2.4	0.25	2.5	5.5	0	DEAD				
East	26	4.2	58	2.5	0.25	2.8	5.2	1	3.9	3.2			
South	26	5.4	65	2.8	0.3	2.8	5.5	1	2.8	2.5			
West	26	4.3	65	2.3	0.2	3.0	4.5	1	4.0	2.1			
Mean	22.75	3.98	64.75	2.50	0.25	2.78	5.18	0.75	$\overset{+++}{3.57}$	2.6	9.0	1.28	1

Yew Barrow (Cont).

Individual No. 7.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	4.1	75	2.3	0.3	2.6	5.9	2	3.2	1.8			
East	18	2.6	78	2.0	0.2	2.4	5.2	0	4.9	2.3			
South	28	4.8	35	2.5	0.3	3.3	5.9	2	5.8	3.5			
West	23	4.0	46	2.1	0.25	2.2	5.4	0	3.3	3.5			
Mean	23.00	3.88	58.50	2.23	0.26	2.63	5.60	1.00	4.05	2.78	12.8	2.29	2

Individual No. 8.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	59	9.0	50	1.9	0.2	2.5	4.4	5	-	-			
East	26	3.2	50	1.8	0.2	2.4	4.0	3	5.1	4.0			
South	20	2.8	34	2.0	0.2	3.0	4.4	1	-	-			
West	25	3.4	45	1.9	0.2	2.0	4.0	0	2.5	1.8			
Mean	32.50	4.60	44.75	1.90	0.20	2.48	4.20	2.25	++ 3.80	2.90	10.8	1.93	2

Yew Barrow (Cont).

Individual No. 9.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	42	5.4	38	2.2	0.25	3.1	4.7	3	-	-			
East	22	2.9	48	2.0	0.25	2.4	5.4	1	-	-			
South	33	4.5	49	2.2	0.3	2.6	6.0	3	6.0	4.0			
West	23	2.9	60	2.0	0.25	1.9	5.2	1	2.0	1.7			
Mean	30.00	3.93	48.75	2.10	0.26	2.50	5.33	2.00	++ 4.00	2.85	9.1	1.18	1

Individual No. 10.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	16	2.5	50	2.1	0.2	2.4	5.0	0	2.7	2.0			
East	13	2.5	88	2.2	0.2	2.2	5.0	0	-	-			
South	24	3.3	94	2.0	0.2	2.0	4.2	1	4.7	3.1			
West	14	2.0	49	1.8	0.2	2.2	4.2	1	-	-			
Mean	16.75	2.58	70.25	2.03	0.20	2.20	4.60	0.50	++ 3.70	2.55	12.2	1.31	1

Yew Barrow (Cont).

Individual No. 11.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	2.2	50	1.9	0.15	2.0	3.8	0	4.0	2.9			
East	24	3.6	49	2.0	0.2	1.9	3.9	2	-	-			
South	21	4.0	32	2.1	0.2	2.2	3.9	0	-	-			
West	15	2.4	32	2.5	0.2	2.4	4.7	1	1.5	1.6			
Mean	19.50	3.05	40.75	2.13	0.19	2.13	4.08	0.75	++ 2.75	2.25	11.4	1.85	2

Individual No. 12.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	22	3.8	62	2.2	0.25	2.0	5.0	1	4.3	4.4			
East	25	5.8	61	2.9	0.3	2.7	6.2	1	5.1	2.2			
South	25	3.9	30	2.2	0.2	2.0	4.9	2	2.9	1.5			
West	20	4.4	50	2.4	0.25	2.5	5.2	6	3.7	3.0			
Mean	23.00	4.48	50.75	2.43	0.25	2.30	5.33	2.50	4.00	2.78	11.8	1.94	1

Yew Barrow (Cont).

Individual No. 13.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	2.6	46	2.0	0.2	2.5	3.9	2	-	-			
East	22	2.8	28	2.3	0.2	2.0	4.9	1	3.8	2.7			
South	30	2.8	54	1.8	0.2	2.3	4.0	2	-	-			
West	43	5.9	60	2.2	0.25	2.5	5.7	2	-	-			
Mean	29.50	3.53	47.00	2.08	0.21	2.33	4.63	1.75	+ 3.80	2.70	17.2	0.94	1

Individual No. 14.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	2.2	68	2.0	0.25	3.0	4.9	1	4.9	3.4			
East	28	3.5	41	1.6	0.25	2.7	5.1	1	5.1	3.5			
South	37	3.5	45	1.6	0.25	2.9	5.3	2	5.9	4.4			
West	18	2.9	32	1.8	0.25	3.0	5.2	2	3.5	2.7			
Mean	25.25	3.03	46.50	1.75	0.25	2.90	5.13	1.50	4.85	3.50	10.2	1.74	2

Yew Barrow (Cont).

Individual No. 15.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	21	3.6	36	2.8	0.25	2.6	5.0	2	-	-			
East	20	4.3	42	2.3	0.25	2.5	5.3	0	5.3	3.3			
South	14	2.9	58	2.4	0.25	2.0	5.2	1	-	-			
West	21	3.9	37	2.3	0.2	2.4	4.8	3	-	-			
Mean	19.00	3.68	43.25	2.45	0.24	2.38	5.08	1.50	$^{+}$5.30	3.30	5.2	2.08	2

Individual No. 16.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	15	1.7	53	1.7	0.2	2.7	4.4	1	-	-			
East	26	4.8	82	3.0	0.3	2.7	5.8	2	4.1	3.5			
South	22	3.5	84	3.0	0.25	2.2	5.0	1	3.4	2.1			
West	31	4.8	30	2.5	0.2	3.0	3.9	2	-	-			
Mean	23.50	3.70	62.25	2.55	0.24	2.65	4.78	1.50	$^{++}$3.75	2.80	14.2	1.41	1

Yew Barrow (Cont).

Individual No. 17.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	34	5.5	43	2.1	0.3	3.0	5.6	2	4.6	3.0			
East	14	2.0	55	1.8	0.2	2.6	3.9	0	1.9	1.5			
South	30	4.0	32	1.5	0.2	2.8	5.0	3	-	-			
West	26	3.4	35	1.8	0.2	3.0	4.5	0	-	-			
Mean	26.00	3.73	41.25	1.80	0.23	2.85	4.75	1.25	$\overset{++}{3.25}$	2.25	15.4	1.63	2

Individual No. 18.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	29	5.0	45	2.3	0.3	3.2	5.6	2	4.3	3.0			
East	31	6.0	48	3.0	0.3	3.4	5.5	2	5.1	3.2			
South	18	2.7	41	2.8	0.2	3.0	4.7	0	2.9	2.0			
West	32	6.0	28	2.4	0.2	2.5	4.6	4	-	-			
Mean	27.50	4.93	40.50	2.63	0.25	3.03	5.10	2.00	$\overset{+++}{4.10}$	2.83	13.6	2.33	2

Yew Barrow (Cont).

Individual No. 19.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	24	4.8	19	4.0	0.25	3.0	5.7	3	5.4	3.3			
East	24	4.0	57	3.2	0.25	2.8	5.3	2	-	-			
South	17	1.9	50	2.0	0.2	2.8	4.2	1	-	-			
West	22	3.8	19	2.8	0.2	2.5	4.4	2	-	-			
Mean	21.75	3.63	36.25	3.00	0.23	2.78	4.90	2.00	$\overset{+}{5.40}$	3.30	13.4	3.09	2

Individual No. 20.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	12	1.2	46	1.7	0.2	2.0	4.0	0	2.0	1.7			
East	22	2.5	54	2.0	0.2	2.6	3.9	2	3.8	2.8			
South	21	2.6	68	1.8	0.2	2.0	4.7	1	-	-			
West	17	1.7	42	1.5	0.2	2.3	3.6	0	2.0	2.0			
Mean	18.00	2.00	52.00	1.75	0.20	2.23	4.05	0.75	$\overset{+++}{2.60}$	2.17	13.6	1.07	1

Yew Barrow (Cont).

Individual No. 21.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	25	4.5	60	1.8	0.2	2.2	4.6	1	2.8	2.0			
East	30	6.3	84	2.3	0.3	2.5	6.3	2	4.3	2.9			
South	20	4.1	66	2.1	0.2	2.4	4.0	6	6.0	3.2			
West	22	4.2	69	2.2	0.2	2.8	5.1	2	-	-			
Mean	24.25	4.78	69.75	2.10	0.23.	2.48	5.00	2.75	$\overset{+++}{4.37}$	2.70	1.48	2	

Individual No. 22.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	18	2.7	43	1.5	0.2	2.3	4.0	0	2.5	2.7			
East	17	3.6	45	2.6	0.25	2.7	5.5	3	-	-			
South	17	3.1	65	2.2	0.2	2.5	3.9	0	-	-			
West	16	2.5	40	2.3	0.25	2.2	4.5	0	-	-			
Mean	17.00	2.98	48.25	2.15	0.23	2.43	4.48	0.75	±2.50	2.70	7.1	1.88	2

Yew Barrow (Cont).

Individual No. 23.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	27	4.8	30	2.9	0.2	3.0	4.3	1	4.2	4.5			
East	22	3.7	100	2.6	0.25	2.5	5.4	2	5.2	2.3			
South	19	3.2	52	2.5	0.2	2.5	3.9	2	3.0	1.3			
West	27	6.5	21	2.5	0.2	2.6	4.3	2	3.6	3.1			
Mean	23.75	4.55	50.75	2.63	0.21	2.65	4.48	1.75	4.00	2.80	10.4	2.08	5

Individual No. 24.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	40	8.7	33	2.5	0.25	2.9	5.4	3	-	-			
East	20	3.5	75	2.1	0.2	2.5	4.9	1	4.6	3.0			
South	25	5.7	67	2.7	0.3	2.8	6.4	1	-	-			
West	25	4.7	45	2.3	0.25	2.6	5.5	2	-	-			
Mean	27.50	5.65	55.00	2.40	0.25	2.70	5.55	1.75	+4.60	3.00	9.6	1.70	2

Yew Barrow (Cont).

Individual No. 25.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	28	4.6	50	2.3	0.25	2.4	5.0	1	-	-			
East	22	3.3	67	2.9	0.3	2.0	6.5	0	-	-			
South	21	2.7	52	2.5	0.3	1.9	6.0	1	2.5	1.8			
West	36	5.5	24	2.7	0.25	2.4	5.3	4	-	-			
Mean	26.75	4.03	48.25	2.60	0.28	2.18	5.70	1.50	+ 2.50	1.80	12.4	1.66	1

Individual No. 26.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	15	2.2	47	2.6	0.2	2.3	4.8	0	2.5	1.8			
East	19	4.3	65	2.8	0.25	2.5	5.6	2	4.8	3.0			
South	32	6.4	38	3.0	0.25	2.5	5.2	0	-	-			
West	19	3.0	53	2.4	0.2	2.5	4.8	1	-	-			
Mean	21.25	3.98	50.75	2.70	0.23	2.45	5.10	0.75	++ 3.65	2.40	16.4	2.52	2

Yew Barrow (Cont).

Individual No. 27.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	27	6.1	25	2.9	0.2	2.7	5.0	3	3.7	3.3			
East	17	2.4	52	2.3	0.2	2.0	4.0	0	5.0	3.0			
South	21	3.9	43	3.2	0.2	2.6	4.5	4	5.9	2.8			
West	27	6.5	39	2.5	0.2	2.3	4.6	5	3.6	3.0			
Mean	23.00	4.73	39.75	2.73	0.20	2.40	4.53	3.00	4.55	3.03	14.5	3.60	9

Individual No. 28.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	26	5.1	41	2.5	0.3	2.0	5.9	2	-	-			
East	15	3.1	53	2.7	0.3	2.4	5.8	1	-	-			
South	29	5.9	74	2.9	0.3	2.0	6.2	1	5.5	4.5			
West	26	5.1	43	2.4	0.25	2.0	5.3	0	-	-			
Mean	24.00	4.80	52.75	2.63	0.29	2.10	5.80	1.00	$\overset{+}{5}$.50	4.50	9.5	2.25	4

Yew Barrow (Cont).

Individual No. 29.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	19	2.3	83	1.3	0.2	2.2	4.5	3	-	-			
East	15	2.0	59	1.9	0.25	2.0	4.7	1	2.2	1.8			
South	29	4.3	55	2.0	0.25	2.3	6.0	3	-	-			
West	30	5.5	68	2.4	0.3	2.6	5.8	4	-	-			
Mean	23.25	3.53	66.25	1.90	0.25	2.28	5.25	2.75	$\overset{+}{2.20}$	1.80	10.2	1.51	1

Individual No. 30.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	8	1.1	22	1.2	0.2	2.0	3.7	0	-	-			
East	21	3.7	49	2.8	0.3	2.4	6.5	2	3.5	2.3			
South	13	1.9	47	2.4	0.3	2.8	5.6	1	3.0	2.0			
West	18	3.6	38	2.3	0.25	2.2	5.6	1	2.5	1.5			
Mean	15.00	2.58	39.00	2.18	0.26	2.35	5.35	1.00	$\overset{+++}{3.00}$	1.93	10.6	1.97	2

Population: Brantingham. Collection date: 4.3.77.

Individual No. 1.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	37	5.6	15.0	2.4	0.25	3.5	5.0	4	4.6	2.7			
East	42	6.5	15.5	2.6	0.20	4.0	5.0	2	4.5	3.6			
South	28	4.6	16.0	2.25	0.20	2.8	4.2	2	3.7	3.2			
West	23	3.4	14.5	2.30	0.20	2.2	4.2	2	2.0	1.6			
Mean	32.50	5.00	15.25	2.37	0.21	3.13	4.60	2.50	3.70	2.78	6.1	0.62	1

Individual No. 2.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	24	4.8	12.0	3.15	0.25	3.5	4.8	1	2.6	2.6			
East	24	4.6	14.5	3.20	0.30	3.4	5.6	3	2.4	2.2			
South	15	2.1	8.4	2.60	0.25	3.5	5.2	2	2.5	1.8			
West	29	7.0	12.0	3.20	0.20	3.8	4.8	1	3.5	3.5			
Mean	23.00	4.63	11.73	3.04	0.25	3.55	5.10	1.75	2.75	2.53	5.5	0.46	2

Brantingham (Cont).

Individual No. 3.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	21	3.15	14.5	2.3	0.2	3.4	4.8	1	2.9	1.5			
East	31	6.7	14.5	1.9	0.2	1.5	4.2	3	4.6	2.9			
South	20	2.7	32.0	2.2	0.25	1.7	5.0	1	3.4	2.0			
West	22	3.9	14.5	2.0	0.21	3.0	4.5	1	3.6	2.5			
Mean	23.50	4.10	18.88	2.10	0.21	2.40	4.62	1.50	3.63	2.23	3.0	0.75	1

Individual No. 4.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	31	6.5	14.5	3.7	0.3	3.5	5.5	4	3.9	2.5			
East	27	4.7	90.0	1.6	0.25	3.7	5.4	2	3.0	2.0			
South	34	6.7	46.0	3.7	0.3	4.1	5.9	2	5.1	2.5			
West	18	4.2	-	3.5	0.2	2.4	5.0	0	DEAD				
Mean	27.50	5.53	50.17	3.13	0.26	3.43	5.45	2.00	4.00	2.33	10.1	0.84	1

Brantingham (Cont).

Individual No. 5.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	34	6.7	36	3.5	0.3	2.8	6.0	4	3.2	2.1			
East	31	5.9	42	3.5	0.25	2.8	5.6	1	3.4	3.1			
South	41	6.7	51	2.1	0.3	3.3	5.0	2	2.0	2.2			
West	27	6.1	46	3.5	0.25	3.1	5.8	2	4.6	2.9			
Mean	33.25	6.35	43.75	3.15	0.28	3.00	5.60	2.25	3.30	2.58	8.0	0.85	1

Individual No. 6.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	36	5.5	60	1.8	0.2	3.5	4.4	4	4.5	2.9			
East	36	6.5	51	1.75	0.2	3.9	4.9	3	5.0	2.9			
South	44	8.1	51	1.6	0.2	3.1	4.3	2	DEAD				
West	21	2.8	69	1.7	0.2	3.1	4.0	2	3.2	2.1			
Mean	34.25	5.73	57.75	1.71	0.20	3.40	4.40	2.75	4.23	2.63	5.1	0.87	3

Brantingham (Cont).

Individual No. 7.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	38	7.6	51	2.6	0.3	3.6	4.6	5	5.7	3.0			
East	62	9.5	42	2.1	0.2	3.7	6.3	4	6.3	2.7			
South	42	7.3	40	2.2	0.2	3.0	4.0	4	6.2	3.4			
West	31	7.0	43.5	2.5	0.2	3.1	5.1	3	5.8	3.1			
Mean	43.25	7.85	44.13	2.35	0.23	3.35	5.00	4.00	6.00	3.05	7.3	0.49	1

Individual No. 8.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	34	6.4	50	2.2	0.3	3.2	4.5	6	4.3	2.7			
East	65	13.1	40	1.7	0.2	3.5	4.8	1	4.2	3.9			
South	44	9.8	45	1.7	0.2	3.3	4.9	5	6.1	3.8			
West	25	7.4	33	1.7	0.2	2.9	4.8	4	2.5	2.0			
Mean	47.00	9.18	42.00	1.83	0.23	3.23	4.75	4.00	4.28	3.10	4.3	0.35	1

Brantingham (Cont).

Individual No. 9.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	22	4.0	32	1.7	0.25	3.1	4.9	2	2.5	1.9			
East	34	6.8	42	2.2	0.25	4.0	5.1	2	4.7	2.7			
South	31	7.1	44	2.15	0.25	3.4	5.3	3	3.4	3.2			
West	21	3.8	42	2.2	0.25	3.1	5.2	1	3.5	3.1			
Mean	27.00	5.43	40.00	2.06	0.25	3.40	5.12	2.00	3.53	2.73	6.1	0.45	1

Individual No. 10.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	3.5	54	2.3	0.3	3.7	5.5	3	3.7	2.1			
East	22	3.5	64	2.1	0.3	3.1	5.8	3	2.7	1.9			
South	28	5.35	56	2.1	0.25	3.6	4.9	0	3.6	2.3			
West	24	4.8	44	2.1	0.25	3.2	4.9	0	4.3	2.8			
Mean	23.50	4.29	54.50	2.15	0.28	3.40	5.27	1.50	3.60	2.28	5.9	0.37	1

Brantingham (Cont).

Individual No. 11.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	37	6.5	50	1.5	0.2	2.0	5.7	3	5.6	3.1			
East	34	6.4	77.5	1.7	0.2	2.2	4.9	3	5.2	3.0			
South	30	5.0	51	1.2	0.2	3.0	5.0	3	5.5	3.2			
West	24	4.5	62	2.1	0.3	3.5	5.3	0	5.1	3.1			
Mean	31.25	5.60	60.13	1.63	0.23	2.68	5.17	2.25	5.35	3.10	6.1	0.56	1

Individual No. 12.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	30	4.3	44	2.5	0.25	3.7	4.7	4	3.5	2.8			
East	31	5.4	40	2.1	0.2	3.1	5.0	4	5.4	4.1			
South	37	6.6	38	2.7	0.25	3.4	6.3	3	5.8	3.6			
West	50	11.4	50	3.1	0.3	4.3	5.0	2	9.1	4.5			
Mean	37.00	6.93	43.00	2.60	0.25	3.63	5.25	3.25	5.95	3.75	10.8	0.75	1

Brantingham (Cont).

Individual No. 13.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	13	1.1	31	1.9	0.2	3.2	5.6	2	3.3	2.4			
East	15	1.9	83	2.0	0.25	3.2	5.2	1	4.5	2.1			
South	29	4.2	63	1.4	0.3	3.9	5.6	1	5.0	4.0			
West	26	4.2	72	2.4	0.25	4.0	4.4	1	4.3	3.0			
Mean	20.75	2.85	62.25	1.93	0.25	3.58	5.20	1.25	4.28	2.88	11.3	1.05	1

Individual No. 14.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	38	7.2	76	2.1	0.25	4.1	5.4	4	4.4	3.4			
East	21	3.4	51	2.0	0.25	3.9	5.5	2	4.5	2.0			
South	15	1.8	79	1.8	0.25	3.6	5.5	2	2.4	2.1			
West	40	8.1	54	2.2	0.3	4.6	5.0	1	4.0	3.0			
Mean	28.50	5.13	65.00	2.03	0.26	4.05	5.35	2.25	3.83	2.63	8.3	0.89	1

Brantingham (Cont).

Individual No. 15.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	32	5.2	29	2.5	0.3	4.0	5.6	2	2.5	3.0			
East	18	3.5	49	2.6	0.3	3.5	5.8	2	2.0	1.9			
South	33	7.3	48	2,35	0.25	2.6	5.6	1	4.1	2.9			
West	16	3.1	71	1.9	0.3	2.4	5.4	1	3.6	2.4			
Mean	24.75	4.78	49.25	2.34	0.29	3.13	5.60	1.50	3.05	2.55	7.9	0.62	1

Individual No. 16.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	42	6.6	64	2.2	0.3	3.6	5.5	5	4.5	3.2			
East	46	9.3	59	2.2	0.3	3.8	5.7	4	5.4	3.8			
South	40	7.0	28	1.9	0.2	3.6	5.8	3	4.6	3.5			
West	33	7.3	48	2.5	0.3	4.0	5.8	2	3.6	2.7			
Mean	40.25	7.55	49.75	2.20	0.28	3.75	5.60	3.50	4.53	3.30	7.5	0.70	1

Brantingham (Cont).

Individual No. 17.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	30	3.7	38	1.9	0.25	2.6	5.9	3	5.3	4.5			
East	20	2.7	80	2.5	0.25	3.4	5.1	3	2.7	2.0			
South	21	2.8	64	2.3	0.3	3.2	5.0	1	3.4	2.7			
West	45	7.8	50	2.8	0.25	3.9	5.6	0	5.8	3.9			
Mean	29.00	4.25	58.00	2.38	0.26	3.28	5.40	1.75	4.30	3.28	10.6	0.64	1

Individual No. 18.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	14	1.1	53.5	1.9	0.2	2.5	6.0	2	2.0	2.0			
East	18	2.8	81	2.35	0.3	3.0	5.6	2	3.1	2.3			
South	44	10.0	84.5	2.9	0.3	4.0	5.0	0	4.6	2.7			
West	24	4.4	65	3.1	0.3	3.4	5.8	0	DEAD				
Mean	25.00	4.58	71.00	2.56	0.28	3.23	5.60	1.00	3.23	2.33	7.2	1.11	4

Brantingham (Cont).

Individual No. 19.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	26	4.2	36	2.6	0.3	3.7	5.3	4	4.3	3.1			
East	15	2.4	80	2.2	0.25	3.1	5.2	1	3.6	2.4			
South	18	2.5	39	2.2	0.25	3.2	4.7	0	3.0	1.6			
West	34	5.4	66	2.1	0.2	3.3	5.5	0	4.5	3.6			
Mean	23.25	3.63	55.25	2.28	0.25	3.33	5.17	1.25	3.85	2.68	4.8	0.35	1

Individual No. 20.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	21	3.7	52	1.8	0.35	3.1	5.0	1	3.1	2.1			
East	25	3.3	50	1.8	0.3	3.3	6.8	3	3.0	2.7			
South	21	2.5	64	1.9	0.35	2.5	6.0	0	3.2	2.9			
West	28	3.7	49	2.2	0.36	3.3	6.9	0	3.4	3.0			
Mean	23.75	3.30	53.75	1.93	0.34	3.05	6.18	1.00	3.18	2.68	6.5	0.75	2

Brantingham (Cont).

Individual No. 21.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	31	4.4	51	2.1	0.25	3.0	6.0	3	3.5	2.9			
East	35	6.7	55	2.8	0.3	3.5	5.4	2	4.1	3.5			
South	23	5.2	41	2.3	0.3	3.6	5.0	1	5.0	3.0			
West	30	5.9	75	2.0	0.3	3.6	5.0	3	DEAD				
Mean	29.75	5.55	55.50	2.30	0.29	3.43	5.60	2.25	4.20	3.13	5.9	0.49	1

Individual No. 22.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	33	4.6	49	1.75	0.25	3.0	4.6	1	4.0	2.9			
East	22	3.1	58	1.9	0.3	2.5	6.0	4	4.4	2.6			
South	40	6.5	51	1.7	0.25	3.1	5.6	1	4.4	2.8			
West	19	2.7	72	2.1	0.3	2.5	5.8	1	3.0	2.0			
Mean	28.50	4.23	57.50	1.86	0.28	2.78	5.50	1.75	3.95	2.58	8.8	0.89	1

Brantingham (Cont).

Individual No. 23.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	50	8.0	62	1.9	0.3	3.2	6.0	4	3.2	2.7			
East	38	4.5	80	1.7	0.25	3.0	5.6	2	4.4	2.3			
South	30	4.2	52	2.1	0.3	3.4	5.0	2	4.0	2.5			
West	25	3.0	75	1.8	0.25	2.4	5.8	1	2.0	2.0			
Mean	35.75	4.93	67.25	1.88	0.28	3.00	5.60	2.25	3.40	2.38	6.1	9.54	1

Individual No. 24.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	49	6.1	40	2.3	0.25	3.5	5.3	5	5.7	3.5			
East	38	4.6	70	2.9	0.25	3.4	5.0	1	3.8	3.2			
South	36	5.5	52	2.2	0.25	3.3	5.8	4	5.0	2.8			
West	34	4.0	53	2.5	0.25	3.3	4.8	2	5.0	2.8			
Mean	39.25	5.05	53.75	2.48	0.25	3.38	5.22	3.00	4.88	3.08	5.3	0.64	2

Brantingham (Cont).

Individual No. 25.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	28	5.9	49.5	2.3	0.3	3.7	5.8	1	3.7	3.1			
East	22	4.3	50	2.3	0.25	3.4	5.6	2	3.5	3.0			
South	19	3.85	43	2.8	0.3	4.0	5.3	2	4.2	3.3			
West	17	3.4	32	2.8	0.25	3.0	5.5	1	4.7	2.9			
Mean	21.50	4.36	43.63	2.55	0.28	3.53	5.55	1.50	4.03	3.08	7.5	0.52	1

Individual No. 26.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	13	2.1	56	2.1	0.3	3.4	5.0	1	3.5	3.2			
East	22	2.9	62	2.0	0.25	3.4	5.9	2	3.1	2.7			
South	34	5.4	45	1.9	0.25	4.0	5.2	1	4.1	3.8			
West	21	2.8	45	2.2	0.25	3.6	4.9	1	3.7	2.8			
Mean	22.50	3.30	52.00	2.05	0.26	3.60	5.25	1.25	3.60	3.13	7.0	0.56	1

Brantingham (Cont).

Individual No. 27.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	17	3.2	58	2.0	0.3	2.9	5.9	2	2.5	2.0			
East	39	6.8	53	2.0	0.25	3.6	5.1	2	6.7	3.6			
South	25	4.4	71	1.6	0.25	3.6	5.0	3	3.4	2.9			
West	26	4.2	53	1.8	0.25	2.8	5.2	0	3.4	2.9			
Mean	26.75	4.65	58.75	1.85	0.26	3.23	5.30	1.75	4.00	2.85	9.6	0.91	1

Individual No. 28.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	-	-	-	-	-	-	-	-	-	-			
East	29	5.7	32	1.9	0.2	3.7	5.8	4	5.0	2.9			
South	50	7.8	54	1.9	0.25	4.2	5.0	3	3.1	2.6			
West	24	3.7	41	1.9	0.25	4.0	3.5	2	3.4	2.6			
Mean	34.33	5.73	42.33	1.90	0.23	3.97	4.76	3.00	3.83	2.70	7.3	0.73	2

Brantingham (Cont).

Individual No. 29.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	3.5	49	2.1	0.25	3.5	4.8	2	2.3	2.0			
East	28	5.2	65	2.3	0.3	3.3	5.8	1	3.9	2.9			
South	22	3.6	64	2.2	0.3	3.0	5.8	3	4.5	2.6			
West	27	4.1	63	1.8	0.25	3.1	6.1	0	3.9	2.9			
Mean	25.00	4.10	60.25	2.10	0.28	3.23	5.57	1.50	3.65	2.60	5.1	0.59	1

Individual No. 30.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	3.3	49	2.5	0.25	2.2	5.1	3	DEAD				
East	21	4.7	59	2.8	0.3	3.1	6.1	1	5.8	3.2			
South	18	2.3	66	2.7	0.25	2.6	5.3	0	3.7	2.9			
West	27	6.6	51	2.5	0.3	3.0	6.3	0	4.6	3.1			
Mean	21.50	4.23	56.25	2.63	0.28	2.73	5.70	1.00	4.70	3.07	7.5	0.78	1

Brantingham (Cont).

Individual No. 31.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	31	5.2	62	2.7	0.25	4.4	5.0	2	4.0	3.2			
East	41	5.9	45	2.2	0.3	4.2	4.5	4	4.7	3.9			
South	18	3.1	38	2.0	0.2	3.8	4.6	1	4.0	3.1			
West	27	3.0	44	2.0	0.25	3.6	6.2	2	2.3	2.4			
Mean	29.25	4.30	47.25	2.23	0.25	4.00	5.08	2.25	3.75	3.15	8.5	0.54	1

Individual No. 32.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	22	5.4	30	3.3	0.3	3.5	6.0	2	4.5	3.4			
East	19	3.5	42	2.5	0.25	2.5	6.1	1	4.8	2.9			
South	23	4.8	38	3.3	0.3	3.4	5.8	1	3.9	2.5			
West	21	5.5	55	4.9	0.35	3.3	6.1	0	4.3	3.5			
Mean	21.25	4.80	41.25	3.50	0.30	3.18	6.00	1.00	4.38	3.08	13.8	2.04	3

Brantingham (Cont).

Individual No. 33.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	35	4.0	48	2.8	0.2	3.5	5.0	5	DEAD				
East	25	2.4	63	2.2	0.2	4.9	4.0	4	3.6	3.7			
South	43	5.2	47	2.3	0.2	4.6	4.7	2	3.5	3.1			
West	20	2.6	36	2.0	0.2	3.6	3.9	2	2.7	2.5			
Mean	30.75	3.55	48.50	2.33	0.20	4.15	4.40	3.25	3.27	3.10	10.5	1.54	3

Population: Guisborough. Collection date: 15.3.77.

Individual No. 1.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	14	1.7	33	1.7	0.2	1.25	4.6	0	1.7	1.5			
East	81	14	36	2.3	0.2	2.5	4.5	10	6.5	4.3			
South	103	19.5	54	2.6	0.25	3.7	5.9	10	4.5	4.0			
West	39	5.0	45	1.5	0.2	3.3	4.3	2	3.5	3.6			
Mean	59.25	10.05	42.00	2.03	0.21	2.70	4.80	5.50	4.10	3.40	6.1	0.68	1

Individual No. 2.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	45	6.5	35	1.7	0.2	3.5	5.0	4	4.3	3.0			
East	78	12.1	43	2.4	0.25	3.5	5.1	7	4.5	3.8			
South	98	15.5	62	2.5	0.3	5.0	6.0	8	4.0	3.7			
West	27	4.1	60	1.8	0.2	3.4	4.6	0	DEAD				
Mean	62.00	9.55	50.00	2.10	0.24	3.85	5.20	4.75	4.30	3.50	6.8	0.71	3

Guisborough (Cont).

Individual No. 3.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	67	19.9	46	2.6	0.25	4.5	6.0	9	5.0	3.5			
East	19	2.0	59	1.9	0.2	1.9	5.0	1	1.0	1.0			
South	25	2.9	49	1.6	0.2	3.0	4.6	2	2.6	2.3			
West	54	6.6	85	2.0	0.25	4.0	5.9	4	4.8	3.9			
Mean	41.25	7.85	59.75	2.03	0.23	3.35	5.40	4.00	3.35	2.68	7.4	2.01	3

Individual No. 4.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	32	5.9	51	2.6	0.3	3.0	5.1	3	3.8	2.8			
East	47	9.2	41	2.4	0.3	4.3	5.5	4	DEAD				
South	48	8.2	58	2.5	0.3	3.2	5.2	3	2.8	2.3			
West	60	13.0	34	2.5	0.3	3.8	5.6	9	7.0	3.8			
Mean	46.75	9.08	46.00	2.50	0.30	3.58	5.35	4.75	4.53	2.97	9.6	2.44	4

Guisborough (Cont).

Individual No. 5.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	38	8.3	48	2.4	0.3	3.0	5.5	3	4.3	2.9			
East	45	10.0	43	2.8	0.3	3.6	6.1	4	3.6	2.8			
South	39	6.2	40	1.5	0.25	2.5	5.1	2	3.5	2.9			
West	34	7.8	52	2.3	0.3	3.5	5.2	3	3.8	3.0			
Mean	39.00	8.07	45.75	2.25	0.29	3.15	5.48	3.00	3.80	2.90	8.7	1.7	2

Individual No. 6.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	27	3.3	36	1.8	0.2	2.6	4.0	2	3.0	2.7			
East	25	3.0	41	2.0	0.2	2.1	5.1	0	2.8	1.8			
South	29	3.6	48	2.0	0.2	3.0	4.9	1	3.5	3.0			
West	22	2.5	75	1.6	0.2	2.5	4.0	0	3.5	2.0			
Mean	25.75	3.10	50.80	1.85	0.20	2.55	4.50	0.75	3.20	2.38	8.5	1.56	2

Guisborough (Cont).

Individual No. 7.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	13	1.2	64	2.0	0.3	2.5	6.0	0	1.9	1.6			
East	24	3.2	49	2.0	0.3	3.1	6.0	2	3.6	2.8			
South	27	3.4	48	1.2	0.25	2.9	5.3	2	3.2	2.4			
West	14	1.4	57	1.3	0.25	1.5	5.1	0	2.0	1.4			
Mean	19.50	2.30	54.50	1.63	0.28	2.50	5.60	1.00	2.68	2.05	9.5	0.95	1

Individual No. 8.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	31	4.5	36	1.6	0.25	3.6	4.9	3	5.2	2.6			
East	24	3.4	39	1.6	0.25	3.9	5.0	3	3.8	2.5			
South	25	3.9	56	1.8	0.3	3.0	5.6	0	3.8	2.4			
West	29	4.4	41	2.0	0.3	3.5	5.2	4	4.0	2.6			
Mean	27.25	4.05	43.00	1.75	0.28	3.50	5.18	2.50	4.20	2.50	10.0	2.40	2

Guisborough (Cont).

Individual No. 9.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	61	12	46	2.0	0.3	3.0	6.0	7	8.0	4.8			
East	33	4.8	43	1.6	0.25	2.5	4.8	1	5.6	3.7			
South	19	2.7	74	2.1	0.3	2.3	5.6	0	3.0	2.2			
West	29	3.3	29	1.5	0.25	2.5	5.0	4	4.2	3.0			
Mean	35.50	5.70	48.00	1.80	0.28	2.58	5.35	3.00	5.20	3.43	8.7	1.26	1

Individual No. 10.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	25	4.3	53	2.8	0.3	4.0	6.2	0	4.0	3.0			
East	24	4.2	34	2.0	0.2	2.0	5.0	0	4.7	2.7			
South	20	3.7	35	2.8	0.3	2.5	5.2	0	3.5	2.2			
West	21	3.8	51	2.7	0.3	2.5	5.5	0	5.0	3.4			
Mean	22.50	4.00	43.25	2.58	0.28	2.75	5.48	0.00	4.30	2.83	11.5	3.62	4

Guisborough (Cont).

Individual No. 11.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	23	3.0	22	1.8	0.2	2.5	4.5	0	3.4	2.5			
East	5	0.3	41	1.5	0.2	3.0	4.1	0	1.8	1.6			
South	84	16	50	3.2	0.3	3.7	6.4	12	9.1	5.3			
West	62	10	58	2.2	0.3	3.0	5.4	7	6.0	3.9			
Mean	43.50	7.33	42.75	2.18	0.25	3.05	5.10	4.75	5.08	3.33	6.8	0.72	2

Individual No. 12.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	28	6.3	52	3.4	0.3	2.3	6.8	2	4.4	2.9			
East	21	3.2	58	2.5	0.3	2.6	5.8	1	4.7	2.7			
South	77	16	66	3.6	0.35	3.8	6.6	15	8.5	8.3			
West	32	5.0	45	2.3	0.3	2.7	5.5	0	3.7	2.6			
Mean	39.50	7.63	55.25	2.95	0.31	2.85	6.18	4.50	5.33	4.13	9.0	2.22	2

Guisborough (Cont).

Individual No. 13.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	19	2.8	50	1.9	0.3	2.8	5.4	1	4.5	3.2			
East	27	5.3	47	1.8	0.3	2.6	6.0	1	5.0	3.6			
South	29	5.8	29	2.3	0.25	3.5	5.4	2	4.4	3.5			
West	25	4.7	58	2.5	0.3	2.7	6.5	0	3.0	2.3			
Mean	25.00	4.65	46.00	2.13	0.29	2.90	5.83	1.00	4.23	3.15	9.7	1.05	1

Individual No. 14.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	27	3.5	26	1.3	0.2	4.0	3.6	0	6.4	3.6			
East	10	1.3	70	1.7	0.2	4.0	5.5	0	DEAD				
South	15	2.5	58	2.1	0.25	3.2	5.8	0	1.5	1.5			
West	14	1.8	38	1.1	0.2	4.0	4.9	0	3.0	2.4			
Mean	16.50	2.28	48.00	1.55	0.21	3.80	4.95	0.00	3.63	2.50	13.8	1.45	1

Guisborough (Cont).

Individual No. 15.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	29	3.0	52	1.6	0.2	2.9	4.6	2	4.0	3.3			
East	13	2.0	40	1.5	0.2	3.4	4.4	0	5.1	3.3			
South	21	3.2	39	2.1	0.25	2.0	5.1	0	2.5	2.1			
West	17	2.0	57	2.7	0.2	3.0	4.7	1	3.6	3.3			
Mean	20.00	2.55	47.00	1.98	0.21	2.83	4.70	0.75	3.80	3.00	10.2	1.72	1

Individual No. 16.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	43	5.9	71	2.2	0.25	3.1	4.8	5	4.6	3.1			
East	32	4.1	57	2.0	0.25	3.4	4.6	2	4.9	3.4			
South	16	2.2	68	1.8	0.2	2.5	4.7	0	1.8	1.4			
West	38	8.7	58	2.0	0.25	3.2	5.5	4	5.2	3.7			
Mean	32.25	5.23	63.50	2.00	0.24	3.05	4.90	2.75	4.13	2.90	6.5	0.95	2

Guisborough (Cont).

Individual No. 17.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	3.8	63	2.2	0.3	3.0	6.3	0	3.2	2.5			
East	20	2.5	56	2.0	0.25	2.6	5.3	0	2.4	2.0			
South	24	4.2	67	2.7	0.3	3.6	5.8	0	2.7	2.1			
West	16	2.3	29	2.7	0.3	2.9	5.9	0	2.5	1.8			
Mean	20.00	3.20	53.75	2.40	0.29	3.03	5.83	0.00	2.70	2.10	8.3	0.91	1

Individual No. 18.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	26	4.5	75	1.7	0.25	2.0	4.7	2	3.4	2.7			
East	31	4.9	42	1.6	0.2	2.4	4.7	0	5.2	3.1			
South	32	6.0	66	2.0	0.3	2.9	5.4	2	5.2	2.7			
West	41	7.0	52	2.1	0.25	3.4	5.4	5	4.9	3.0			
Mean	32.50	5.60	58.75	1.85	0.25	2.68	5.05	2.25	4.68	2.88	8.1	1.15	1

Guisborough (Cont).

Individual No. 19.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	27	3.8	47	2.3	0.3	2.9	5.5	0	1.9	1.7			
East	24	3.7	53	2.1	0.25	2.7	5.2	0	2.1	1.5			
South	20	2.6	60	1.75	0.25	3.0	4.6	0	4.1	3.0			
West	29	5.2	51	2.3	0.3	3.0	6.0	0	2.1	1.7			
Mean	25.00	3.83	52.75	2.11	0.28	2.90	5.33	0.00	2.55	1.90	10.2	1.89	2

Individual No. 20.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	24	6.3	40	3.2	0.3	2.3	5.6	1	4.1	2.4			
East	17	2.8	49	2.0	0.2	2.0	4.6	0	2.2	1.9			
South	5	0.7	47	2.2	0.2	1.8	4.5	0	DEAD				
West	26	8.6	33	3.4	0.3	3.0	5.5	2	5.3	3.6			
Mean	18.00	4.60	42.25	2.70	0.25	2.28	5.05	0.75	3.87	2.63	6.6	1.26	1

Guisborough (Cont).

Individual No. 21.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	19	2.1	66	1.5	0.25	2.0	4.8	0	4.6	3.1			
East	16	1.7	85	1.3	0.2	1.5	4.2	0	2.0	1.4			
South	25	3.5	47	1.6	0.25	2.5	5.0	0	1.9	1.6			
West	21	2.3	86	1.1	0.2	1.5	4.5	0	3.3	2.7			
Mean	20.25	2.40	71.00	1.38	0.23	1.88	4.63	0.00	2.95	2.20	9.0	2.90	2

Individual No. 22.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	32	4.0	45	1.7	0.25	2.4	5.0	3	5.2	3.0			
East	21	3.2	36	2.0	0.25	2.7	5.3	2	3.0	2.6			
South	22	3.0	76	2.5	0.3	2.6	5.9	0	2.8	2.0			
West	26	3.2	56	1.7	0.25	1.8	4.9	2	2.4	1.9			
Mean	25.25	3.35	53.25	1.98	0.26	2.38	5.28	1.75	3.35	2.38	7.0	1.03	1

Guisborough (Cont).

Individual No. 23.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	39	9.6	41	3.7	0.3	3.0	5.7	4	7.0	3.9			
East	16	4.2	53	5.0	0.3	3.2	6.0	0	DEAD				
South	13	2.5	75	2.5	0.2	1.5	4.7	0	DEAD				
West	19	3.4	31	2.7	0.25	3.0	4.5	0	3.0	2.2			
Mean	21.75	4.93	50.00	3.48	0.26	2.68	5.23	1.00	5.00	3.05	9.0	1.23	1

Individual No. 24.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	20	3.8	45	2.1	0.25	3.0	5.4	2	3.5	2.8			
East	18	3.9	43	2.7	0.3	3.0	5.6	3	5.3	2.6			
South	20	3.5	40	2.8	0.3	3.0	5.2	1	3.8	2.5			
West	18	3.6	37	2.4	0.35	2.6	5.8	2	3.0	2.2			
Mean	19.00	3.70	41.25	2.50	0.30	2.90	5.50	2.00	3.90	2.53	12.0	2.58	2

Guisborough (Cont).

Individual No. 25.

	NLY	LYG	AL	LL	BL	LP	DL	NBY	BL	BB	HT	DT	NB
North	24	2.8	74	2.1	0.2	3.0	4.1	0	4.2	2.8			
East	15	1.8	49	1.5	0.2	2.5	4.1	1	2.0	1.9			
South	8	1.1	65	1.2	0.2	1.3	3.8	0	DEAD				
West	21	4.1	57	2.4	0.3	2.5	6.1	0	3.0	1.7			
Mean	17.00	2.45	61.25	1.80	0.23	2.33	4.53	0.25	3.07	2.13	11.0	1.34	1

APPENDIX 2.

Raw data of the cold hardiness experiment.

A. Conductivity results after freezing at the control and test temperatures.

B. Conductivity results after killing at + 120°C. (Conductivity units:- 10^{-5} ohms $^{-1}$ cm $^{-1}$).

Population: Butser Hill. **Test month**: November, 1977.

A.

Replicates.

°C.	1	2	3	4	5
+2	1.75	1.75	2.00	2.00	1.88
-2	2.00	2.00	2.00	1.75	1.94
-6	2.00	2.00	2.00	1.75	1.94
-10	2.25	2.50	2.50	2.25	2.38
-14	3.00	3.00	3.00	3.50	3.13
-18	4.25	3.75	5.25	3.75	4.25

B.

°C.	1	2	3	4	5
+2	17.25	18.0	19.0	18.00	18.06
-2	19.75	20.50	19.00	19.25	19.63
-6	19.00	18.25	19.00	17.50	18.44
-10	20.00	20.75	20.0	19.75	20.13
-14	18.50	20.50	19.25	18.50	19.19
-18	18.75	18.50	18.50	19.00	18.69

Population: Wyre Forest.

A.

Replicates.

°C.	1	2	3	4	5
+2	5.00	5.75	5.00	4.50	5.00
-2	4.50	5.00	5.00	4.25	5.75
-6	5.50	4.50	5.50	5.00	5.25
-10	6.00	5.75	6.00	6.00	6.00
-14	8.00	7.00	8.00	8.25	7.00
-18	9.00	9.50	10.00	9.50	12.00

B.

°C.	1	2	3	4	5
+2	53.00	54.00	52.50	51.50	51.00
-2	50.00	53.00	52.50	54.50	53.00
-6	53.00	52.00	51.00	52.00	50.00
-10	53.50	53.25	51.50	53.00	54.00
-14	55.50	53.00	51.50	54.00	54.75
-18	51.00	52.00	55.75	52.00	54.25

Population: Overton Hall.

A.

Replicates.

°C.	1	2	3	4	5
+2	3.50	3.00	3.00	3.00	3.00
-2	3.50	3.00	3.50	3.50	3.50
-6	3.75	4.00	3.75	3.50	3.25
-10	4.25	4.50	5.00	5.00	5.00
-14	6.50	6.00	6.50	6.50	8.00
-18	10.00	6.00	8.00	9.00	10.00

B.

°C.	1	2	3	4	5
+2	33.25	33.50	33.50	34.00	34.50
-2	34.00	32.50	35.00	35.00	36.00
-6	35.00	35.50	34.50	33.50	33.00
-10	33.00	34.50	36.00	35.00	35.50
-14	34.00	35.00	33.50	34.50	35.50
-18	37.00	30.50	32.50	32.00	32.50

Population: Yew Barrow.

A.

Replicates.

°C.	1	2	3	4	5
+2	1.50	2.00	1.50	2.00	2.00
-2	1.50	2.00	2.00	1.75	2.00
-6	2.00	2.00	2.00	2.00	2.50
-10	3.00	3.00	3.00	3.50	2.75
-14	7.00	6.00	6.00	6.00	7.00
-18	-	8.50	7.00	9.50	10.50

B.

°C.	1	2	3	4	5
+2	22.00	27.50	26.00	24.50	25.50
-2	24.00	27.50	25.00	24.50	25.25
-6	24.50	27.00	23.00	28.00	25.50
-10	26.00	27.00	26.00	23.50	24.50
-14	29.50	28.00	27.00	27.00	26.50
-18	-	28.00	25.50	28.50	22.00

Population: Brantingham.

A.

Replicates.

°C.	1	2	3	4	5
+2	5.50	5.00	5.00	7.00	5.50
-2	6.50	5.50	7.00	8.00	6.50
-6	9.00	9.00	8.50	8.00	8.50
-10	10.00	10.50	10.00	12.00	12.00
-14	12.50	14.00	12.00	10.00	11.00
-18	13.50	11.00	14.00	11.50	13.00

B.

°C.	1	2	3	4	5
+2	38.00	39.50	39.00	45.00	40.50
-2	41.50	43.00	39.50	43.50	41.00
-6	42.50	43.00	41.50	41.50	45.00
-10	41.50	42.50	42.50	41.00	41.50
-14	43.00	44.00	44.00	41.50	43.00
-18	41.50	41.00	43.00	44.00	41.00

Population: Guisborough.

A.

Replicates.

°C.	1	2	3	4	5
+2	5.50	6.00	5.00	5.00	5.00
-2	4.50	5.00	5.50	5.00	4.00
-6	5.00	5.00	5.00	6.00	4.50
-10	6.50	6.50	6.00	6.00	5.50
-14	14.00	9.50	9.00	10.50	10.00
-18	15.00	14.50	14.00	14.00	11.50

B.

°C.	1	2	3	4	5
+2	41.00	48.00	49.00	47.00	48.00
-2	44.00	42.00	47.00	46.00	41.00
-6	47.00	44.00	42.50	46.00	44.50
-10	46.00	45.00	44.50	44.50	47.00
-14	46.00	46.00	47.00	46.00	42.00
-18	48.00	46.00	42.00	45.00	44.00

Population: Butser Hill. **Test month**: January, 1978.

A.

°C.	Replicates.				
	1	2	3	4	5
+2	3.75	3.50	3.00	2.75	2.75
-2	2.50	2.50	2.25	3.00	2.75
-6	2.50	2.75	2.75	2.50	3.00
-10	3.00	3.25	3.50	3.25	3.00
-14	4.00	3.25	4.75	4.00	4.00
-18	5.00	5.00	4.75	4.75	4.25

B.

°C.	1	2	3	4	5
+2	31.50	30.00	29.50	31.00	31.25
-2	28.00	32.00	31.00	30.00	29.50
-6	29.50	29.00	29.00	31.00	29.25
-10	32.50	32.50	32.50	30.00	33.50
-14	31.25	30.00	32.50	32.50	34.25
-18	31.75	32.50	31.75	31.50	30.50

Population: Wyre Forest.

A.

Replicates.

°C.	1	2	3	4	5
+2	3.00	2.75	3.00	3.00	3.00
-2	3.50	3.00	3.00	3.00	3.00
-6	3.50	3.75	3.75	3.00	3.25
-10	4.00	4.00	4.00	3.50	3.50
-14	6.25	5.75	6.00	6.75	6.00
-18	9.00	7.25	9.00	8.00	8.50

B.

°C.	1	2	3	4	5
+2	33.00	35.00	35.00	33.00	34.75
-2	37.25	31.50	32.25	35.75	35.50
-6	36.00	34.25	36.25	33.50	35.50
-10	33.00	35.00	35.75	35.00	33.50
-14	35.75	33.00	33.50	36.00	35.50
-18	34.00	36.00	36.25	35.00	39.00

Population: Overton Hall.

A.

Replicates.

°C.	1	2	3	4	5
+2	4.00	4.25	4.25	4.25	4.25
-2	4.00	4.75	4.00	4.00	4.00
-6	3.75	4.00	4.00	3.75	4.00
-10	4.75	4.50	4.25	3.75	4.25
-14	6.00	5.00	5.00	5.00	5.75
-18	5.00	6.50	5.50	5.75	6.00

B.

°C.	1	2	3	4	5
+2	36.25	36.00	38.50	35.00	36.75
-2	36.50	37.00	35.25	38.00	39.00
-6	36.00	34.00	39.75	38.00	35.50
-10	41.00	35.50	37.25	37.50	38.00
-14	35.50	38.25	31.75	38.00	38.00
-18	39.25	38.50	36.75	38.00	38.00

Population: Yew Barrow.

A.

Replicates.

°C.	1	2	3	4	5
+2	2.75	3.00	3.50	2.75	2.75
-2	2.50	2.50	3.00	3.00	2.75
-6	3.00	3.00	3.00	3.50	-
-10	3.75	3.75	3.50	3.75	3.50
-14	4.75	5.25	4.75	4.00	3.25
-18	3.25	6.00	4.25	6.00	5.75

B.

°C.	1	2	3	4	5
+2	33.00	33.00	33.50	29.00	30.75
-2	31.50	30.75	33.00	32.75	28.25
-6	32.00	35.00	35.25	35.25	-
-10	33.00	30.00	32.50	27.00	33.50
-14	29.50	31.75	33.00	32.50	31.75
-18	33.75	30.50	29.50	31.50	29.00

Population: Brantingham.

A.

Replicates.

°C.	1	2	3	4	5
+2	3.75	3.75	3.50	3.50	5.00
-2	3.25	4.25	4.00	3.50	3.75
-6	4.25	3.75	4.25	4.25	3.25
-10	4.50	6.00	5.50	4.50	4.75
-14	5.25	5.00	5.50	5.00	5.25
-18	5.00	5.75	5.75	6.00	6.00

B.

°C.	1	2	3	4	5
+2	38.50	37.00	40.00	41.00	41.25
-2	35.00	40.00	40.00	41.00	41.50
-6	40.50	41.00	43.00	40.00	41.00
-10	40.00	41.75	41.50	42.25	42.50
-14	37.75	40.00	41.00	39.50	39.00
-18	39.00	40.50	40.50	40.25	41.75

Population: Guisborough.

A.

Replicates.

°C.	1	2	3	4	5
+2	4.00	4.00	4.50	3.75	4.75
-2	6.00	3.75	4.00	4.00	3.75
-6	4.25	4.25	3.25	4.25	6.00
-10	4.50	5.25	4.75	6.00	7.00
-14	5.00	5.25	7.25	5.50	5.50
-18	13.00	11.00	9.00	8.50	11.00

B.

°C.	1	2	3	4	5
+2	49.00	47.50	49.50	49.50	50.00
-2	49.50	48.50	48.00	50.50	48.00
-6	50.00	48.50	43.50	48.00	51.50
-10	50.00	45.50	48.00	50.00	47.25
-14	47.50	45.75	47.00	46.00	44.25
-18	45.00	49.00	48.00	45.75	48.50

Population: Butser Hill. **Test month:** March, 1978.

A.

Replicates.

°C.	1	2	3	4	5
+2	1.50	1.50	1.25	1.75	1.75
-2	1.50	2.00	1.75	1.50	1.75
-6	1.75	1.75	1.50	1.50	1.50
-10	2.00	1.75	2.00	1.75	1.75
-14	3.50	2.75	2.75	3.50	3.50
-18	7.50	6.25	6.25	7.75	-

B.

°C.	1	2	3	4	5
+2	14.00	13.25	12.75	13.75	11.75
-2	11.75	13.00	12.25	13.75	13.00
-6	11.50	12.75	12.00	13.00	11.75
-10	13.00	12.25	13.00	12.00	12.25
-14	12.75	13.50	12.25	13.75	14.00
-18	14.00	14.00	13.00	15.00	-

<u>**Population**</u>: Wyre Forest.

A.

<u>Replicates.</u>

°C.	1	2	3	4	5
+2	3.25	3.25	3.50	3.25	3.5
-2	3.75	3.50	3.75	3.75	3.5
-6	3.50	3.25	4.00	3.50	3.75
-10	4.00	4.25	4.25	5.00	4.50
-14	7.00	7.00	7.00	6.75	6.00
-18	11.00	11.25	12.00	10.75	11.75

B.

°C.	1	2	3	4	5
+2	29.00	29.00	28.00	30.00	28.50
-2	29.00	25.25	28.25	29.25	29.00
-6	26.75	26.00	31.00	29.25	29.00
-10	25.00	26.00	29.25	29.25	29.50
-14	26.25	26.75	28.25	30.25	28.25
-18	30.25	29.00	29.00	29.50	29.25

Population: Overton Hall.

A.

Replicates.

°C.	1	2	3	4	5
+2	4.75	4.25	5.00	4.00	4.50
-2	4.00	4.00	4.00	4.00	3.75
-6	4.00	4.75	4.00	4.25	3.75
-10	4.25	4.00	5.50	5.00	5.00
-14	8.75	8.75	8.50	8.25	8.00
-18	16.25	12.25	12.00	13.00	18.00

B.

°C.	1	2	3	4	5
+2	30.25	32.00	31.75	27.75	30.00
-2	29.00	27.00	27.25	29.00	29.00
-6	31.75	31.50	29.25	30.25	30.00
-10	28.00	27.00	30.75	27.75	28.25
-14	27.50	28.00	28.00	29.00	29.50
-18	30.50	26.25	27.75	26.25	31.00

Population: Yew Barrow.

A.

Replicates.

°C.	1	2	3	4	5
+2	2.00	1.75	1.75	1.50	1.75
-2	2.00	1.75	1.50	2.00	2.00
-6	2.25	2.00	2.00	2.00	2.25
-10	2.50	2.25	2.50	2.25	2.25
-14	4.25	3.00	4.50	4.25	3.75
-18	5.75	5.75	6.25	6.25	5.00

B.

°C.	1	2	3	4	5
+2	17.25	16.50	13.50	14.25	15.00
-2	15.50	14.75	15.00	14.25	15.75
-6	17.00	16.00	15.50	17.25	15.00
-10	15.50	17.00	16.75	16.50	15.50
-14	17.00	15.25	16.00	16.50	16.25
-18	16.25	16.00	17.25	16.75	15.75

Population: Brantingham.

A.

Replicates.

°C.	1	2	3	4	5
+2	4.50	4.00	4.50	3.50	4.00
-2	5.50	4.75	5.00	4.75	4.50
-6	5.25	5.25	4.75	5.00	5.00
-10	5.75	5.00	5.25	5.25	5.50
-14	7.25	6.00	7.25	7.00	6.25
-18	8.00	7.50	7.50	7.75	7.75

B.

°C.	1	2	3	4	5
+2	31.50	31.00	33.25	30.00	32.00
-2	30.50	32.50	32.75	31.25	31.50
-6	30.00	32.00	27.75	33.50	32.00
-10	32.50	32.00	30.50	32.50	31.75
-14	31.25	31.50	30.00	31.75	29.50
-18	30.00	29.50	29.50	30.00	29.00

Population: Guisborough.

A.

Replicates.

°C.	1	2	3	4	5
+2	4.75	7.00	9.50	6.25	7.00
-2	6.25	6.00	8.00	12.25	6.75
-6	10.50	9.25	12.00	8.00	8.50
-10	12.25	12.25	11.75	9.75	9.25
-14	13.25	19.00	18.00	19.00	14.75
-18	22.50	28.50	19.25	-	-

B.

°C.	1	2	3	4	5
+2	39.25	44.00	42.50	44.00	44.75
-2	39.50	40.00	45.25	46.00	44.00
-6	44.25	43.00	49.00	42.75	43.00
-10	49.00	47.25	48.25	42.00	41.75
-14	44.50	46.00	48.75	48.75	43.75
-18	48.75	47.75	48.00	-	-

Population: Butser Hill. **Test month:** May, 1978.

A.

Replicates.

°C.	1	2	3	4	5
+2	2.00	1.75	2.00	2.00	2.00
-2	2.25	2.25	2.00	2.25	2.00
-6	6.00	5.50	5.75	6.00	6.00
-10	12.75	13.50	14.25	14.00	13.00
-14	17.25	16.00	16.75	15.00	16.25
-18	16.00	27.00	16.50	17.25	18.50

B.

°C.	1	2	3	4	5
+2	15.25	16.00	16.75	16.00	17.50
-2	17.25	17.25	17.25	16.25	16.75
-6	18.00	17.25	17.00	17.00	18.75
-10	18.00	18.50	18.25	18.50	17.50
-14	19.50	18.75	18.75	18.00	18.00
-18	17.75	19.00	18.25	19.00	20.00

Population: Wyre Forest.

A.

Replicates.

°C.	1	2	3	4	5
+2	2.00	2.00	2.00	2.00	2.00
-2	2.25	2.00	2.00	2.25	1.75
-6	4.25	3.75	4.25	3.25	4.00
-10	15.00	14.00	12.25	10.25	12.00
-14	15.75	18.00	17.25	17.25	17.50
-18	18.25	19.25	17.50	18.0	19.50

B.

°C.	1	2	3	4	5
+2	16.25	18.25	16.25	16.00	17.50
-2	18.00	17.75	16.25	18.25	17.75
-6	18.00	17.25	18.00	17.75	18.25
-10	20.00	19.25	19.00	15.50	17.00
-14	19.25	20.75	19.75	20.00	19.75
-18	20.00	21.00	19.25	20.5	21.00

Population: Overton Hall.

A.

Replicates.

°C.	1	2	3	4	5
+2	2.25	2.50	3.00	2.25	2.00
-2	2.50	2.50	4.00	2.50	2.50
-6	3.75	3.00	3.50	3.50	3.25
-10	11.25	11.75	11.75	12.00	11.00
-14	21.25	21.00	20.00	19.50	19.75
-18	23.00	22.75	22.25	22.00	23.00

B.

°C.	1	2	3	4	5
+2	22.50	23.00	23.00	22.00	22.25
-2	21.00	19.25	21.50	22.50	21.75
-6	23.00	21.75	22.75	21.50	22.75
-10	24.50	22.00	24.75	24.5	23.25
-14	24.50	24.00	23.00	22.50	23.00
-18	25.00	24.25	24.00	23.50	24.75

Population: Yew Barrow.

A.

Replicates.

°C.	1	2	3	4	5
+2	2.00	2.00	2.00	2.00	1.75
-2	2.00	2.00	2.25	2.00	1.75
-6	5.50	5.50	6.50	6.00	6.00
-10	13.00	13.50	13.75	13.25	14.75
-14	19.00	18.50	20.00	19.00	18.25
-18	20.50	19.50	20.00	19.00	20.50

B.

°C.	1	2	3	4	5
+2	20.25	19.50	18.75	20.0	18.00
-2	19.00	19.25	18.50	20.25	18.75
-6	19.00	18.50	20.25	18.75	19.75
-10	19.50	20.25	20.00	19.25	20.00
-14	22.00	21.00	22.50	20.75	20.75
-18	22.25	20.75	22.00	21.00	22.25

Population: Brantingham.

A.

Replicates.

°C.	1	2	3	4	5
+2	2.00	1.75	2.00	2.00	2.00
-2	2.75	2.25	2.25	2.00	2.50
-6	2.25	2.75	2.50	2.75	1.75
-10	7.25	7.00	7.75	7.50	12.50
-14	14.25	13.75	13.75	12.25	14.75
-18	14.25	13.75	14.25	15.00	14.25

B.

°C.	1	2	3	4	5
+2	14.25	15.00	14.25	15.00	14.25
-2	15.00	15.75	16.00	15.00	16.75
-6	14.50	16.25	15.25	11.00	11.50
-10	16.50	15.25	15.50	15.00	17.25
-14	16.50	16.25	17.00	15.00	17.25
-18	16.00	16.00	17.00	17.00	16.25

Population: Guisborough.

A.

Replicates.

°C.	1	2	3	4	5
+2	2.75	2.25	2.50	2.25	3.00
-2	2.25	2.50	2.25	2.25	2.50
-6	3.00	3.00	3.00	2.75	3.00
-10	9.75	9.25	9.00	9.25	11.00
-14	27.50	17.25	18.25	16.00	18.00
-18	20.50	18.75	19.00	21.00	22.00

B.

°C.	1	2	3	4	5
+2	21.00	20.00	19.75	19.25	19.25
-2	19.00	19.25	18.25	20.75	20.50
-6	21.00	20.75	22.25	21.00	20.00
-10	21.50	21.25	19.00	18.75	22.75
-14	21.25	21.25	22.75	22.00	22.00
-18	22.50	21.25	21.00	23.00	24.50

Population: Butser Hill. **Test month**: July, 1978.

A.

Replicates.

°C.	1	2	3	4	5
+2	2.50	2.25	2.50	2.25	2.50
-2	2.25	2.25	2.50	2.25	2.25
-6	5.25	6.00	7.00	6.25	5.75
-10	13.00	14.25	15.00	14.00	13.25
-14	20.50	21.50	19.50	-	19.75
-18	20.50	20.50	21.50	20.00	20.00

B.

°C.	1	2	3	4	5
+2	19.00	19.50	21.25	19.50	20.00
-2	20.50	20.00	21.00	19.00	20.00
-6	20.00	20.75	20.00	20.00	21.00
-10	21.50	21.25	22.00	20.75	21.50
-14	21.00	21.75	20.25	-	20.75
-18	20.25	20.25	21.00	20.00	19.25

Population: Wyre Forest.

A.

Replicates.

°C.	1	2	3	4	5
+2	2.25	2.75	2.75	3.00	2.75
-2	2.25	2.50	2.50	3.00	3.00
-6	10.00	9.25	11.00	7.50	12.25
-10	19.75	20.25	19.75	21.00	19.25
-14	20.25	20.75	19.25	19.75	21.75
-18	20.00	19.75	18.75	20.25	21.50

B.

°C.	1	2	3	4	5
+2	20.50	19.75	18.50	20.00	19.25
-2	17.00	18.00	17.75	20.00	20.75
-6	19.00	21.50	22.25	18.25	24.00
-10	22.00	21.75	21.50	22.25	22.75
-14	21.00	21.50	20.75	20.25	22.25
-18	20.00	20.50	20.00	20.75	21.75

Population: Overton Hall.

A.

Replicates.

°C.	1	2	3	4	5
+2	2.25	2.25	2.25	2.25	2.50
-2	2.50	2.50	2.50	2.25	2.25
-6	7.50	6.25	5.50	2.50	5.75
-10	18.75	17.25	18.00	18.25	16.25
-14	22.50	21.50	21.75	22.50	22.00
-18	22.00	22.25	20.00	22.50	21.50

B.

°C.	1	2	3	4	5
+2	21.50	24.00	23.00	23.25	24.00
-2	24.00	23.50	24.00	23.00	21.25
-6	21.25	22.00	21.00	23.00	21.75
-10	23.25	21.50	23.75	22.25	20.00
-14	22.75	22.00	22.50	23.00	22.50
-18	20.50	21.25	20.00	21.50	21.00

Population: Yew Barrow.

A.

Replicates.

°C.	1	2	3	4	5
+2	1.25	1.50	1.50	1.50	1.50
-2	1.50	1.75	1.75	1.50	1.75
-6	7.50	7.25	8.00	8.50	7.25
-10	13.50	13.75	13.00	14.00	13.75
-14	17.00	16.50	16.00	16.00	16.25
-18	15.50	16.50	15.00	16.50	14.50

B.

°C.	1	2	3	4	5
+2	11.50	12.50	14.00	12.50	14.00
-2	11.75	12.50	13.75	12.00	13.50
-6	13.25	14.00	14.25	14.00	13.50
-10	16.00	15.25	16.00	16.00	15.50
-14	17.50	17.50	16.75	16.75	17.25
-18	15.50	17.00	16.00	17.75	15.50

Population: Brantingham.

A.

Replicates.

°C.	1	2	3	4	5
+2	1.5	1.75	1.50	1.50	1.75
-2	2.0	2.00	1.75	2.00	2.00
-6	2.00	8.25	8.25	9.00	8.25
-10	15.50	15.75	15.25	15.00	14.00
-14	16.75	16.00	17.00	16.00	17.00
-18	16.00	16.00	15.50	16.25	-

B.

°C.	1	2	3	4	5
+2	14.75	16.25	15.50	17.00	15.50
-2	18.00	16.00	17.00	16.25	15.25
-6	13.75	15.00	15.00	16.00	15.00
-10	17.00	18.00	17.00	17.00	17.00
-14	17.75	17.50	18.75	16.75	19.00
-18	16.50	17.00	17.25	16.75	-

Population: Guisborough.

A.

Replicates.

°C.	1	2	3	4	5
+2	1.75	2.25	1.5	1.75	1.75
-2	2.0	1.5	1.75	1.75	1.75
-6	5.5	2.0	5.25	6.25	5.5
-10	15.00	16.25	15.5	16.00	14.00
-14	21.25	22.00	21.75	21.00	19.75
-18	22.50	20.00	18.25	21.00	20.25

B.

°C.	1	2	3	4	5
+2	16.50	17.50	19.00	20.00	17.50
-2	17.25	21.00	19.00	17.75	16.75
-6	19.00	18.50	21.25	18.75	15.75
-10	21.00	20.75	20.75	19.75	19.50
-14	21.00	22.50	22.25	22.00	21.50
-18	22.00	19.75	18.25	21.00	20.50

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