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Factors affecting the early growth and form of Fraxinus excelsior L. in Britain

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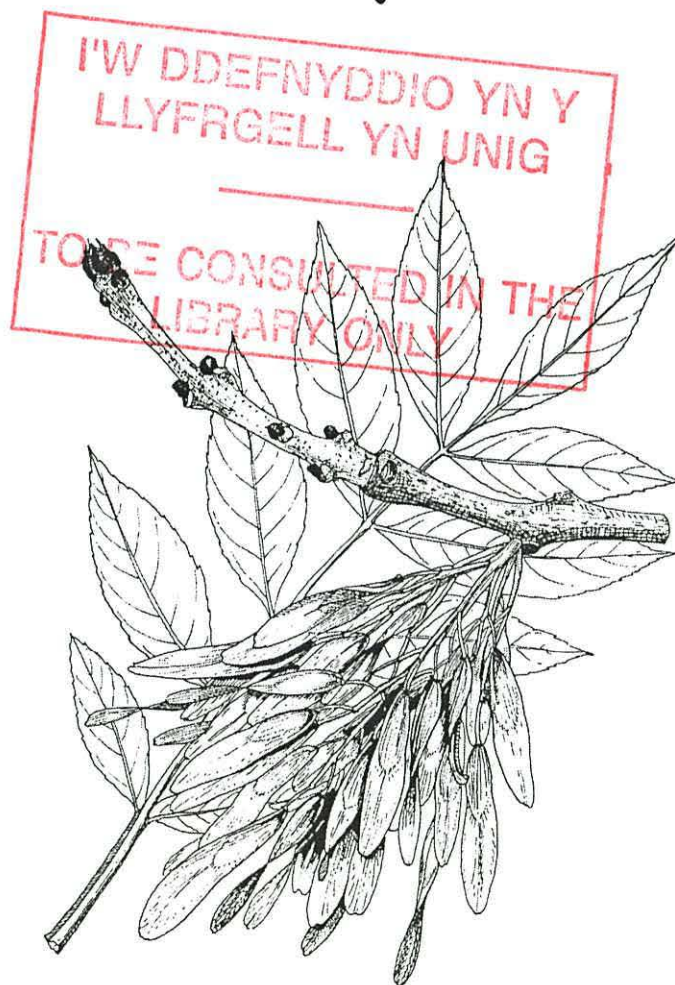
Abstract

The work described in this thesis is an investigation of factors affecting the early growth and form of ash (*Fraxinus excelsior* L.), particularly (i) the effects of initial spacing; (ii) the effects of mixture design with other broadleaved species, and (iii) the relationships between forking, incidence of frosts and the presence of ash bud moth (*Prays fraxinella* Bjerk.).

In the spacing experiments there was a negative relationship between height, stem diameter, stem volume and initial spacing, i.e. growth was poorer at wider spacings. Analysis of the data showed that there was no intraspecific competition. The most likely hypothesis to explain the results is that trees at closer spacings shelter each other and the improved growth is the result of enhanced microclimate.

In the mixture experiments two patterns of growth were observed. Firstly, in the ash:cherry experiment, two rapidly growing species altered their allocation of assimilates to different parts of the plant to maintain a position in the upper canopy. Secondly, in the ash:oak and ash:beech experiments, a two-tier canopy formed with ash in the upper canopy and interspecific competition resulted in an early nursing effect on the ash. In both patterns of growth, competition affected stem diameter and the shape of the tree, whilst there were only short-term effects on height.

To study the relationships between forking, frosts and ash bud moth, 42 sites in southern Britain were surveyed. Generally higher levels of forking coincided with a greater number of frosts in April and May, when ash is usually breaking bud. However, the survey did not produce further evidence for a link between frosts and forking because meteorological data had been recorded remotely and were therefore not an accurate measure of on-site temperatures. Ash bud moth was found in approximately 0.2% of 4106 buds sampled and it is concluded that this is unlikely to be a serious cause of forking of newly planted ash trees.

Chapter summaries

Chapter 1 Introduction, background information and thesis objectives

Ash *(Fraxinus excelsior* L.) was the third most common broadleaved species recorded in the last census when it covered over 70 000 hectares of forest (Locke, 1987). The attraction of ash is that it offers the prospect of the production of valuable timber on relatively short rotations. Optimal growth conditions for ash can be described using the Ecological Site Classification of Pyatt *et al*. (2001). Ash grows best on sites where the climate is 'warm' (>1376 day-degrees >5.6 °C), soil moisture is 'fresh' to 'very moist' (generally meaning that depth to the winter water table is between 40 cm and 100 cm) and soil nutrient status is 'rich' and 'very rich' (generally soil pH in the range 5.0 to 7.5).

Ash has a monopodial trunk which grows rhythmically (Rauh, 1939), i.e. it has a period of extension beginning with bud break in early May and ceasing with the formation of the new terminal bud later in the summer. In general, ash leaves are preformed and the buds are determinate (Hallé *et al*., 1978). Hence the vegetative shoot is fully developed in the dormant bud and the number of foliage leaf primordia will be essentially the same as the number of foliage leaves on the mature shoot.

The work described in this thesis is an investigation of factors affecting the early growth of ash with the following objectives: (i) to examine the effects of initial spacing on growth and form; (ii) to investigate the effects of mixtures of other broadleaved species on growth and form; (iii) to quantify the level of forking in planted ash trees < 6 years old; (iv) to investigate population levels of ash bud moth *(Prays fraxinella* Bjerk.) in ash plantations assessed for forking; and (v) to examine the relationships between amount of forking, incidence of frosts and other site factors.

Chapter 2 The effects of initial spacing on growth and form

The effects of initial spacing on growth and form were investigated using two replicate Nelder experiments (Nelder, 1962) at two sites, with spacings in the range 0.77 m to 4.86 m, and a randomized block design with three spacings of 2.0 m, 5.0 m and 10.0 m. In both Nelder experiments there was a negative relationship between spacing and the three variables height, stem diameter and stem volume, i.e. growth was poorer at wider spacings. A similar relationship between spacing and both height and stem diameter was also apparent in the randomized block experiment. Analysis of the data showed that there was no intraspecific competition and a number of hypotheses are examined which may explain the observed results. The most likely one is that trees at closer spacings shelter each other and the consequent improved growth is the result of enhanced microclimate.

Chapter 3 The effects of other broadleaved species on growth and form

The effects on growth and form of mixtures of ash with cherry (*Prunus avium* L.), oak (*Quercus petraea* (Matt.) Lieb. and *Q. robur* L.) and beech (*Fagus sylvatica* L.) were investigated using a balanced two-component competition experiment described by Boffey and Veveers (1977). In general two patterns of growth were observed. Firstly, in the ash:cherry experiment, two rapidly growing species altered their allocation of assimilates to different parts of the plant to show a plastic response to interspecific competition, and both species maintained a position in the upper canopy. Secondly, in the ash:oak and ash:beech experiments, a two-tier canopy formed with ash in the upper canopy and interspecific competition resulted in an early nursing effect on the ash. In both patterns of growth, competition affected stem diameter and the shape on the tree with few, and only short-lived, effects on height. The effect of mixtures on the form of ash trees was investigated by a study of bud and branch demography. A small number of significant effects were observed which showed increased numbers of buds and branches on ash trees growing with increased proportions of the other species in the mixture. However, none of the effects lasted for more than a year and hence no demographic patterns were apparent.

Chapter 4 The influence of spring frosts, ash bud moth and site factors on forking

Forking below 6 m is a serious defect in ash trees if production of quality timber is an important objective of management. Forty-two sites in southern Britain were surveyed to examine the proportion of trees that had forked and to investigate possible causes of forking (in particular incidence of frosts and ash bud moth). In total, 69% of 4147 trees had at least one fork with 29% having more than one. Between 1991 and 1994, 19% of trees forked but in 1995 and 1996 the figure was much higher at 39%. Both 1995 and 1996 had many frosts in April and May, when ash is usually breaking bud, whereas in 1993 and 1994 frosts in the same period were less common. There is thus an implication that late spring frosts may be an important cause of forking. However, the survey did not produce further evidence for a link between frosts and forking because meteorological data had been recorded remotely and were probably not an accurate measure of on-site temperatures. Ash bud moth was found in approximately 0.2% of 4106 buds sampled and it is concluded that this is unlikely to be a serious cause of forking of newly planted ash trees in southern Britain.

Chapter 5 Concluding discussion

Explanations for the effects observed in the thesis are considered in terms of a detailed mechanistic model of tree growth described by Landsberg (1986).

Contents

Figures and Tables

Chapter 3 Effects of other broadleaved species on growth and form

Chapter 4 The influence of spring ash bud moth (*Prays fraxinella* Bjerk.) and site factors on forking

Tables

Figures

Chapter 5: Concluding discussion

Tables

Figures

Acknowledgements

I am very sorry, *Pyrophilus*, that to the many (elsewhere enumerated) difficulties which you may meet with, and must therefore surmount, in the serious and effectual prosecution of experimental philosophy I must add one discouragement more, which will perhaps as much surprise as dishearten you; and it is, that besides that you will find (as we elsewhere mention) many of the experiments published by authors, or related to you by the persons you converse with, false and unsuccessful (besides this, I say), you will meet several observations and experiments which, though communicated for true by candid authors or undistrusted eye-witnesses, or perhaps recommended by your own experience may, upon further trail, disappoint your expectation, either not at all succeeding constantly or at least varying from what you expected.

Robert Boyle (1673) *Concerning the Unsuccessfulness of Experiments.*

Chapter 1

Introduction, background information and thesis objectives

1.1 Importance and distribution

Ash *(Fraxinus excelsior* L.[1]) was the third most common broadleaved species recorded in the last *Census of Woodlands and Trees 1979-1982* (Locke, 1987) when it covered over 70 000 hectares of forest and represented 12% of the area of broadleaves in Britain. A recent analysis of planting funded by the Forestry Commission has shown that ash was the second most common broadleaved species planted after oak (*Quercus robur* L. and *Q. petraea* (Matt.) Lieb.) (Harmer and Forrester, 1994). The attraction of ash is that it offers the prospect of the production of valuable timber on relatively short rotations (Kerr and Evans, 1993) and is Britain's 'most versatile hardwood' (R. Venables, *pers. comm.*). It also has the advantage, compared with many other broadleaves, of being relatively free from attack by grey squirrels (*Sciurus carolinensis* Gmelin.) (Evans, 1984). These attributes have led to much interest in the species, and studies by Helliwell (1982) and Kerr (1995) have described the silvicultural characteristics of ash in Britain. On a wider scale, ash is also an important species in the rest of Europe (Thill, 1979; Asche, 1995; Duflot, 1995; Joyce *et al.*, 1998), and is present in parts of western Asia and north Africa.

Ash is widely distributed throughout Britain and occurs in many of the National Vegetation Classification (NVC) woodland types described by Rodwell (1991). It is a major component of woodland types W8 (*Fraxinus excelsior-Acer campestre-Mercurialis perennis*) and W9 (*Fraxinus excelsior-Sorbus aucuparia-Mercurialis perennis*) growing on soils derived from calcareous parent materials. Ash can also be locally common in woodlands typical of moderately base rich mineral soils in the wetter parts of Britain (W7: *Alnus glutinosa-Fraxinus excelsior-Lysimachia nemorum*), and woodlands on freely draining base rich soils in the south-east lowlands which are generally limited to steep faces of chalk escarpments (W12: *Fagus sylvatica-Mercurialis perennis*). The presence of ash in NVC woodland types is summarized in Table 1.1.

Münch and Dieterich (1925) described two physiological races of ash in Germany, one adapted to dry limestone soils (*Kalkesche*) and the second to moist fertile soils (*Wasseresche*). The main difference between these two races was described in terms of

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[1] Authorities throughout are according to Stace (1991) or Mitchell (1974) for non-native trees.

1

leaf morphology: the midribs and main lateral veins of the former are thickly covered with hairs and those of the latter are quite smooth. However, a later study by Weiser (1995) in Germany found no evidence for distinct physiological races, neither did Helliwell (1982) nor Kerr (1995) in central southern England.

Table 1.1 Summary of the presence of ash in National Vegetation Classification woodland types

NVC woodland type		Presence			
Code	Woodland type	Major component	Locally common	Uncommon or rare	Not usually present
W1	Salix cinerea - Galium palustre				✓
W2	Salix cinerea - Betula pubescens – Phragmites australis				✓
W3	Salix pentandra - Carex rostrata				✓
W4	Betula pubescens - Molinia caerulea			✓	
W5	Alnus glutinosa - Carex paniculata			✓	
W6	Alnus glutinosa - Urtica dioica			✓	
W7	Alnus glutinosa - Fraxinus excelsior - Lysimachia nemorum		✓		
W8	Fraxinus excelsior - Acer campestre - Mercurialis perennis	✓			
W9	Fraxinus excelsior - Sorbus aucuparia - Mercurialis perennis	✓			
W10	Quercus robur - Pteridium aquilinum - Rubus fruticosus			✓	
W11	Quercus petraea - Betula pubescens - Oxalis acetosella			✓	
W12	Fagus sylvatica - Mercurialis perennis		✓		
W13	Taxus baccata			✓	
W14	Fagus sylvatica - Rubus fruticosus			✓	
W15	Fagus sylvatica - Deschampsia flexuosa				✓
W16	Quercus spp - Betula spp - Deschampsia flexuosa				✓
W17	Quercus petraea - Betula pubescens - Dicranum majus			✓	
W18	Pinus sylvestris - Hylocomium splendens				✓

Based on Whitbread and Kirby (1992).

1.2   Site requirements

Previous accounts of the site requirements of ash in Britain such as those by Kerr (1995) have attempted to describe the range of sites on which ash will grow. The development of the Ecological Site Classification (ESC) allows a more objective approach to defining the most suitable sites for ash (Pyatt *et al.*, 2001).   ESC assumes that three principal factors can describe a site: climate, soil moisture and soil nutrient regime. Each of these factors is divided into zones; there are seven climate zones, eight soil moisture zones and six soil nutrient zones. The three factors can be thought of as forming the axes of a cube which, if divided into the zones described above, would represent 7 × 8 × 6 = 336 'mini-cubes', or site types, for the whole of Britain.   Tree species suitability for each zone has been determined as 'optimal', 'suitable' or 'unsuitable'. To define an overall site suitability, rules for combinations of factors have been developed, e.g. 'optimal' for climate and 'suitable' for soil moisture and soil nutrient regime would be an overall 'suitable'. This section describes the site requirements of ash in Britain using mainly ESC criteria; more detailed accounts of the influence of water, nutrients and light on growth are discussed in section 1.3.

1.2.1   Climate

The main climatic parameters used in ESC are accumulated temperature (day-degrees above 5.6 °C) and moisture deficit (precipitation minus potential evapotranspiration). Figure 1.1 shows that ash is 'optimal' on sites in the 'warm' parts of Britain, except the most dry, and is 'suitable' on a high proportion of 'cool' sites. The distribution of these sites in Britain is in general agreement with Kerr (1995), who stated that ash would grow well in all parts of Britain on suitable soils. However, in some areas in the more northerly and westerly parts of Britain wind may become an important constraint to productive growth. In ESC climate is principally defined by warmth and wetness; however, winter cold, continentality, windiness and aspect can also be used as refinements. The latter two indicate that for sites with a DAMS score (Detailed Aspect Method of Scoring; see Quine and White, 1992) of more than 19 ash is 'unsuitable'.

An aspect of climate that is not fully taken into account by ESC, but is important for ash, is unseasonal frost in the early autumn and late spring. Ash has been shown to be very sensitive to late spring frosts with opening buds of seedlings being killed after 18 hours exposure at −3 °C (Wardle, 1961). This may affect the form of a tree because the terminal bud is flanked by a pair of lateral buds in the axils of the uppermost leaves of the shoot.

Figure 1.1 Ecological Site Classification climatic zones for ash

		Accumulated temperatures (day-degrees > 5.6 °C)						
		>1925	1925-1626	1625-1376	1375-1101	1100-876	875-676	675-500
Moisture deficit (mm)	>180							
	141-180		WARM DRY					
	100-140				COOL DRY			
	81-100							
	61-80		WARM MOIST			COOL MOIST		
	41-60							
	11-40		WARM WET			COOL WET		SUB ALPINE
	0-10							

Key

Not found in Britain	
Unsuitable	
Suitable	
Optimal	

If the terminal bud is lost or damaged and fails to elongate in the spring, there are two possible successors which, if both develop, will form a fork.

1.2.2   Soil moisture and soil nutrient regime

In terms of the ESC soil moisture zones, ash will grow optimally on sites that are 'very moist', 'moist' and 'fresh', and will be suitable on 'wet' and 'slightly dry' sites. Ash will also grow optimally on sites in soil nutrient zones 'rich' and 'very rich', and will be suitable on 'medium' and 'carbonate' sites. This information has been combined for ash on the ESC soil quality grid in Figure 1.2 (page 7). This shows that ash will grow best on base rich soils which have high levels of soil moisture; these are generally typical of the NVC woodland types W8 and W9 (Rodwell, 1991). Plant indicators of these types of site are listed in Table 1.2, based on information in Popert (1950) and Pyatt *et al.* (2001).

Table 1.2 Vascular plant indicators of good ash sites

Common name	Latin name	ESC soil nutrient regime	ESC soil moisture regime
bluebell	Hyacinthoides non-scripta	Rich	Fresh
male fern	Dryopteris filix-mas	Rich	Fresh
wood avens	Geum urbanum	Rich	Fresh
germander speedwell	Veronica chamaedrys	Rich	Fresh
pignut	Conopodium majus	Rich	Fresh
cocksfoot	Dactylis glomerata	Rich	Fresh
common hemp-nettle	Galeopis tetrahit	Rich	Fresh
dog's mercury	Mercurialis perennis	Very Rich	Fresh
cleavers	Galium aparine	Very Rich	Fresh
ground ivy	Glechoma hederacea	Very Rich	Fresh
burdock	Arctium nemorosum	Very Rich	Fresh
wood sedge	Carex sylvatica	Very Rich	Fresh
hogweed	Heracleum sphondylium	Very Rich	Fresh
yellow archangel	Lamiastrum galeobdolon	Very Rich	Fresh
bugle	Ajuga reptans	Rich	Moist
false brome	Brachypodium sylvaticum	Rich	Moist
red campion	Silene dioica	Rich	Moist
rosebay willowherb	Chamaenerion angustifolium	Rich	Moist
wood spurge	Euphorbia amyedaloides	Rich	Moist
primrose	Primula vulgaris	Rich	Moist
ramsons	Allium ursinum	Very Rich	Moist
stinging nettle	Urtica dioica	Very Rich	Moist
hedge woundwort	Stachys sylvatica	Very Rich	Moist
enchanter's nightshade	Circaea lutetiana	Very Rich	Moist
tufted hair grass	Deschampsia cespitosa	Rich	Very Moist
rough meadow-grass	Poa trivialis	Rich	Very Moist
wood horsetail	Equisetum sylvaticum	Rich	Very Moist
wood speedwell	Veronica montana	Rich	Very Moist
lesser celandine	Ranunculus ficaria	Very Rich	Very Moist

Source: Popert (1950) and Pyatt *et al.* (2001).

Recent work in Belgium has generated site index curves for ash. The parameters in the model were related to topography, soil depth, soil moisture and geological strata (Claessens *et al.*, 1999). The favourable and unfavourable influences on the growth of ash in this study are shown in Table 1.3, and broadly support the conclusion that ash grows well on nutrient rich sites with a good water supply.

Table 1.3 Factors affecting the productivity of ash in Wallonia, Belgium

Factor	Favourable	Unfavourable
Topography	Valleys and hollows H50 = 27.5 m	Plateaux and slope >10° H50 = 24.2 m
Soil depth	>100 cm H50 = 26 m	<40 cm H50 = 22.6 m
Soil moisture	Permanent water-table H50 = 27.5 m	Without water-table H50 = 24.5 m
Geological strata	Alluvium H50 = 28.1 m	Famenne, Dinant, Loess H50 = 24.8 m

H50 = height at age 50 years.
Source: Claessens *et al.* (1999).

1.3 Influence of water, nutrients and light on growth

1.3.1 Water

Compared with other broadleaved trees, ash has the ability to transpire large volumes of water (Ladefoged, 1963; Braun, 1977). This was investigated by Kozlowski *et al.* (1974) for white ash (*Fraxinus americana* L.) and compared with sugar maple (*Acer saccharum* Marsh.). Their study found that white ash had fewer but larger stomata (length 26.7 µm, density 118 mm^{-2} compared with 15.3 and 504 for sugar maple), less efficient stomatal closure and higher water loss through the cuticle due to lower cuticular resistance.

On a site with good water supply, Besnard and Carlier (1990) recorded a maximum stomatal conductance of 16×10^{-3} m s^{-1} for ash. This compares with values in the range of 2 to 5×10^{-3} m s^{-1} reported for a wide range of north temperate broadleaved tree species in reviews by Hinckley *et al.* (1978) and Körner *et al.* (1979). Similar values have been recorded for fast growing broadleaved trees, for example, 20×10^{-3} m s^{-1} for grey alder

(*Alnus incana* (L.) Moesch) and 16×10^{-3} m s^{-1} for grey willow (*Salix cinerea* L.) (Besnard, 1987 cited in Besnard and Carlier, 1990) and 14×10^{-3} m s^{-1} for some poplars (Pallardy and Kozlowski, 1981). The importance of site water status for the productive growth of ash has been demonstrated by Kassas (1950), Frochot *et al.* (1992) and Levy *et al.* (1992), but, of course, many sites where ash grows do not have ideal water conditions. In fact the range of sites, in terms of water status, where ash grows is quite surprising. Iremonger and Kelly (1988) showed that ash seedlings can tolerate flooding to ground level for two growing seasons and Wardle (1961) observed that when water is severely limited ash remains a shrub.

Figure 1.2 Ecological Site Classification soil quality grid for ash

		Soil nutrient regime					
		Very poor	Poor	Medium	Rich	Very rich	Carbonate
Soil Moisture Regime	Very Dry						
	Mod. Dry						
	Slightly Dry						
	Fresh						
	Moist						
	Very Moist						
	Wet						
	Very Wet						

Key

Unsuitable	
Suitable	
Optimal	

The site studied by Besnard and Carlier (1990) was an alluvial forest in the upper Rhône valley in France, and the maximum stomatal conductance (16×10^{-3} m s^{-1}) was recorded for that part of the day when the amount of light exceeded 700 µmol.m^{-2} s^{-1}. During the study the minimum leaf water potential never fell below -2 MPa, a figure in the range which would trigger stomatal closure of several other broadleaved species (Hinckley *et al.*, 1978). Besnard and Carlier (1990) suggested that light was the main factor controlling the aperture of stomata and that, in this environment of good water supply, microclimatic factors other than light only limit stomatal opening in dry and very warm weather.

Further information on water relations is provided by a study of ash growing in the foothills of the Alps where summer droughts are common (Carlier et al., 1992); this is a contrast to the alluvial site studied by Besnard and Carlier (1990). In the foothills of the Alps, the water requirements of ash were much more moderate than those on the alluvial site, mainly due to a much lower maximum stomatal conductance and better control of stomatal opening. Partial closure of stomata occurred at midday or earlier, but this did not prevent the leaf water potential falling to -5.5 MPa. This level is usually associated with trees of dry or desert regions, and yet no damage was observed on the ash trees, although drought symptoms were noted on other tree species.

Three strategies for responding to water stress have been described by Ludlow (1989): escape, avoidance and tolerance. Plants with an escape strategy have a life cycle during which they rarely experience water shortage (e.g. desert annuals); those with the avoidance strategy have tissue which is very sensitive to water loss and prevent large decreases in leaf water potential by minimising water loss or increasing water uptake (e.g. desert succulents). Plants with the tolerance strategy, which best describes the response of ash to water stress, have tissues that can tolerate dehydration. Work by Carlier et al. (1992) and Peltier and Marigo (1996) have indicated that osmotic changes and elastic adjustment of the cell walls both contribute to the drought adaptation mechanisms of ash.

Another element in the tolerance strategy in response to moisture stress is altered growth; it is frequently reported that ash is very sensitive to moisture stress (Helliwell and Harrison 1979; Kolb et al., 1990). The link between moisture stress and growth was investigated by Aussenac and Levy (1983) in a study of potted trees of five-year-old English oak (*Quercus robur* L.) and four-year-old ash. In controlled conditions, water supply was withheld until predawn water (base) potential reached -1.9 MPa. As the soil dried the stomatal conductance of oak decreased much more quickly than that of ash with a low value (i.e. 1×10^{-3} m s^{-1}) occurring at xylem water potential of twigs of -1.5 MPa for oak and - 4 MPa for ash. In response to soil drying both species stopped growing when predawn water (base) potential reached -1.1 MPa, although this occurred earlier in ash due to its higher rate of transpiration. The results of this study require careful interpretation as the trees were of different ages and the two species have different patterns of growth, with ash having predetermined growth extending generally in one flush and oak growing intermittently in a series of flushes. However, the results are a good example of altered growth of ash as part of its strategy of tolerance of water stress.

1.3.2   Nutrients

Ash is generally considered to be a demanding species in terms of nutrient requirements, reflected in the ESC soil nutrient preferences for 'rich' and 'very rich' sites. On these soils, and some others, ash should have minimum foliar nutrient concentrations of 2.3% nitrogen, 0.22% phosphorus and 0.9% potassium, which Taylor (1991) recommends for optimal growth. Figures for other nutrients are given by Bergmann (1983 quoted in Tobolski, 1995). The importance of foliar nitrogen concentrations for good height growth has been demonstrated by Gordon (1964) for ash growing in the Lake District. Using data from 31 stands, height/age relationships were developed and these were used to estimate height at a standard age of 50. This height was then related to foliar nitrogen concentration. The equation:

$$y = 58.31\, x - 83.7 \qquad\qquad \text{[1.1]}$$

where y = estimated tree height at 50 years in feet (metres = feet $\times$ 0.305) and x = foliar nitrogen as % dry weight, was found to explain 77.7% of the variation in height within the range of foliar nitrogen (1.8 to 2.6 %).

Miller (1984) suggested that broadleaved species were generally 'site demanding' rather than 'nutrient demanding' because their observed site requirements relate more to an inability to obtain nutrients from the soil rather than actual high nutrient requirements for growth. This is a possible explanation for the results of Culleton *et al.* (1996), who found no response to a range of fertilizers applied during establishment on a fertile mineral soil in Ireland, and Evans (1986) who reported increased diameter increment of stands of ash, aged 35 and 49, in response to nitrogen and potassium fertilizer. The sites used by Culleton *et al.* (1996) may have had soil nutrient availability which was equal to, or in excess of, that needed for ash, whereas the site used by Evans (1986) had lower availability and the trees therefore showed a response to fertilizer. It is interesting that these examples do not fit the guiding principles for forest fertilization put forward by Miller (1981), which suggest that a response from the young trees studied by Culleton *et al.* (1996) was more likely than from the older trees investigated by Evans (1986). These results emphasize the complexity of studying the nutrient requirements of ash trees and other woody plants. A further point for ash is that the distribution of nitrogen in above ground parts of ash trees is similar to that in herbaceous plants, i.e. the leaves and petioles are important sinks for nitrogen (Gebauer and Stadler, 1992).

The most common symptom of nutrient related problems reported for ash is chlorosis, which is a consequence of excessive supply of carbonate, and iron and manganese (Marscher, 1986), usually associated with calcareous soils. This is one reason why it is recommended to plant ash on sites with a minimum depth of soil of 30 cm above chalk or limestone (Kerr and Evans, 1993); these sites are described as 'carbonate' in ESC. Hutchinson (1970) described the general consequences of chlorosis for plants and showed that ash was much more prone to desiccation when its foliage was chlorotic.

1.3.3   Light

The effects of light on the growth of trees is complex and a wide range of approaches have been taken to detect, measure and quantify competition for light (Hart, 1988; Cannell and Grace, 1993). Studies within the genus *Fraxinus* have ranged from the effects of light on the development of mycorrhiza (Borges and Chaney, 1993), to the effects on dry matter partitioning (Jones and McLeod, 1990) and tree form (Harris and Bussak, 1993). An early study of the effects of light on the growth of ash by Van Miegroet (1970) investigated changes in leaf characteristics in response to changes in light intensity, light quality and photoperiod. The aim was to improve understanding of the empirical classifications of *light demanding* and *shade tolerance* frequently used by silviculturists. The work demonstrated that such terms are an over-simplification and that the light requirements of a tree can change under the influence of a range of factors, particularly water supply and tree age.

The light requirements of ash change over different stages of development (Savill, 1991). The canopy leaves of trees and older saplings are distinguishable from juvenile leaves of seedlings, young saplings and young coppice shoots. In adult foliage, only sun leaves are developed whereas in juvenile foliage both sun and shade leaves are present (Wardle, 1961). The main difference between sun and shade leaves is that shade leaves are thinner because they generally have no or only a single layer of palisade cells, whereas sun leaves have two distinct layers. The ability of young seedlings to produce shade leaves enables new regeneration to survive under canopies for many years (Okali, 1966; Tapper, 1992; Tabari *et al.*, 1998). A study by Wardle (1959) found that the compensation point of young ash regeneration was reached at 7-9% of full daylight. However, in many W8 type woodlands there is a dense carpet of dog's mercury (*Mercurialis perennis* L.) in the field layer. In such situations Gardner (1976) has estimated that the half-life of ash seedlings is 7-8 months with the main cause of death being attack by damping-off fungi (Long, 1966). These characteristics are all part of the regeneration pattern of ash, which depends on the existence of persistent juveniles that develop rapidly in response to canopy opening (Tapper, 1992 and 1993).

Like most other tree species, adult ash trees take advantage of increased availability of resources, such as light, to increase their rate of growth; silviculturists encourage this by thinning. However, knowledge of the dynamics of even-aged stands of ash is poor; for example, to date, there is no explanation for the common observation that the window for a response to thinning is narrower for ash than for some other broadleaved species (Kerr, 1995). Ongoing work by Goff *et al.* (1995), Ottorini *et al.* (1996) and Goff and Ottorini (1996) is investigating relationships between crown development and stem volume increment and should ultimately lead to a better understanding of the stand dynamics of ash.

1.4   Patterns of shoot and root growth

1.4.1   Shoot growth

The pattern of shoot growth in ash conforms to the model described by Rauh (1939). Tree architecture is determined by a monopodial trunk which grows rhythmically and so develops tiers of branches which are morphogenetically identical with the trunk. Many temperate deciduous tree species exhibit this rhythmic growth, which has been defined by Hallé and Martin (1968) as one in which shoots have a marked endogenous periodicity of extension (the alternative is continuous growth where there is no periodicity of extension). In ash the period of extension growth begins with bud-break in early May (although understorey trees can flush much earlier) and ceases at the formation of the new terminal bud, generally in July. Detailed accounts of rhythmical growth in *Fraxinus* have been given by Gill (1971) for white ash, Merrill (1990) for green ash (*Fraxinus pennsylvanica* var. *subintegerrima* (Vahl.) Fern.), and Collin *et al.* (1995) for ash under controlled conditions.

In general, ash leaves are preformed and the buds are determinate (Hallé *et al.*, 1978). Hence the vegetative shoot is fully developed in the dormant bud and the number of foliage leaf primordia will be essentially the same as the number of foliage leaves on the mature shoot. The study by Gill (1971) was one of the first on white ash, although it was limited to comparing only 15 terminal buds of opposite branches. More detailed work by Remphrey and Davidson (1994a) and Davidson and Remphrey (1994) has shown that green ash has the capacity for both preformation and neoformation; the latter is where shoots are not entirely preformed in the resting bud and a proportion of the leaves are formed during the growth season. This was the first report of neoformation in *Fraxinus* and was shown to be an important part of the species' recovery strategy after pruning or the loss of terminal buds in late spring frosts. Observations indicating that ash has the capacity

for neoformation have been made during the course of work presented in this thesis (section 3.4).

In ash, there have been detailed studies of the physiology of the terminal bud and its entry and exit from dormancy (Barnola *et al.*, 1986a and b; Lavarenne *et al.*, 1986; Cottignies, 1990). However, a review by Collin and Badot (1997) concluded that the research was too fragmentary to propose a reliable model explaining the growth and development of ash. One interesting result was the response of ash to defoliation after the cessation of shoot elongation under controlled conditions of 14 h light at 27±1 °C /10 h dark at 19±1 °C (Collin *et al.*, 1994). Up to 40 days after the end of shoot elongation, defoliation caused immediate flushing of the terminal bud and a resumption of shoot elongation. Under the conditions described, the ash trees produced in five months the same stem growth as planted ash trees after two years. The use of defoliation as a method of enhancing growth of ash during establishment may be worthy of further examination, although, even if similar results were obtained under field conditions, there may be enhanced risk of damage from unseasonal frosts.

1.4.2   Root growth

Difficulties of studying roots means that there is much less information on root growth of ash than on other aspects of its biology. The morphology of ash roots has been described by Majid (1954), Köstler *et al.* (1968) and Wardle (1961). Generally the root system is of a typical 'plateroot' type with long, shallow horizontal roots from which laterals grow vertically downwards. This type of root system mainly exploits the upper horizons of the soil (Rust and Savill, 2000). For example, Wardle (1961) observed a much greater concentration of roots in the top 5 cm of soil with greater densities in fen peat or sandy soils (1500 cm of root per 85 cm^3) than in heavier loams (230-400 cm of root per 85 cm^3). The lower limit of rooting depth is usually set by the permanent water table. The roots are generally of two types. 'Coarse' roots (>0.5 mm diameter) are persistent and can withstand long periods of poor aeration. 'Fine' roots are more numerous, mostly die after one year, and are killed if the water table rises temporarily. The root mass of ash, for equivalent stem diameters, is greater than that of beech (*Fagus sylvatica* L.), sycamore (*Acer pseudoplatanus* L.) or English oak (Köstler *et al.*, 1968). Savill and Rust (2000) indicate that ash is one of the most aggressive root competitors of all economically important broadleaved tree species in northern Europe.

Root growth is related to soil temperature, the lower limit being 4 °C to 6 °C and the upper limit 30 °C. Collin *et al.* (1995) recorded continuous root growth under controlled

conditions (14 h light at 27±1 °C /10 h dark at 19±1 °C). The change in the permeability of ash roots in response to drought has been studied by Wiersum and Harmanny (1983). They compared ash with five other tree species representative of urban tree planting (*Ulmus × hollandica* Mill. 'Groeneveld', *Acer pseudoplatanus* 'Negeria', English oak, *Populus × canadensis* Moench 'Robusta' and *Salix alba* L. 'Belders'). The results showed that ash was relatively slow to adjust the permeability of its roots in response to drought, but that on rewatering recovery was similar to that of the other species. These results are further evidence for ash being classified as having a strategy of tolerance in relation to water stress, as discussed in section 1.3.1.

Harmer (1996) studied seedlings of ash, sycamore and oak grown in swards of *Deschampsia flexuosa* (L.) Trin. and *Poa trivialis* L.cv. Ino Daehnfeldt, and in weed free conditions. The results showed the tolerance of weed competition declined in the order of oak>ash>sycamore; it was also shown that in response to competition oak produced more fine roots (< 2 mm in diameter) although, interestingly, there was no difference between ash and sycamore in this respect. The ability of leafy cuttings of ash to root in different propagation environments has been studied by Jinks (1995). More detailed studies, such as the one by Arnold and Struve (1989) on green ash, would be an important contribution to further understanding of the rooting of ash.

Tobolski (1995) reports that roots of ash trees are generally heavily mycorrhizal, and that the association is generally with endomycorrhizae and belongs to an arbuscular type of symbiosis. He quotes several examples of arbuscular mycorrhizae increasing the growth of *Fraxinus* species and proposes a strategy of inoculation to improve the performance of seedlings when they are out-planted. However, the subject of mycorrhizal associations in ash has received little attention in forest research in Great Britain.

1.5   Silvicultural practice

1.5.1   Establishment

1.5.1.1   Artificial regeneration

General silvicultural experience is that ash is relatively easy to establish compared with oak or beech (Kerr, 1995). Hodge (1991), drawing on work by Struve (1990) in the USA, attributed this to the varying root morphologies of these species, with ash being described as a 'fine rooted' species. Hodge argues that, assuming careful lifting in the nursery, ash will have more intact root tips when planted than oak or beech, which are more coarsely

rooted. However, this is a simplistic treatment of an observation (easy establishment) which is probably the product of many factors. As described in section 1.4.2, ash, and without doubt the other two species, have both fine and coarse roots. Studies linking root morphology to field survival in northern red oak (*Quercus rubra* du Roi) and sweet gum (*Liquidamber styraciflua* L.) have indicated the importance of first-order lateral roots (Ruehle and Kormanik, 1986; Kormanik, 1986) rather than the balance between different root-size classes. Other contributory factors to ease of establishment would include the ability of dormant ash to survive and grow after desiccation and rough handling. This has been examined by McKay *et al.* (1999) who reported greater than 95% survival of ash after 36 hours of desiccation and 10 drops from 1 m above the ground, although treatments did have effects on growth. In the same paper, data were also presented which show that ash has a root:shoot ratio (dry weight basis) of 3.35, compared with 2.49 for beech and 0.48 for silver birch (*Betula pendula* Roth). These data suggest that in early growth after germination, ash invests heavily in developing a root system to supply water and nutrients, which are essential during establishment.

The recommended minimum sizes of planting stock for bare-rooted ash are 5 mm root collar diameter and 20 cm height; cell grown stock should be 6 mm and 60 cm respectively (British Standards Institution, 1984). It is recommended that a spot or band of at least 1 m^2 around the plant should be kept weed free for at least three years after establishment to maximise water and nutrient availability to the tree (Davies, 1987). An added benefit of weed control is that exposed mineral soil is usually more efficient at absorbing heat than soil covered with vegetation. A warmer soil will improve plant root growth and overnight re-radiation may also reduce frost damage, which is particularly important for this frost tender species. Ash grows well in treeshelters (Potter, 1991).

If timber production is an objective, a maximum initial spacing of 2.0 m × 2.0 m is recommended for planting bare land and 2.5 m × 2.5 m for restocking (Kerr and Evans, 1993). The lower density on restocking sites assumes that there will be some natural regeneration of woody species to supplement stocking. However, these recommendations are a result of observation and experience as there is little objective information on the relationship between initial spacing, growth and form for broadleaved trees in Britain. Work described in Chapter 2 of this thesis presents new information on this subject for ash.

Early side shelter is essential for the establishment of ash, and it has been recommended that it should not be planted pure on exposed ground (Maurer, 1963; Evans, 1984). The underlying reason for this recommendation is probably the reduction of water loss from

transpiration in order to ensure that growth is maximised. Suitable shelter can be provided by planting in mixture with compatible species such as Norway spruce (*Picea abies* (L.) Karst.), European larch (*Larix decidua* Mill.) or other broadleaved species (Kerr and Evans, 1993). Further work investigating the growth and form of ash when grown with other broadleaved species is described in Chapter 3 of this thesis.

If the initial form or growth of ash is poor then stumping back should be considered. This practice of cutting back top growth in the years after planting, as long as there are live buds above ground, stimulates resprouting; one of the new shoots can then be selected as a straight new stem. Kerr (1995) described an example where stumping back has been used to produce what he considers to be one of the best stands of ash in Britain, at Garnon's Estate in Herefordshire.

1.5.1.2   Natural regeneration

A recent analysis of data on the Forestry Commission Woodland Grant Scheme database (Harmer and Forrester, 1994) revealed that of 31 578 hectares approved for broadleaved regeneration in Britain under the Woodland Grant Scheme between June 1991 and September 1993, 7165 hectares (22%) was for natural regeneration, and of this an area of 240 hectares (3%) was approved for pure ash natural regeneration. In the same period, 4006 hectares (56%) of natural regeneration of mixed broadleaves were also approved, of which ash was likely to make up a large proportion. Detailed advice on the natural regeneration of broadleaved trees is given in Harmer and Kerr (1995).

Throughout Britain, ash shows a strong capacity to regenerate naturally both in woodland and non-woodland situations (Hodge and Harmer, 1996; Harmer *et al.*, 1997). Seed production usually begins when the trees are 20-30 years old and seed is produced annually thereafter, but with intervals of 3 to 5 years between heavy crops (Picard, 1982). Samaras fall from trees between September and March but some trees can hold them for a complete season. The samaras are not usually dispersed very far from the parent tree; a formula for calculating horizontal dispersal distance in Farmer (1997) shows that samaras released from a 25 m tall white ash in a gentle wind (2 m sec^{-1}) would fall between 30 and 50 m away from the parent tree. Ash seed is 'doubly dormant', requiring a period of moisture and warmth followed by chilling for dormancy to be broken; this explains why most natural regeneration appears in the second spring after a seedfall (Wagner, 1996).

Ash will regenerate freely on sites where it will not thrive as adult trees, such as compacted clays or dry soils over chalk. Evans (1984) states that on such sites regeneration will usually disappear after 3-4 years. Ash will also regenerate freely in woodlands with a field layer of dog's mercury, a common association in W8 and W9 woodland types. However, when this field layer of dog's mercury is dense, regeneration is inhibited (Wardle, 1961). Optimum conditions for natural regeneration of ash are found in woodlands with a complete canopy (and in which dog's mercury and other competing vegetation are therefore controlled by shading), and from which browsing mammals are excluded or are present at very low densities. As described previously, the regeneration pattern of ash depends on the existence of persistent juveniles that develop rapidly in response to canopy opening (Tapper, 1992; 1993).

The flowers of ash display 'total sexual confusion' (Mitchell, 1974) and the following categories were described by Schultz (1892, cited in Wardle, 1961): (i) exclusively male trees; (ii) trees purely female or purely hermaphrodite; (iii) trees purely male in some years, in others years mostly male, but also with some female and hermaphrodite flowers; (iv) trees predominantly male, but with always a few female and hermaphrodite flowers on particular branches. It has been suggested that female trees are of generally poor form (Evans, 1984; Garfitt, 1989) and, if true, this could lead to the removal of large proportions of female trees in selective thinning, endangering future possibilities for natural regeneration. However, recent investigations have found little evidence for a relationship between tree form and sex (Groves, 1992; Pavani, 1989).

1.5.2   Stand silviculture

Once established, whether by artificial or natural regeneration, the objective of silviculture aimed at quality timber production should be to produce a straight, defect free bole 6 m in length and of 40-60 cm diameter at breast height. Trees can be grown to sizes in the upper part of this diameter range in 50 years on good sites but on poor sites, it can take anything up to 80 years (Kerr and Evans, 1993; Pilard-Landeau and Goff, 1996).

1.5.2.1   Thinning

There is a general consensus in the literature on how to thin ash (Kerr and Evans, 1993; Pilard-Landeau and Goff, 1996). The main principle is that crown competition should be minimized to encourage fast growth. Once a tree has reached 6-7 m in height from initial stocking densities of about 2500 stems per hectare, frequent crown thinning is required to perpetuate a live crown over at least one-third of the height of the tree. However, despite

these recommendations the most frequently observed problem in the stands observed by Kerr (1995) was under-thinning. An observation by Kerr (1995) is that once a tree is constrained and the crown becomes small, it responds poorly to further thinning; however, there is little, or no, experimental evidence for this.

Thinning to improve stand quality will be greatly assisted if 300–350 trees per hectare are identified in winter between the first and second thinning, and permanently marked by painted bands or spots (Kerr and Evans, 1993). Subsequent crown thinnings should aim to favour this sub-population of trees, but it is also important to remove some of the marked trees when necessary, as only 120–150 trees per hectare are usually required in the final crop.

The effects of growing space on the volume production and wood properties of ash were investigated by Oliver-Villanueva and Becker (1993). In general, their results indicated that trees with the most growing space had the largest volume and that wood properties were not compromised by rapid growth. The increased mean ring width of trees with most growing space was associated with an increased percentage of latewood, a reduced heartwood percentage (because trees reached target diameter more quickly) and increased wood density, elasticity and strength. The only disadvantage of increased growing space was the increased shrinkage and swelling of the wood. These general findings were supported by Denne and Whitbread (1978), who found no relationship between ring width and fibre length in ash.

1.5.2.2   Stem defects

The two most frequent stem defects in stands of ash are canker and forking. Ash cankers can be caused by the bacterium *Pseudomonas savastanoi* pv. *savastanoi* (Smith) Young *et al.*, or the fungus *Nectria galligena* Bres. apud Strasser. Bacterial canker is characterized by a general swelling of the stem and the presence of brown corky tissue (Strouts and Winter, 1994); with fungal canker there is death of tissue and some swelling at the edges of the canker due to callus production (Boa, 1981). Cankered trees should be removed by thinning at the earliest opportunity.

Forked ash trees can be classified into two groups: those which have persistent forking up the main stem and fastigiate branches (this form of forking is most likely to be genetic and trees should be removed in early thinnings), and those which have one single fork. Likely causes of a single fork include unseasonal frost, attack by ash bud moth and damage by birds or wind to the soft green shoot after emergence from the bud. If such forks are below

17

6 m in height, trees should be removed; however, if the fork is high in the crown there may be a case for leaving the tree, depending on the distribution of other potential final crop trees. Further work investigating the populations of ash bud moth and the influence of site factors on forking is described in Chapter 4 of this thesis.

Grey squirrel damage is relatively rare on ash, and in this respect the species has an advantage over other fast growing broadleaves such as sycamore and Norway maple (*Acer platanoides* L.). Both *Acer* species are favoured by squirrels, and if present in small proportions in ash woodlands, can be managed as a sacrificial decoy to grey squirrels. Such a policy may cause environmental concern as both sycamore and Norway maple are often considered invasive species. However, work by Waters and Savill (1992) demonstrated the phenomenon of alternation between ash and sycamore in British woodlands and has led to a reappraisal of the belief that sycamore is strongly invasive and dominating in such woodlands.

1.5.2.3   Pruning

Much recent tree planting has been at spacings wider than those recommended to ensure the production of quality timber (Kerr, 1993). Formative pruning can be used to improve the quality of timber in such stands. This should be achieved by removing forks and large branches annually between January and November using a sharp knife or secateurs until a single stem 6 m long is produced (Kerr, 1992).

Traditional high pruning is expensive and costs increase rapidly with increasing branch size and height up the stem. Hence high pruning is only advisable if branches are less than 5 cm in diameter, should be concentrated on final crop trees, and should be done to a height of 6 m.

1.5.3   Wood properties

In common with other broadleaved species it is generally recommended to fell ash in winter, when the cambium is dormant. Felling in the summer and leaving logs in the wood can predispose the timber to splits and checks due to rapid drying. There is constant demand for well-grown ash of good quality and because this usually exceeds supply it is possible to command good prices. A few exceptional trees with completely white timber, and between 20 and 40 cm in diameter, make sports-grade ash that fetches a premium price. An unusual and profitable market is the export to Ireland of material suitable for hurley sticks (Fitzsimmons and Luddy, 1986).

The most significant timber defect in ash is a darkening of the centre of the stem often called 'black heart' (Kerr, 1998). This condition does not affect the physical properties of the wood but it is disliked by the timber trade and can significantly depress the value of logs; few stands are free of this defect and hence white ash is highly prized.

1.6 Thesis objectives

The objectives of the work described in this thesis are.

1. To examine the effects of initial spacing on the early growth and form of ash.

2. To examine the growth and form of ash planted in mixture with oak, beech and cherry (*Prunus avium* L.).

3. To quantify the amount of forking present in recently planted ash stands.

4. To investigate population levels of ash bud moth in recently planted ash stands.

5. To examine the relationships between forking, incidence of frosts and other site factors in recently planted ash.

Chapter 2

The effects of spacing on initial growth and form

2.1 Introduction

2.1.1 General principles of the effects of density on plant growth

In this chapter the main interest is in the effects of spacing on the growth and development of newly planted ash trees. The effects of spacing on natural populations of non-woody plants have been well studied by agronomists and plant ecologists and these form a useful context for the present study (Harper, 1977; Milthorpe and Moorby, 1979; Begon *et al.*, 1996). The effects of spacing can be viewed at the level of the population, the individual and, because growth can be a modular process (White, 1979; Harper 1981), organs within individuals. In the early stages of growth of monospecific populations there will be few, if any, density dependent effects on the mean size of individuals. However, with continued growth and increasing levels of intraspecific competition the average size of plants becomes increasingly related to density. In general the relationship is that yield per plant is inversely proportional to total yield, i.e. at high densities the mean size will be low and at low densities the mean size will be high. In addition, the total yield per unit of area is independent of density over a range of densities (the law of constant final yield), though this does not apply at extremes.

Analysis of populations in which intraspecific competition is operating usually shows predictable distributions of individuals. Generally the distributions are skewed to the right, i.e. populations have a few large individuals and many small ones; this is referred to as the 'hierarchy of exploitation' by Harper (1977). The larger individuals are then at a competitive advantage compared with their smaller rivals and grow independently of competition, whereas the smaller trees are more affected by competition, leading to size differences being accentuated and in some cases distributions becoming bi-modal (Ford, 1975). These differences can be caused by initial differences in germination time or the ability of individuals to sustain growth and development.

Eventually, any monospecific population will reach a point where some individuals can no longer modify growth in response to competition or are out-competed by dominant neighbours. At this point the plant will die and the population will be undergoing density-dependent mortality. The rate of mortality has been investigated in a wide range of

situations and generally has been found to be constant; it can be described using the equation:

$$w = Kd^{-3/2} \qquad\qquad [2.1]$$

where w is the mean plant weight, d is the density and K is a constant; this is known as the '-3/2 power law' (Yoda *et al.*, 1963).

White (1980) plotted the results of 31 studies of self-thinning populations of 11 herbs and 20 woody plants[2] and used the -3/2 power law to derive a relationship between average plant dry weight and surviving plant density. This shows that mortality would commence in trees planted at an initial spacing of 2.0 m × 2.0 m (i.e. 0.25 trees m^{-2}) when they were between 100 kg (10^5 g) and one tonne (10^6 g) in weight. Assuming that a mature ash tree has branchwood equal to 40% of its merchantable volume and a volume to weight ratio of 1.3 (Hamilton, 1975), a one tonne ash tree would be approximately 19 m tall and 30 cm in diameter at breast height (i.e. the average size of a tree at age 40, in the yield table for ash, General Yield Class 8, planted at 1.5 m × 1.5 m after five management table thinnings (Hamilton and Christie, 1971)).

2.1.2 The importance of initial spacing in forestry

The changes described above are familiar to foresters; for example density dependent mortality is apparent from scrutiny of any set of yield tables such as those presented by Hamilton and Christie (1971). Density dependent changes in size distribution have also been reported by Ford and Newbold (1970) for sweet chestnut (*Castanea sativa* L.), for Sitka spruce (*Picea sitchensis* (Bong.) Carr.) by Ford (1975), and for a range of species by Hamilton and Christie (1974). A common factor in all these studies is that competition had been apparent for many years and the stand would be described as being in the *stem exclusion phase* according to the classification of Oliver and Larson (1996).

The main reasons why spacing is of great interest to foresters are: (i) the decision on spacing is a major factor affecting cost – close spacing requires more trees and therefore will be more expensive, and (ii) closer spacings can induce branch mortality sooner and provide a greater pool of stems from which to select the final crop, both of which help improve tree form and timber quality (MacKenzie, 1951). However, until relatively recently

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[2] Of the 20 woody species eight were either moderately or heavily shade tolerant.

the effects of spacing on growth, form and wood properties had been much discussed but little studied. This fact has been illustrated by Evert (1973) who compiled a bibliography on initial tree spacing covering the period 1920-1972; of 388 references only 49 (12.6%) contained data from spacing experiments, and many of these were unreplicated.

2.1.3   Brief review of spacing experiments on trees

One reason for the paucity of such studies is the problems that spacing poses in terms of experimental design. Randomized designs, introduced by Fisher (1922), have some important and well-known advantages and have been widely used in silvicultural experiments. However, where spacing experiments are concerned randomization may have some disadvantages; for instance, if the spacing is maintained using a square pattern for all densities then one may either keep a constant number of plants per plot, in which case the plots are all different sizes and difficult to fit together in a block (McClain *et al.*, 1994). The alternative is to have all plots the same size, in which case the closer spacings may have an unnecessarily large number of plants and the means of different treatments will be estimated with varying degrees of accuracy.

An alternative systematic design was first proposed by Nelder (1962), and these designs have subsequently been used in a number of studies (e.g. Smith, 1978; Eastham and Rose, 1990; Galinski *et al.,* 1994; Xie *et al.,* 1995; Gaul and Stuber, 1996; Knowe and Hibbs, 1996). Nelder (1962) described a number of different designs, but the most commonly used in forest science has been his *1a* design, an example of which is shown in Figure 2.1 (page 25). In this design the length of radii to each arc (r_1, r_2...r_n) increases according to a geometric progression, so that the area available for each tree gets larger from the centre to the outside of the circle. Within each arc, the area available for each tree (Figure 2.2, page 28) is constant and the square root of this area gives the equivalent square spacing for the same area per plant. The design overcomes some of the problems discussed above with randomized experiments; however, this has to be balanced against the fact that it is a systematic design and uses single tree plots.

Despite the paucity of experiments, over the past 20 years a body of literature has built up on the subject of the effects of initial spacing on growth and form. A number of studies, selected on the basis that results were reported for a similar time span to that used in this thesis (i.e. between one and five years), are summarized in Table 2.1. These show that despite the general principles described above, results vary with species, site and the range of spacings studied. This confirms that there are no short cuts; replicated field trials with clear objectives are the only way to collect appropriate data.

Table 2.1 Summary of spacing studies in which results were reported after one to five years

Species[a]	Age (years)	Spacing range (m)	Effect of increased spacing on:			Reference
			Shoot dry weight (g)	Height (m)	Stem diameter (mm)	
Alnus rubra	4	0.31- 6.50	↑	↑	↑	Giordano and Hibbs (1993)
Eucalyptus camaldulensis	2.6	3 × 1.5 - 4 × 3	↑	↔	↑	Bernado *et al.* (1998)
Pinus taeda	5	2.0 - 6.4	n/a	↓	↑	Piennar and Shiver (1993)
Pseudotsuga menziesii	5	0.17 - 1.2	↑	↑	↑	Cole and Newton (1987)
Populus clones	3	0.5 - 1.5	↑	↑	↑	Debell and Harrington (1997)
Pinus sylvestris	1	0.03 - 0.1	↑	↓	↑	Jinks and Mason (1998)
Pinus nigra subsp. *laricio*	1		↑	↓	↑	
Pseudotsuga menziesii	1		↑	↔	↑	
Pseudotsuga menziesii	4	1.83- 5.77	n/a	↓	↓	Scott *et al.* (1998)

Key: ↑ - significant increase; ↓ - significant decrease; ↔ - no significant effect; n/a - results not presented in paper.
[a] For authorities to species see references.

The objective of the work described here was to examine the effects of initial spacing on the early growth and form of ash. Two approaches were used, a Nelder type *1a* experiment and a randomized block design with equal plot areas.

2.2 Materials and methods

2.2.1 Nelder experiments

2.2.1.1 Neroche 46 P1995

2.2.1.1.1 Site description

The experiment is situated on an ex-pasture site within the area of Neroche Forest, approximately six miles south of Taunton (50°56′N, 3°05′W). The site is 305 m above sea level (asl) and slopes gently with a western aspect. It is exposed to the south west but is protected on the north side by a 20 m tall beech hedge and from the east by a compartment of Scots pine (*Pinus sylvestris* L.) about 15 m tall. The soil is a brown earth classified by Avery (1980) as a paleo-argillic brown earth which overlies Keuper marls from the Triassic period. In terms of the Ecological Site Classification (ESC) for tree growth the site lies within the warm moist zone described by Pyatt *et al.* (2001). The ESC Decision Support System (Ray, 2001) describes the site as 'suitable' for ash; the other decision categories are 'optimal' and 'not suitable' (see section 1.2).

Soil samples taken at the site in February 1992 produced the following mean values: pH 5.9; phosphorus 15 mg kg^{-1}, potassium 108 mg kg^{-1}, magnesium 143 mg kg^{-1}; organic matter 8%; nitrogen 0.44% (of oven dry soil). Ash foliage samples were taken in June 1997 and gave results of (as a % of dry weight): nitrogen 2.6, phosphorus 0.11 and potassium 0.71. Sampling was repeated in July 1998 and gave results of nitrogen 3.2, phosphorus 0.22 and potassium 1.1. With reference to Taylor (1991) these figures indicate that phosphorus and potassium concentrations were low for ash. However, no fertilization has taken place at the site before or after planting. Water table measurements were available for a neighbouring experiment and data for the 1994 growing season showed that generally the water table was 60–100 cm below the soil surface. This was a particular problem in 1996 when there was a dry spring.

2.2.1.1.2 Experiment design and details of establishment

In March 1995 three Nelder fans of type *1a* (Nelder, 1962) were planted inside a deer and rabbit proof fence. Planting stock was ash 1+1 transplants which were on average 38.6 cm tall and 4.2 mm stem diameter (5 cm above ground after planting). The experiment was intended to study spacings in the range 1.0 × 1.0 m to 4.0 × 4.0 m, and the method to generate appropriate Nelder fans covering this range is shown in Appendix 2.1. Each of the fans used was a semi-circle with a radius of 23.75 m, each with 10 arcs and 13 rays with the outer most arcs and rays being guard rows (Figure 2.1). Table 2.2 shows the areas available for each of the trees in the arcs and the square spacings which would make a similar area available to each plant. The fans were orientated differently to take account of any systematic variation on the site.

Figure 2.1 Experiment layout of Neroche 46 and Swadlincote 1

r_1 = 2.24m
r_2 = 2.91m
r_3 = 3.78m
r_4 = 4.92m
r_5 = 6.40m
r_6 = 8.32m
r_7 = 10.81m
r_8 = 14.05m
r_9 = 18.27m
r_{10} = 23.75m

• Guard row trees
○ Assessment trees
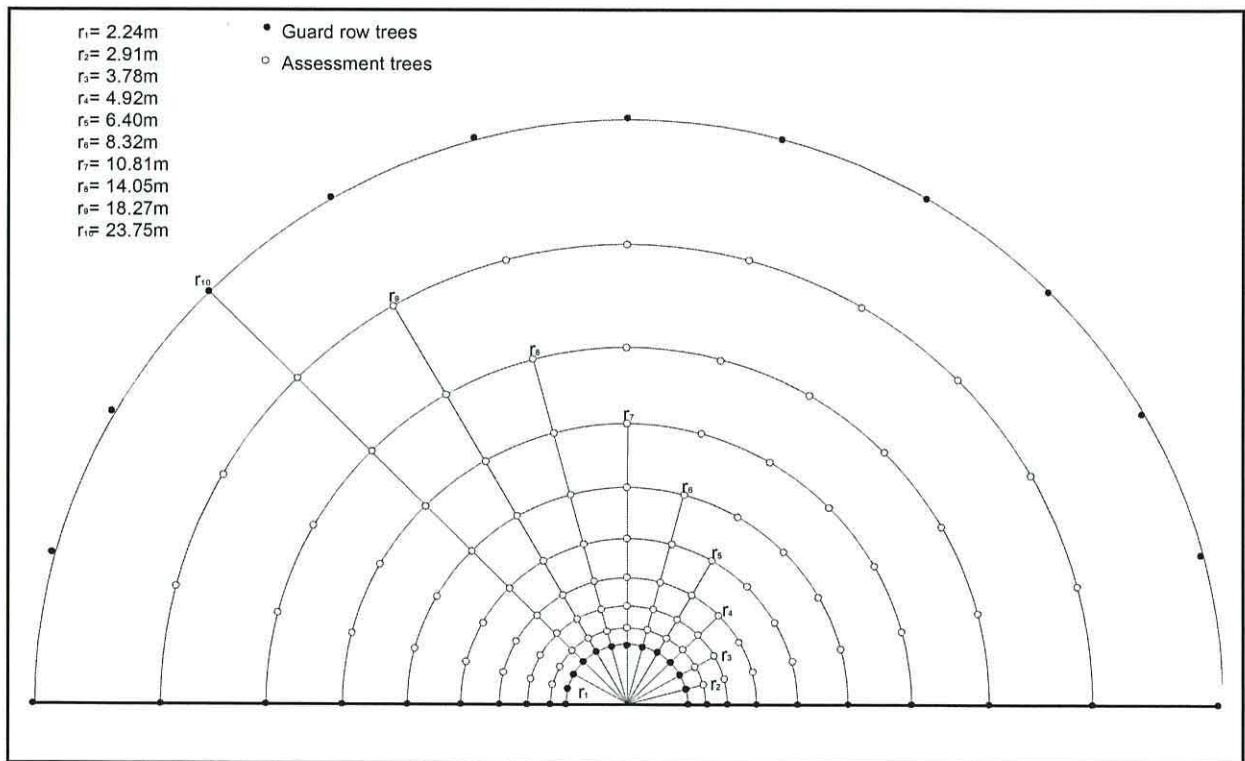
Initially trees were planted into weed free spots which were at least 1.0 m in diameter. These had been produced using pendimethalin (4 litres ha^{-1}) and propyzamide (Kerb flowable at 3.75 litres ha^{-1}) applied as a pre-plant treatment in December 1994. Subsequent control in the summer was by guarded application of glyphosate (2 litres ha^{-1}) and glufosinate ammonium (3 litres ha^{-1}). The latter was applied later to clean up areas missed by the glyphosate; it is not translocated and there is less risk of damage to trees then from glyphosate (Willoughby and Dewar, 1995). In winter, propyzamide

was used as described above. The initial spots were maintained for one year, and after this each fan plus a 1 m buffer received complete weed control for the duration of the experiment. Unfortunately an over-zealous application of atrazine applied at 9 litres ha^{-1} occurred in December 1998. This was the rate given in Willoughby and Dewar (1995), but the rate had been revised to 6.5 litres ha^{-1} in Willoughby (1996). The result was that 16% of trees in the experiment were killed and, because of the soil-acting nature of the herbicide, the growth of many others was impaired.

Table 2.2   Details of Nelder experiment layout (Neroche 46 and Swadlincote 1)

Arc number	Distance from centre (m)	Area available for each tree (m^2)	Equivalent number of trees ha^{-1}	Equivalent square spacing (m) [1]
1	2.24	Guard row	-	-
2	2.91	0.597	16750	0.77
3	3.78	1.013	9871	1.01
4	4.92	1.716	5827	1.31
5	6.40	2.898	3450	1.70
6	8.32	4.885	2047	2.21
7	10.81	8.249	1212	2.87
8	14.05	13.959	716	3.74
9	18.27	23.598	423	4.86
10	23.75	Guard row	-	-

[1] These spacings, rounded to one decimal place, have been adopted as the standard nomenclature for spacing treatments.

2.2.1.1.3 Growth assessments

Each tree was measured for total height (nearest cm) and stem diameter (nearest mm at a marked point 5 cm above the ground) immediately after planting and annually in October of each year until the last assessment in August 1999. The last assessment unaffected by the atrazine application was in October 1998. During 1995 four trees died, and these were replaced in October 1995 from a reserve of trees from the initial planting which had been planted at 50 cm × 50 cm adjacent to the Nelder fans; no other replacement occurred. For each assessment the height:stem diameter ratio was calculated for each tree by dividing the height (in cm) by the stem diameter (in mm).

In August 1999, after the damaging atrazine application, each tree was assessed as 0 = dead, 1 = growth affected, 2 = alive and healthy. In October 1999 random sampling was used to identify four rays in each of the three fans which were removed in a destructive harvest of shoots and roots; as there were eight treatment trees in each

ray this gave a maximum of 8 × 4 × 3 = 96 trees. Each tree was excavated by hand using spades; the main lateral roots were located and excavated, maintaining as much fine root material as practical. This was facilitated by friable soil and dry, fine weather. Each tree which was dead or had growth affected (scored as 0 or 1) was separated into: (i) roots (all material below the root collar); (ii) central stem (root collar to tip of leader [or tip of tallest branch if taller than leader]) and (iii) branches. For each tree which was still alive (scored 2) the 1999 increment of the stem and branches was separated from the rest of the plant and treated as a sub-set of (ii) and (iii) above. Branches and stems were cut into 30 cm sections and placed into labelled polythene bags; the roots had as much soil as possible removed by vigorous shaking, and were also placed complete into larger bags with appropriate labels. The samples were then transported to Alice Holt Research Station for dry weight determination.

The samples were stored in cool, dry conditions and the polythene bags were ventilated to minimise the risk of fungal degrade. Processing took place between October 1999 and March 2000 and very little mildew or mould was observed. Preparation for drying consisted of cutting samples into small pieces, less than 5 cm long, and where the stem or root was greater than 3 cm diameter the sample was also split longitudinally to ensure even drying. Samples were placed in metal trays in an oven at 85°C; samples were dried to constant weight which generally took 48 hours. Samples were weighed to the nearest 0.1 g immediately after removal from the oven.

2.2.1.1.4 Form assessments

The form of each of the trees was assessed by calculating the branch:central stem dry weight ratio. During the course of the experiment a number of non-destructive form assessments were also made: (i) bifurcation ratio (Steingraeber and Waller, 1986), (ii) length of longest branch and (iii) a form score (3 = strong straight central stem, 2 = central stem apparent but not straight and 1 = no central stem apparent). However, no clear patterns or relationships emerged from analysis of the non-destructive assessment data and results are not presented in the thesis.

2.2.1.1.5 Leaf area investigation

Appendix 2.2 explains the method used to derive an equation which could be used to estimate the leaf area of an ash tree using the length of the leaf:

$$y = 0.37x + 0.01752\,x^2 \qquad\qquad \text{[2.2]}$$

where y = estimated area of leaf (cm^2) and x = length of leaf (cm).

In August 1997 and August 1998 all trees from fan 1 were assessed for: (i) number of leaves, and (ii) length of every 10th leaf (nearest mm). Some trees had very few leaves, and where there were fewer than 50 leaves, five were measured for length. Using this information and equation [2.2] the foliage area of all ash trees in fan 1 was estimated.

2.2.1.2   Swadlincote 1 P1998

A second set of three Nelder experiments was also established in January 1998 at the Swadlincote Demonstration Woodland in the National Forest (Kerr and Williams, 1999) (52° 45'N, 1°34'W). The ESC Decision Support System (Ray, 2001) describes the site as 'suitable' for ash. The main differences between establishment of this experiment and that of Neroche 46 were: (i) the use of 0.75 m treeshelters to protect each tree, (ii) the use of complete weed control throughout the establishment phase, and (iii) only total height and stem diameter at a marked point 5 cm above ground were measured.

2.2.2   Analysis of data from Nelder experiments

Figure 2.2 Area available for growth for each tree in the Nelder experiment
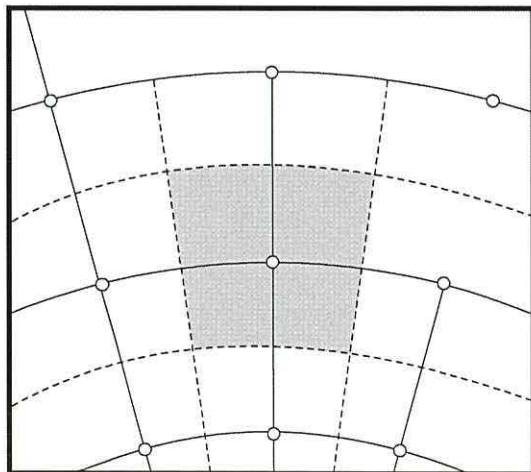
Each assessed tree was assumed to have an area available for growth (Figure 2.2); the method of calculating this and dealing with missing trees is shown in Appendix 2.3. The square root of this area is equivalent to the spacing between trees if they were planted on a square grid. Spacing is also synonymous with the term 'mean distance to nearest neighbour' which is commonly used in the scientific literature.

The objective of the work was to investigate the influence of spacing on growth and form of ash trees; hence spacing, as defined above, has been used as an explanatory variable in the analyses described below.

2.2.2.1   Growth and dry weight data

Analysis of the growth data from the Nelder fans was a two stage process. Firstly, the spacing was calculated for each arc of each fan taking into account any missing trees[3] (Appendix 2.3), and the mean height, mean stem diameter and mean height:diameter ratio for each arc of each fan were calculated.   Secondly, the means and their variances were plotted out to inspect the possible form of their relationship with spacing.   Initially, data were fitted to a multiple linear regression in Genstat (Anon, 1993) using the model:

$$y_{ij} = \alpha + \delta_i + \beta x_j + \lambda x_{ij} + \varepsilon_{ij} \qquad [2.3]$$

where: y = height, stem diameter or height:diameter ratio ; x = spacing (m) as a variate; α (constant), δ (change in constant for blocks), β (slope) and λ (interaction of spacing and blocks) are model parameters; ε = errors.   Terms were fitted in the order shown above but in all cases the interaction between fans and spacing was not significant. The final model used therefore only included:

$$y_{ij} = \alpha + \delta_i + \beta x_{ij} + \varepsilon_{ij} \qquad [2.4]$$

This model produced three parallel straight lines, one for each fan, with the same gradient but different y-axis intercepts. For each model residuals were investigated to ensure that they were normally distributed and that there was no systematic change in relation to fitted values (Cook and Weisburg, 1982). It was noted, for the height and stem diameter data for October 1997 and October 1998, that variances were heterogeneous ($P \leq 0.05$ using Bartlett's Test for homogeneity of variances (Snedecor and Cochran, 1980)).   In an attempt to deal with this problem a logarithmic transformation was carried out but this had little effect on the structure of the residuals. Therefore for clarity and ease of interpretation the linear regression model was used.

---

[3] Four trees died in 1995 and were replaced using trees which had been on-site since April 1995, hence it has been assumed in the analysis that all trees were planted in March 1995.

The height data from April 1995 to October 1998 were analysed using a parallel curve analysis in Genstat (Anon., 1993). A number of functions were investigated but the most appropriate, in terms of percentage variance accounted for and the ability of the curve fitting procedure in Genstat to converge in under 30 iterations, was an exponential function of the form:

$$y_{ij} = \alpha_j + \beta_j . \rho^{x_i} + \varepsilon_{ij} \quad j = 1...8 \qquad [2.5]$$

where: y = height; x = assessment date (fitted as a variate); j = spacings (of which there were eight); α, β and ρ are model parameters; ε = errors. Parallel curve analysis in Genstat allows four levels of similarity to be investigated: (i) a single curve to all the data (α, β and ρ are all constant); (ii) parallel curves (β and ρ are constant); (iii) common nonlinear parameters (ρ is constant); (iv) separate nonlinear parameters (α, β and ρ are all different). The form of the model shown in [2.5] is where ρ is constant.

In addition to comparing field performance using height, diameter and the ratio between them, the duration of transplant check was also investigated using the Transplant Shock Index (TSI) proposed by South and Zwolinski (1997). The index is defined as the slope of a linear relationship between initial height and height increment in a given year. A negative slope indicates that plants are experiencing transplant check, while a positive slope suggests plants have recovered from check. If the slope is close to zero then the trees are considered to be recovering from shock. A TSI was calculated for each spacing from 1995 to 1997.

The height and diameter distributions at each spacing for data from October 1997 and October 1998 were investigated by fitting a Normal (Gaussian) distribution; the null hypothesis was that the distribution was normal. For each distribution the mean, skewness and kurtosis were calculated. The goodness of fit was indicated by the residual deviance which has an asymptotic chi-squared distribution with the specified degrees of freedom.

For each tree destructively harvested the following dry weight variables were calculated for the period of growth up to the end of 1998: (i) central stem (stem excluding branches), (ii) branches, (iii) root, (iv) shoot (central stem+branches), (v) total (central stem+branches+root), (vi) shoot:root ratio and (vii) central stem:branch ratio. For trees unaffected by residual herbicide there was confounding caused by growth during 1999; branch and central stem increments were removed, but the rest of the increment could not be 'peeled off' the remaining stem and branches. An attempt

was made to correct for this using height and diameter data from October 1998 and August 1999; however, as the shape of the trees was not known it was judged that these 'adjusted' data were poorer than the empirical data. The dry weight data were continuous and normally distributed so were analysed using the same model ([2.3]) as the height and diameter data. The difference between the weight and growth data was that in the former means for each spacing/fan combination were calculated from four values, while in the latter they were from 11 values.

2.2.2.2   Leaf area data

The leaf area for each tree was estimated and a mean was calculated for each spacing in fan 1. An exponential model was then fitted to the data using Genstat. For the August 1997 data all models approached their limiting form but the best fit was an exponential model of the form:

$$y_{ij} = \alpha + \beta \rho^{x_i} + \delta x_j + \varepsilon_{ij} \qquad [2.6]$$

For the August 1998 data a standard exponential model was found to give the best fit and had the form:

$$y_i = \alpha + \beta \rho^{x_i} + \varepsilon_i \qquad [2.7]$$

In both equations above, y = leaf area (cm^2), x = spacing, α, β, δ, ρ are model parameters and ε = errors.

2.2.3   Randomized block experiment

2.2.3.1   Site details

The experiment (North Wyke 3 P1988) was established on a grassland site which belongs to the Institute of Grassland and Environmental Research (IGER) 6.5 km northeast of Okehampton, Devon (50° 47′N, 4°55′W). The topography of the area is gently undulating and the site lies at 175 m asl and slopes (5°) to the south. Tatter flag measurements from 1988 and 1989 (data not shown) confirmed that the site was very sheltered according to the classification of Mackie and Gough (1994).

The soil is a surface water gley classified by Avery (1980) as a pelo-stagnogley soil which overlies Millstone grit and Culm measures from the Carboniferous period; the

soil pH is 6.1. The drainage status of the area was described as 'poor' by IGER in 1987 and this was confirmed by observations when visiting the experiment, particularly in winter. In terms of Ecological Site Classification for tree growth the site lies within the warm moist zone described by Pyatt *et al.* (2001). The ESC Decision Support System (Ray, 2001) describes the site as 'suitable' for ash.

2.2.3.2   Experimental design and details of establishment

The experiment was established as a silvo-pastoral experiment. It was a split plot design with four main plots (tree spacing), two sub-plots (species) and three blocks. The tree spacings used were 10 m × 10 m (100 stems per hectare (sph)), 5 m × 5 m (400 sph), 2 m × 2 m (2500 sph) (the forestry control) and no trees (the grazing control); the two species planted were ash and sycamore. The area, number of trees planted and number of trees assessed in the plots are summarized in Table 2.3.

Table 2.3 Numbers of trees planted and assessed in the randomized block spacing experiment (North Wyke 3)

Spacing treatment	Plot information	Block 1	Block 2	Block 3
10 m	Plot area (ha)	0.48	0.48	0.48
	Trees in plot	48	48	48
	Trees assessed	24	24	24
5 m	Plot area (ha)	0.38	0.33	0.28
	Trees in plot	120	110	90
	Trees assessed	25	25	25
2 m	Plot area (ha)	0.11	0.11	0.12
	Trees in plot	210	200	216
	Trees assessed	96	96	100
	Trees assessed from Sep 1995+	25	25	25

All trees assessed were in a central plot; for example, in the 10 m spacing treatment there was only one guard row.

All trees were planted in November 1987 as good quality 1+1 transplants. In the 10 m and 5 m spacing treatments trees were protected by 1.5 m treeshelters, while trees at 2 m spacing were enclosed by a rabbit proof fence. Weed control was to keep a 1 m diameter spot around each tree 90% free of weeds for the first four years; this was achieved using glyphosate (2 litres ha^{-1}) which was applied as a guarded spray in the 2 m spacing plots. Some supplementary hand weeding occurred in the 2 m spacing treatment to remove invading forbs, some of which were noxious.

Before planting, 60 kg ha^{-1} of P_2O_5 and 20 kg ha^{-1} of K_2O fertilizer were applied to the area and lime was added to give a pH of 6.5. Throughout each season 160 kg ha^{-1} of nitrogen was applied to the 10 m and 5 m spacing treatments as standard agricultural practice to improve the grazing quality. Sheep grazed in the 10 m and 5 m spacing treatments and sheep numbers were adjusted to maintain a sward height of between 4 and 6 cm.

All trees in the 10 m and 5 m spacing treatments and selected trees in the 2 m spacing treatment were pruned in April of 1992, 1995 and 1998; data were recorded for the amount of material cut but were not available for investigation. The objective of the pruning was to produce trees with 5 m of clear timber; the experiment plan specifies that any one lift must not remove more than one-third of the live crown.

2.2.3.3   Survival and growth assessments

The height and survival of trees were measured in April 1988 and then annually until January 2000, except at the end of the 1992 growing season when there was no assessment. Stem diameter at 20 cm above ground level[4] was measured in January 1992 and at breast height (1.3 m above ground) in September 1995, February and October 1998 and January 2000. For each occasion when a diameter was assessed a height:diameter ratio was calculated by dividing the height (in cm) by the diameter (in mm). At the end of 1988 all dead trees were replaced but this beating-up was not repeated.

2.2.4   Analysis of data from the randomized block experiment

To treat the experiment as an ash spacing experiment all plots without trees and those with sycamore were ignored in the analysis. Data were subjected to analysis of variance as a randomized block experiment with three treatments (10 m, 5 m and 2 m spacings) and three blocks. The sums of squares were partitioned as shown in Table 2.4.

Table 2.4 Analysis of growth assessments: partitioning of sums of squares

Source of variation	Degrees of freedom
Blocks	2
Spacing	2
Residual	4
Total	8

---

[4] For trees in treeshelters this was done using a small door cut in the side of the treeshelter.

In addition, the height data from April 1988 to January 2000 were analysed using a parallel curve analysis in Genstat (Anon., 1993). A number of functions were investigated but the most appropriate, in terms of percentage variance accounted for and the ability of the curve fitting procedure in Genstat to converge in under 30 iterations, was a logistic function of the form:

$$y_{ij} = \alpha_j + \frac{\gamma_j}{1 + \exp(-\beta_j(x_i - \mu_j))} + \varepsilon_{ij} \quad j = 1...3 \qquad [2.8]$$

where: y = height, x = assessment date (as a variate), j = spacings (of which there were three), α, β, μ, γ are model parameters and ε = errors. The four levels of similarity examined were: (i) a single curve to all the data (α, γ, β and μ all constant); (ii) parallel curves (γ, β and μ all constant); (iii) common nonlinear parameters (β and μ were constant); (iv) separate nonlinear parameters (α, γ, β and μ were all different). The form of the model shown in [2.8] is where all parameters are different.

2.3 Results

2.3.1 Nelder experiments

2.3.1.1 Survival and growth

Over the four growing seasons between April 1995 and October 1998 growth was generally slow in the first two, as trees established, and was then rapid in the last two years (detailed results are in Appendix 2.4). Average height increments in 1995 and 1996 were 5.2 cm and 8.6 cm, while in 1997 and 1998 they were 87.7 cm and 141.7 cm. These patterns were also reflected in the stem diameter increments for the four years which were (in date order) 1.4 mm, 1.9 mm, 4.7 mm and 7.5 mm. Throughout this period survival was excellent: four trees died in 1995, three died in 1996, seven in 1997 and two in 1998 out of 450 in total. There was no relationship between survival and spacing.

There was no significant effect of spacing on height during the first two years of the experiment. However, it was apparent that growth in fan 3 was better than in fans 1 and 2; for example, in October 1996 at 1.3 m spacing the mean height of trees in fan 3 was 12.6 cm and 22.6 cm greater than in fans 1 and 2 respectively (Appendix 2.4). After the third growing season, in October 1997, there was a highly significant negative

relationship between spacing and height, i.e. trees at the closer spacings were taller than those at wider spacings (Figure 2.3). The same pattern was also evident after four years growth, in October 1998 (Figure 2.4); the extent to which spacing affected height (i.e. the gradient of the line) had increased by a factor of 2.6 compared with October 1997. The fitted equations are summarized in Table 2.5.

Table 2.5 Coefficients of linear models of a response variable of height fitted against the explanatory variables spacing and fan for Neroche 46

Assessment	Nelder Fan	Constant $(\alpha+\delta)^1$	Coefficient of spacing$(\beta)^1$	Model:% variance and significance	Significance of spacing^2
Oct. 1995	1	47.5	-0.516	20.2^{ns}	ns
	2	44.0			
	3	45.2			
Oct. 1996	1	50.1	0.659	73.9***	ns
	2	45.0			
	3	63.5			
Oct. 1997	1	91.9	-6.95	86.1***	***
	2	78.7			
	3	141.3			
Oct. 1998	1	163.8	-17.81	84.8***	***
	2	145.3			
	3	241.5			

^{1} Form of model shown in equation [2.4].
^{2} From accumulated analysis of variance table; ns - not significant, *** $P \leq 0.001$.

Results for stem diameter were very similar to those for height (Figures 2.5 and 2.6). For example, results were not significant for the first two years and then in October 1997 and October 1998 there was a significant negative relationship between spacing and stem diameter, i.e. trees at the closer spacings were thicker than those at wider spacings. The fitted equations are summarized in Table 2.6 (page 40).

Over the course of the investigation height:stem diameter ratios varied between 5.87 (cm mm^{-1}) and 11.14 (cm mm^{-1}) but there was never a significant relationship with spacing (Table 2.7, page 40, and Appendix 2.4).

The general form of the relationship between growth and spacing, i.e. that both height and stem diameter are increased at close spacing, was repeated in the results after two growing seasons in the Nelder experiment at Swadlincote (Figures 2.7, 2.8 and Appendix 2.5). The main difference between the results from the two experiments was that the term for *fans* was not significant and therefore a model with the same parameters could be used for all three fans.

35

Figure 2.3 Effects of spacing on height of ash trees in October 1997 at Neroche 46
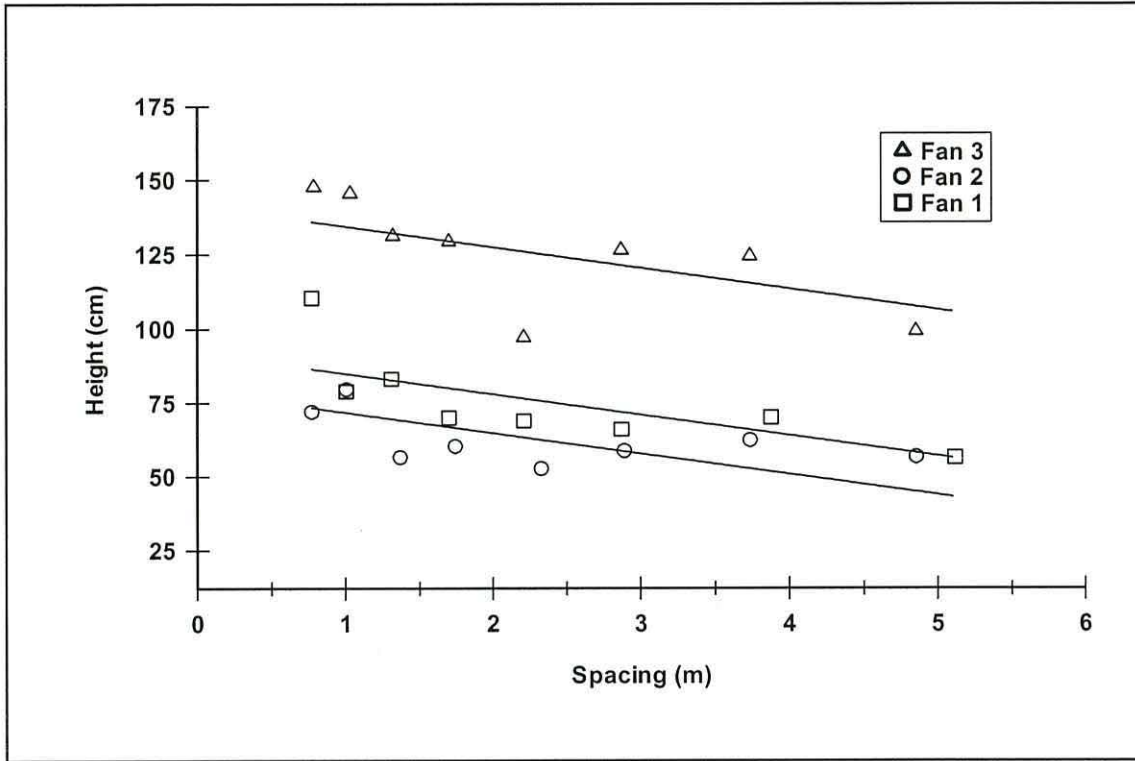
Figure 2.4 Effects of spacing on height of ash trees in October 1998 at Neroche 46
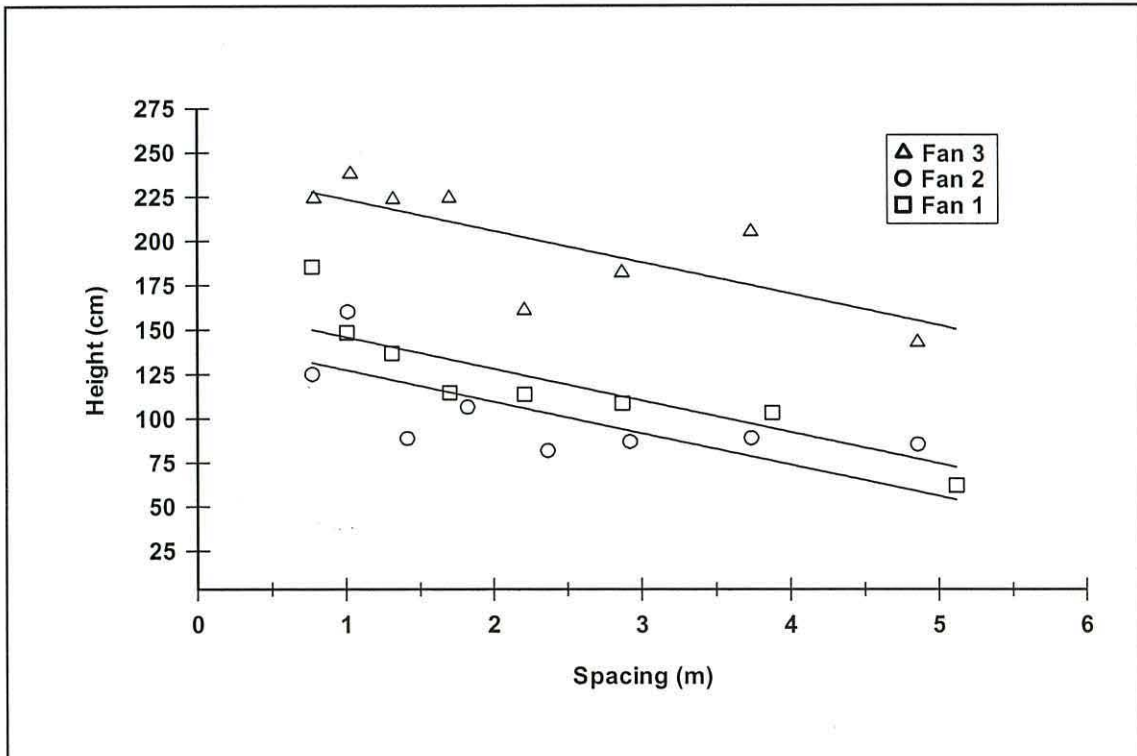
Figure 2.5 Effects of spacing on stem diameter of ash trees in October 1997 at Neroche 46
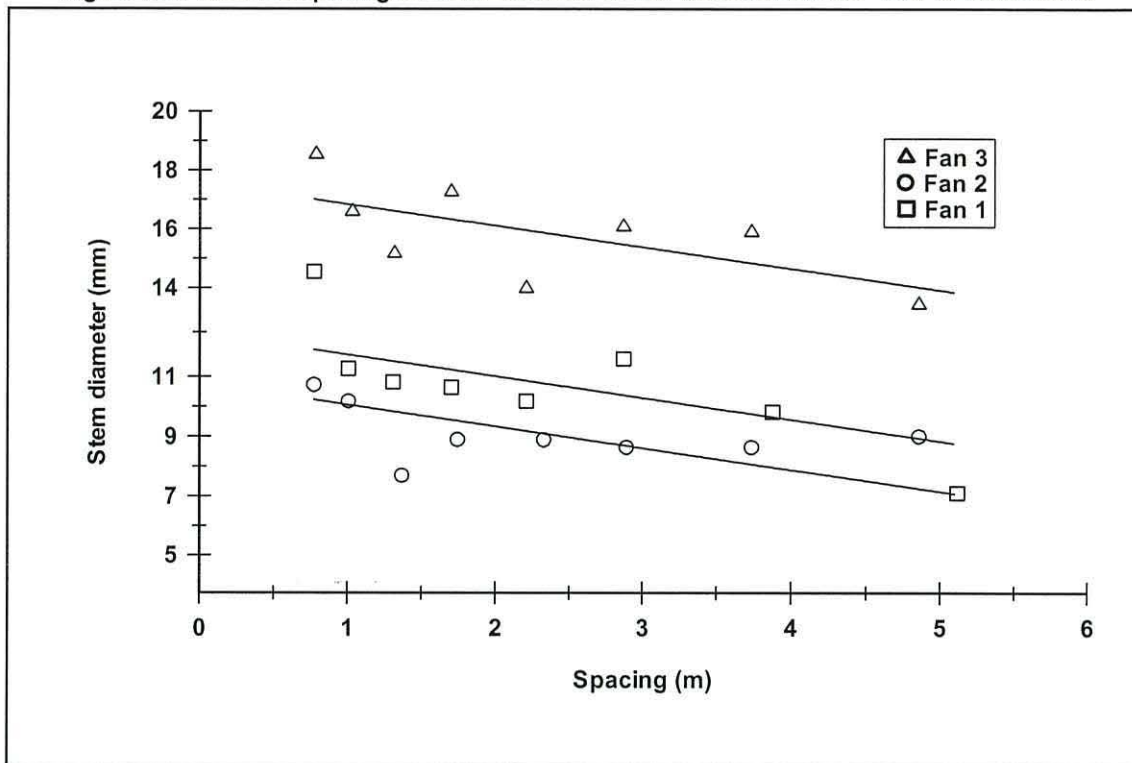
Figure 2.6 Effects of spacing on stem diameter of ash trees in October 1998 at Neroche 46

37
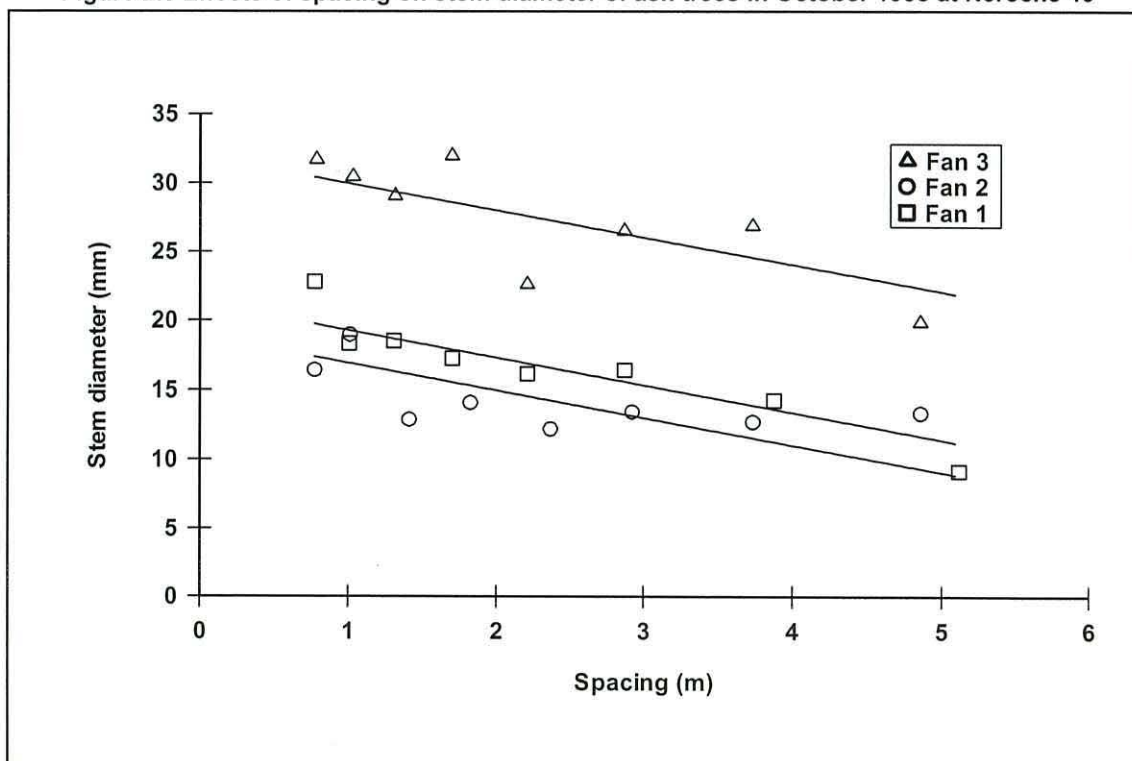
Figure 2.7 Effects of spacing on height after two growing seasons at Swadlincote 1
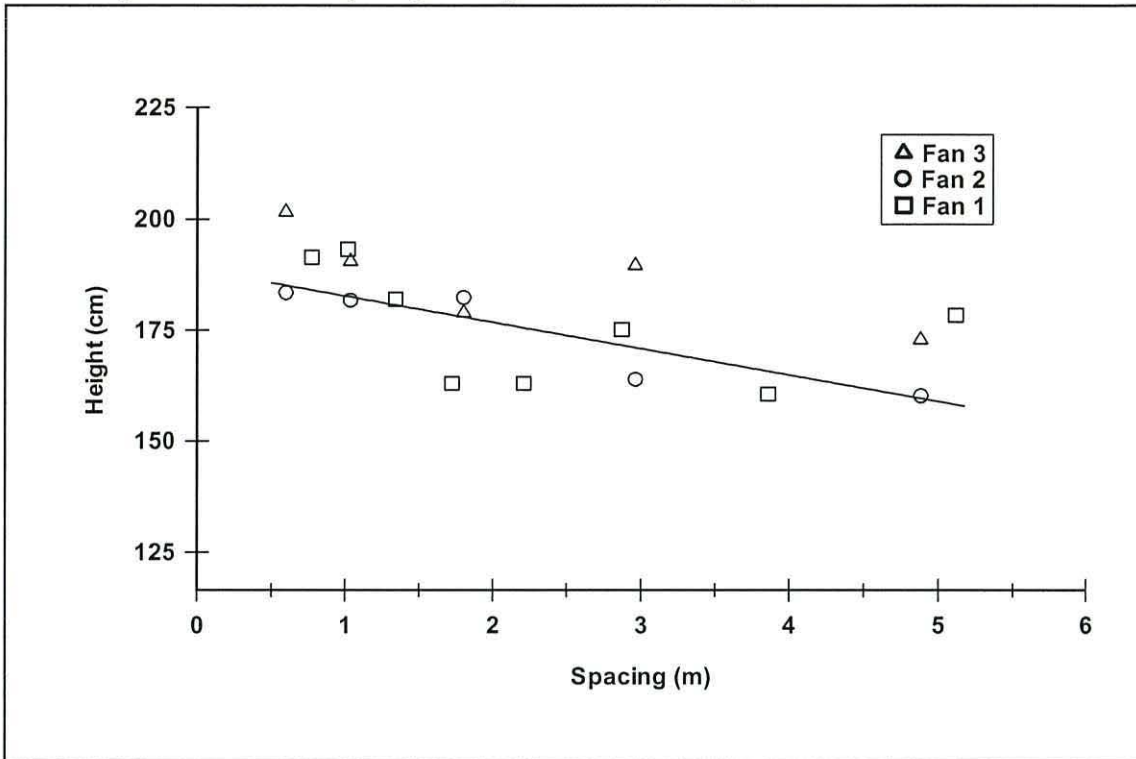
Figure 2.8 Effects of spacing on stem diameter after two growing seasons at Swadlincote 1
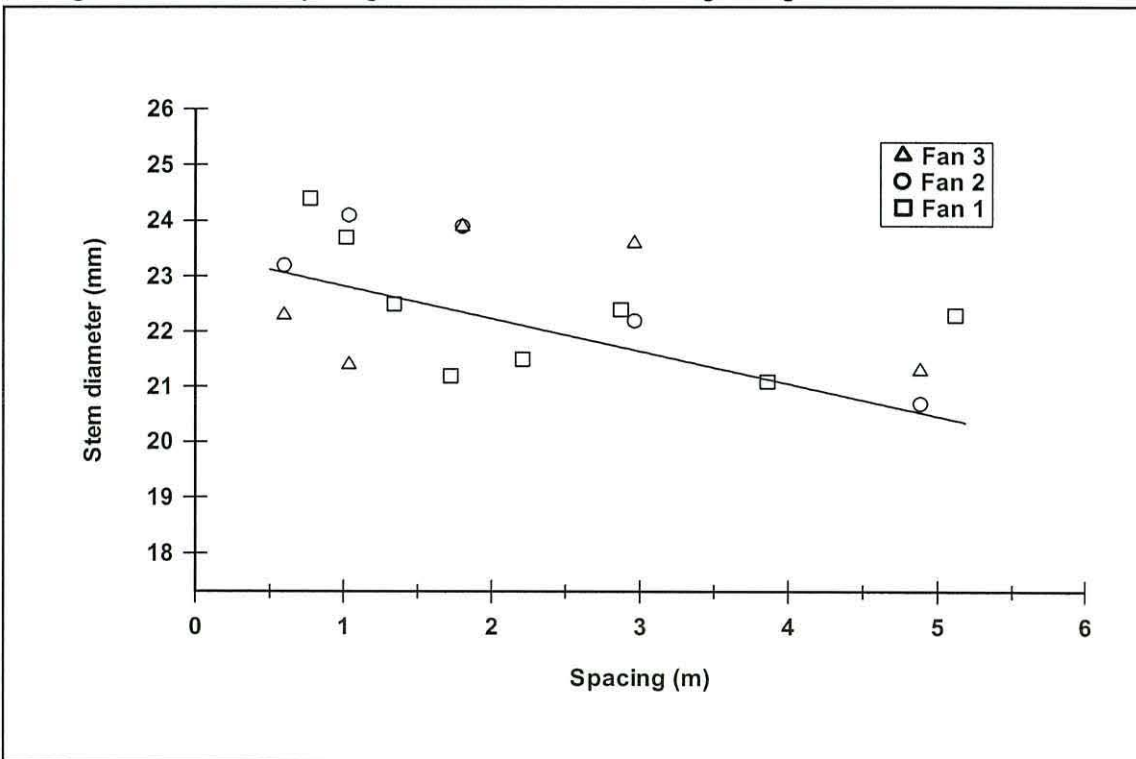
Figure 2.9 Effects of spacing on height at Neroche 46: results of parallel curve analysis

For clarity, only results from four spacings are presented
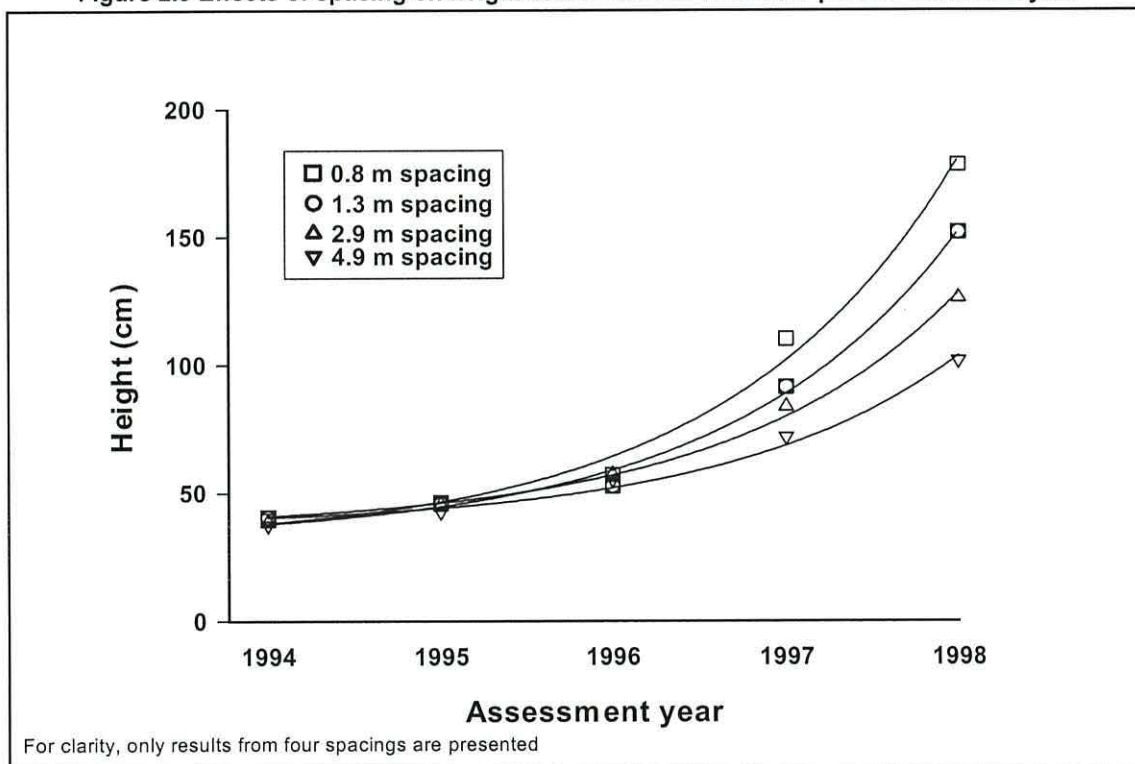
Table 2.6 Coefficients of linear models of a response variable of stem diameter fitted against the explanatory variables spacing and fan for Neroche 46

Assessment	Nelder Fan	Constant $(\alpha+\delta)^1$	Coefficient of spacing$(\beta)^1$	Model:% variance and significance	Significance of spacing^2
Oct. 1995	1	6.26	-0.114	61.3***	ns
	2	5.61			
	3	7.12			
Oct. 1996	1	6.94	0.213	74.7***	ns
	2	6.26			
	3	8.94			
Oct. 1997	1	12.47	-0.728	85.6***	***
	2	10.79			
	3	17.57			
Oct. 1998	1	21.27	-1.97	88.6***	***
	2	18.92			
	3	31.96			

[1] Form of model shown in equation [2.4].
[2] From accumulated analysis of variance table; ns - not significant; *** $P<0.001$.

Table 2.7 Summary of height:stem diameter ratios in Neroche 46 and North Wyke 3

Assessment	Maximum (cm mm^{-1})	Minimum (cm mm^{-1})	Mean (cm mm^{-1})	Significance of spacing^1
(a) Neroche 46 (Nelder experiment)				
October 1995	11.14 (2.2 m)	6.06 (0.8 m)	7.63	ns
October 1996	8.26 (1.3 m)	6.49 (4.0 m)	7.00	ns
October 1997	8.79 (1.0 m)	5.87 (2.2 m)	7.25	ns
October 1998	8.27 (1.0 m)	6.31 (2.2 m)	7.22	ns
(b) North Wyke 3 (randomized block experiment)				
January 1992	11.6 (10 m)	6.6 (2 m)	9.49	***
September 1995	13.9 (10 m)	9.6 (2 m)	11.66	*
February 1998	10.4 (5 m)	8.5 (10 m)	9.37	ns
October 1998	9.9 (10 m and 2 m)	7.5 (10 m)	9.10	ns
January 2000	10.9 (2 m)	7.7 (10 m)	9.32	ns

Figures in brackets indicate the spacing at which the value occurred.
[1] ns - not significant; * $P\leq0.05$; *** $P\leq0.001$.

Parallel curve analysis of the height–age growth curves confirmed the relationship between height growth and spacing (Figure 2.9). The best model included spacing, assessment date and the interaction of the two terms, but did not require the non-linear parameter to be estimated separately (Table 2.8); it accounted for 98.8% of the total variance. Figure 2.9 clearly shows that trees at different spacings were on similar

growth trajectories for the first two years but were clearly on different ones between the assessments in October 1996 and October 1998.

The diameter distributions were normal for all spacings in October 1997 and at all spacings except 2.9 m in October 1998 (Appendix 2.6). The distribution at 2.9 m was bi-modal with three trees being much larger than the others at both assessment dates, though only in October 1998 did this confer non-normality.The skewness parameter for all distributions at both dates was positive and therefore distributions were skewed to the right.

Table 2.8 Model parameters for the parallel curve analysis of Neroche 46

Spacing (m)	Model parameters[1]		
	α	β	ρ
0.8	30.4	3.64	
1.0	25.6	3.73	
1.3	31.8	2.91	
1.7	29.1	2.94	
2.2	33.8	2.12	2.105
2.9	36.3	2.22	
3.7	34.6	2.36	
4.9	37.0	1.61	

[1] Form of model shown in equation [2.5].
NB. α = asymptote; β = difference between where the function meets the y axis, and where the asymptote meets the same axis; ρ = rate of exponential increase (ρ is the only non-linear parameter).

Results for height distributions were more complex and are illustrated for October 1997 in Figure 2.10 (page 43) and for October 1998 in Figure 2.11 (page 44); other statistics from the comparison of distributions are given in Appendix 2.7. In October 1997 only two distributions were normal, those at 0.8 m and 3.7 m. There was evidence of bi-modality in the distributions at 1.0 m, 1.3 m, 1.7 m and 2.9 m spacings. All distributions were skewed to the right and therefore had more small diameters than large diameter trees. All except one distribution had negative kurtosis which indicated they were 'pointy' (showed *leptokurtosis*) compared with the bell-shaped normal distribution.

In October 1998, six of the distributions were normal and two were not normal, these were at 1.3 m and 4.9 m spacing and were bi-modal. All but one of the distributions were skewed to the right and the skewness parameter generally increased with wider spacings. The exception to this was at 1.3 m spacing which showed a distribution with two sub-populations of roughly equal size and therefore was not skewed. As in October 1997 the kurtosis parameter indicated that all the distributions were 'pointy' (showed *leptokurtosis)* compared with the bell-shaped normal distribution.

There was no clear pattern of change in distributions between 1997 and 1998. Four distributions did not change and were either normal (0.8 m, 3.7 m) or not normal

(1.3 m, 4.8 m). The other four distributions were all not normally distributed in October 1997 and changed to being normal in October 1998.

The dry weights of the central stem, branches and roots of trees at different spacings are summarized in Table 2.9 and Appendix 2.8. Data were variable with coefficients of variation commonly in excess of 100%. Analysis of data showed there was a significant negative relationship between both central stem dry weight (Figure 2.12, page 45) and root dry weight (Figure 2.13), and spacing. Trees at wide spacing therefore had lower dry weights of the central stem and roots than trees at closer spacings. In addition, there was a significant positive relationship between shoot:root ratio and spacing (Figure 2.14, page 46). These results suggest that at close spacings trees were partitioning dry matter roughly equally between shoot and root (shoot:root ratio ≈ 1). As spacing increased, trees partitioned a greater proportion of their dry matter to the shoot, and at the widest spacing the shoot:root ratio was ≈ 2. The fitted equations for the significant relationships are in Table 2.10 (page 47); no other relationships between dry weight parameters and spacing were significant (Appendix 2.8).

Table 2.9 Dry weights of central stem, branches and roots from Neroche 46

Spacing (m)	Mean central stem dry weight (g)	Mean branch dry weight (g)	Mean root dry weight (g)
0.8	378.2 (116%)	37.9 (133%)	251.1 (106%)
1.0	339.3 (130%)	30.4 (160%)	335.5 (135%)
1.3	472.2 (119%)	61.0 (168%)	493.2 (119%)
1.7	336.0 (88%)	17.4 (134%)	309.4 (92%)
2.2	374.2 (92%)	85.8 (187%)	374.1 (76%)
2.9	368.8 (96%)	59.1 (175%)	315.8 (108%)
3.9	213.5 (68%)	25.1 (131%)	116.2 (68%)
4.9	233.4 (80%)	47.8 (131%)	124.8 (120%)

Figures in ( ) are coefficients of variation.

In 1995 TSI values at all spacings were close to zero or negative, indicating that all trees were still in transplant shock (Figure 2.15, page 46). However, in 1996 there was a contrast between trees growing at the three closest spacings, in which TSIs were positive and indicated recovery from transplant shock, and those at the wider spacings which had lower values close to zero. In 1997 TSI values indicated that trees at all spacings had recovered from transplant shock.

Figure 2.10 Height distributions of ash trees in October 1997 at Neroche 46.

43
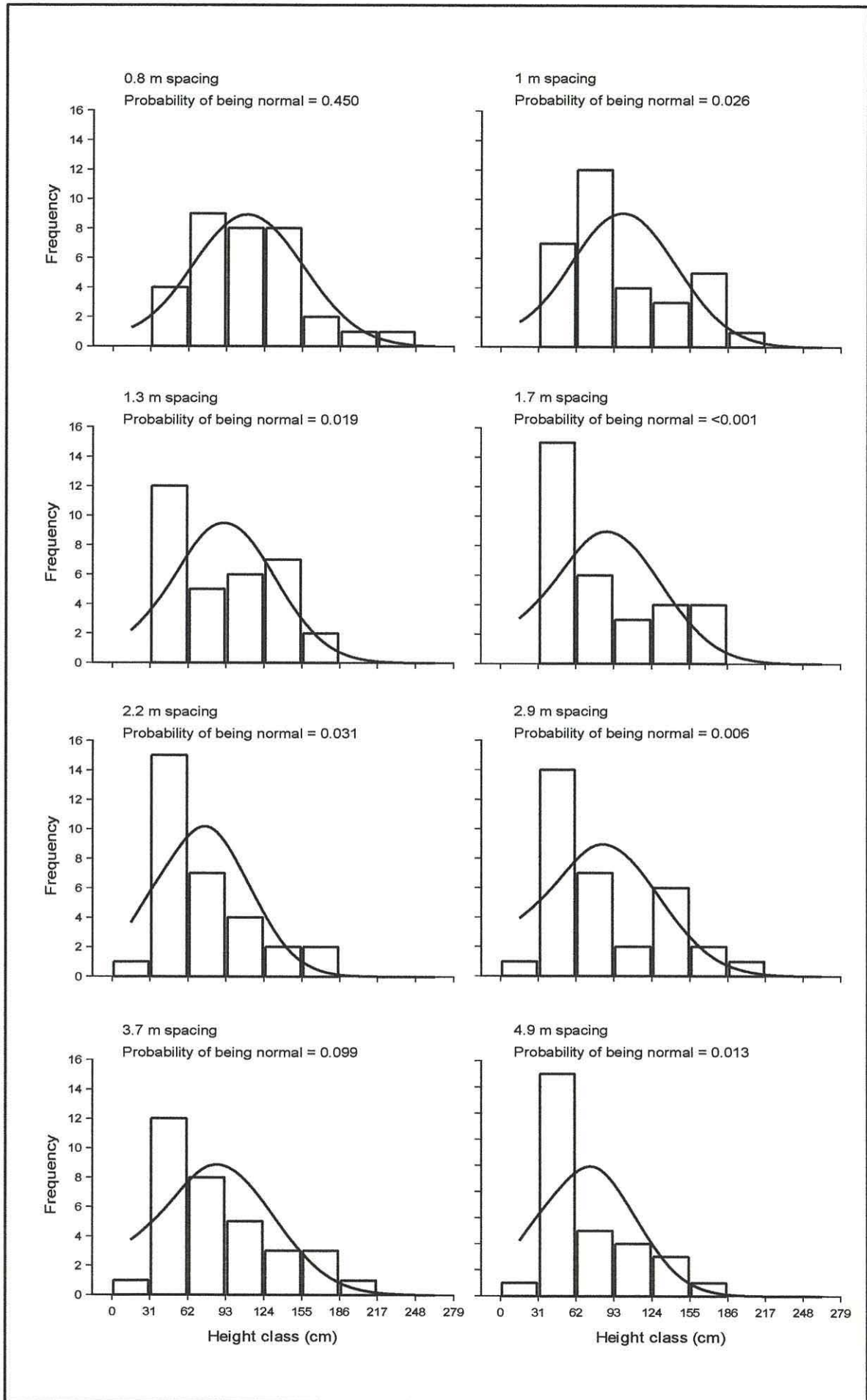
Figure 2.11 Height distributions of ash trees in October 1998 at Neroche 46.
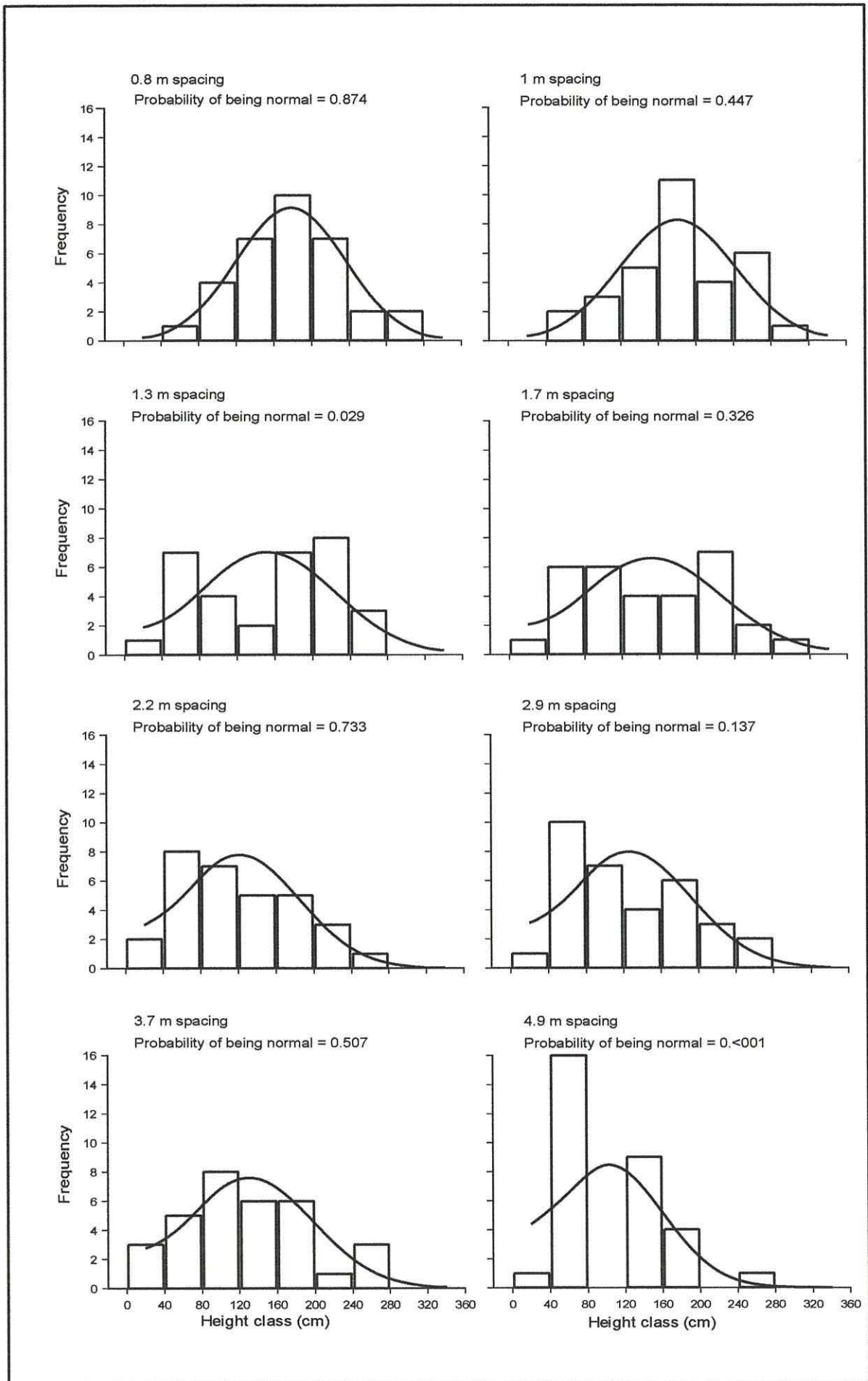
Figure 2.12 Effects of spacing on stem dry weight of ash trees in October 1999 at Neroche 46
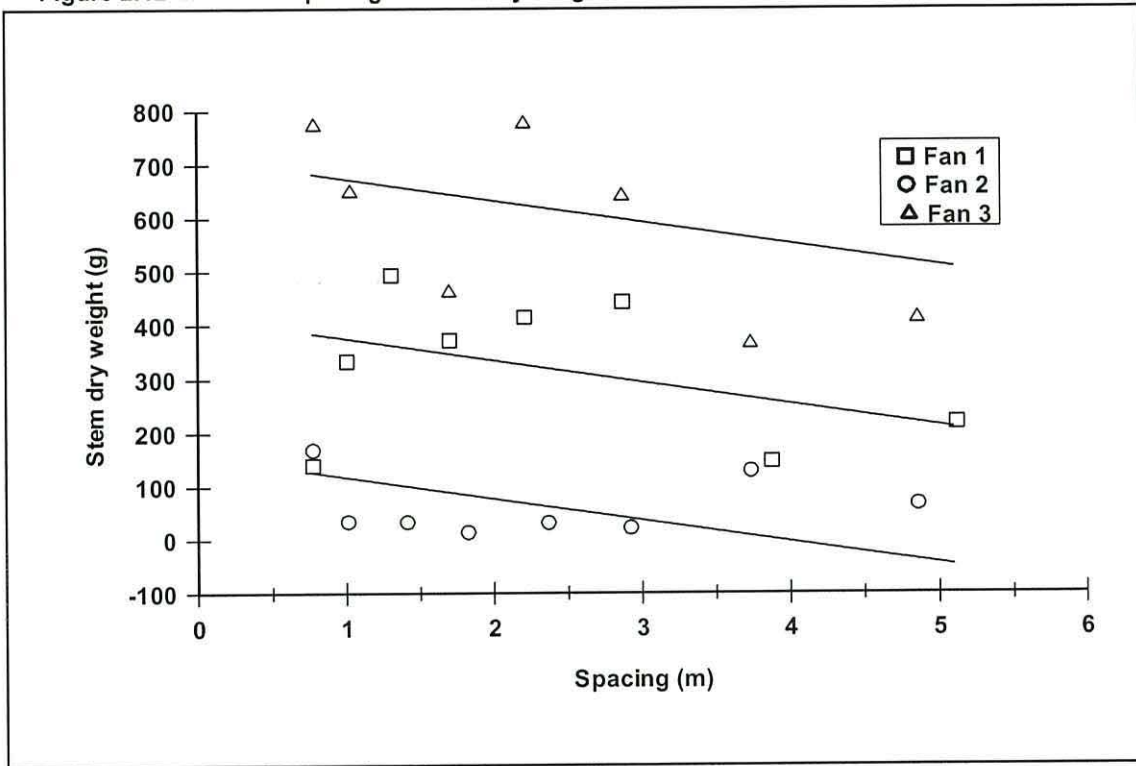
Figure 2.13 Effects of spacing on root dry weight of ash trees in October 1999 at Neroche 46
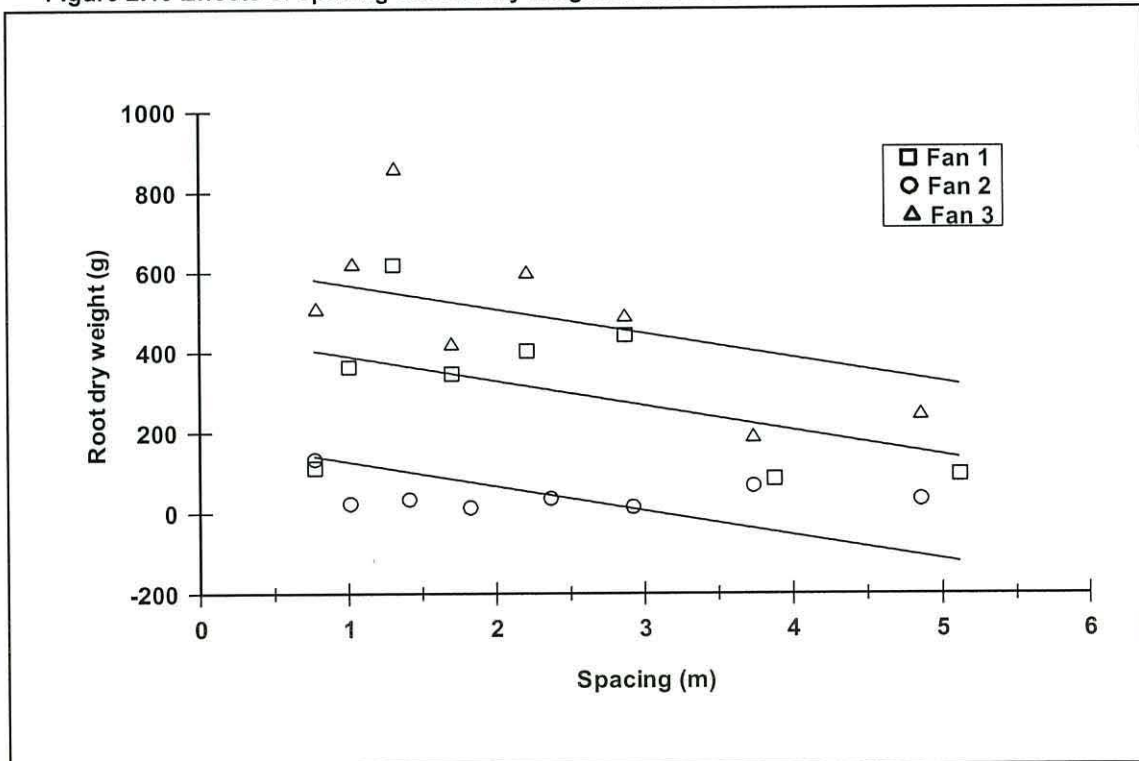
Figure 2.14 Effects of spacing on shoot:root ratio of ash trees in October 1999 at Neroche 46
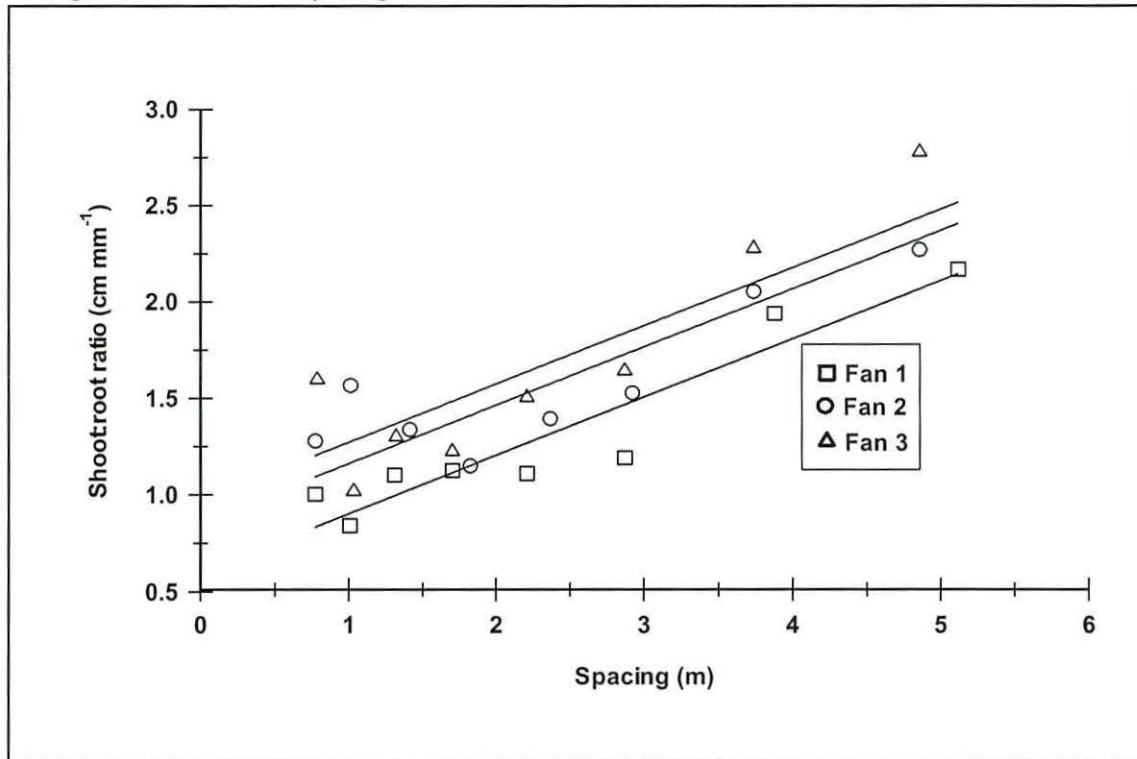
Figure 2.15 Transplant shock index of ash trees after one, two and three growing seasons at Neroche 46
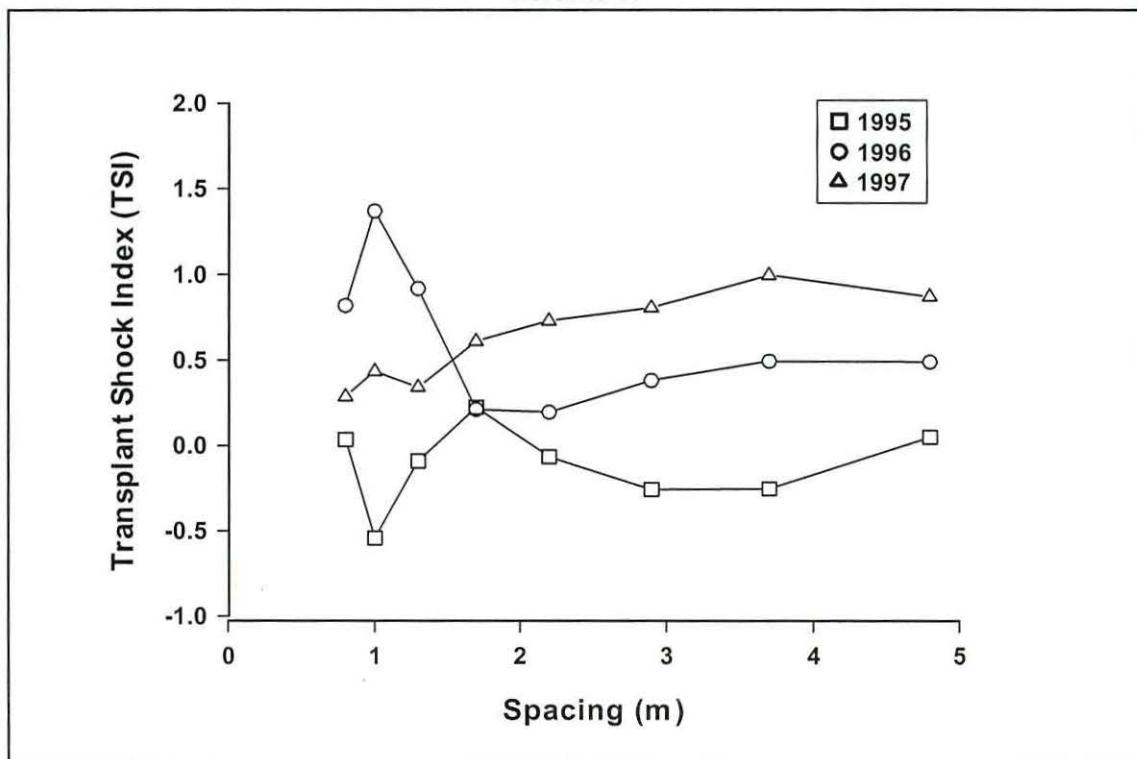
Table 2.10 Coefficients of linear models of various dry weight response variables against the explanatory variables spacing and fan for Neroche 46

Response variable	Nelder Fan	Constant $(\alpha+\delta)^1$	Coefficient of spacing $(\beta)^1$	Model:% variance and significance	Significance of spacing^2
Stem dry weight	1	415.6	-40.4	76.7***	*
	2	158.1			
	3	714.1			
Branch dry weight	1	30.3	0.54	42.9**	ns
	2	6.5			
	3	94.6			
Top (stem + branch) dry weight	1	464.0	-41.8	73.6***	ns
	2	170.6			
	3	817.5			
Root dry weight	1	451.2	-60.3	64.2***	**
	2	188.0			
	3	628.6			
Stem: branch ratio	1	44.2	-5.13	(^{3})	ns
	2	43.2			
	3	37.8			
Shoot:root ratio	1	0.60	0.302	78.9***	***
	2	0.86			
	3	0.97			

[1] Form of model shown in equation [2.4] but y = response variables as shown above.
[2] From accumulated analysis of variance table; *** $P\leq0.001$, ** $P\leq0.01$, * $P\leq0.05$, ns not significant.
[3] Residual variance exceeded variance of response variate.

2.3.1.2   Form measurements

Analysis of the central stem:branch dry weight ratio indicated that there was no significant relationship with spacing (Appendix 2.8).

2.3.1.3   Leaf area

Analysis of the leaf area data indicated that in 1997 and 1998 leaf area decreased exponentially with increased spacing (Figures 2.16 and 2.17, Table 2.11). In 1997 this decrease was from 400 cm^2 per tree at the closest spacing to 150 cm^2 at the widest spacing; in 1998 the reduction over the same range of spacings was from 800 cm^2 per tree to 300 cm^2 per tree. At both assessment dates data were quite variable; however, this did not mask the relationship between leaf area and spacing.

Figure 2.16 Relationship between mean leaf area and spacing in August 1997 at Neroche 46: fan 1
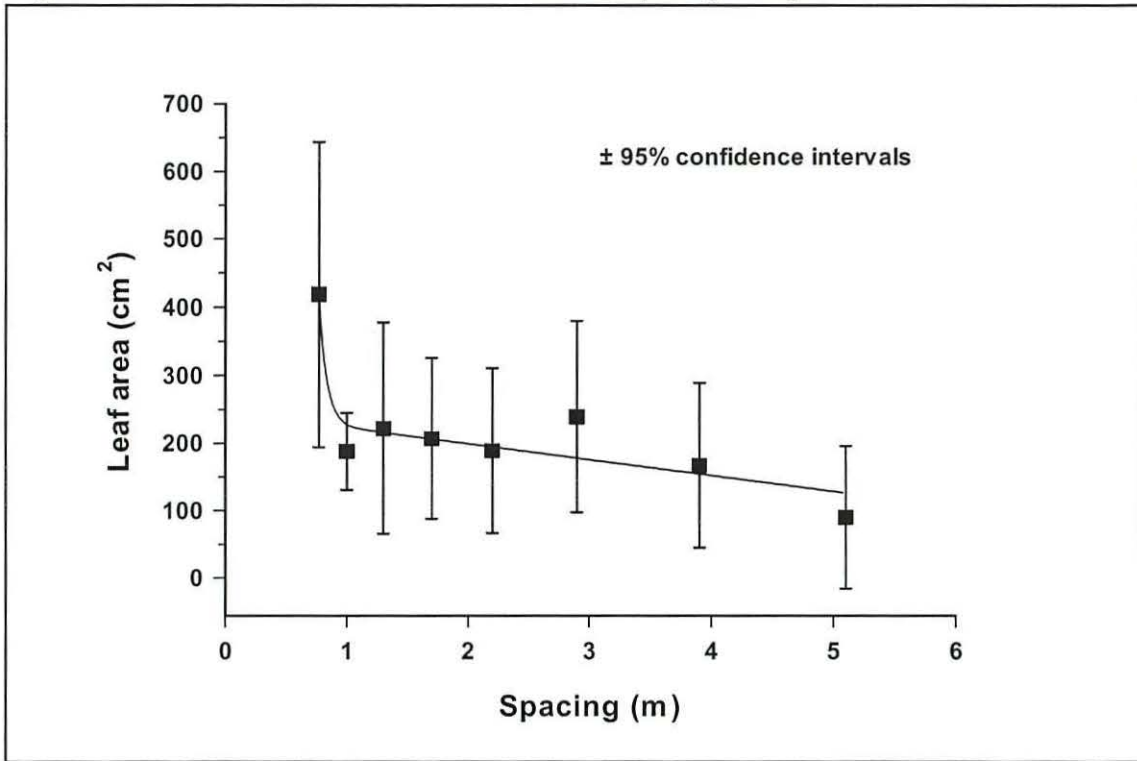
Figure 2.17 Relationship between mean leaf area and spacing in August 1998 at Neroche 46: fan 1
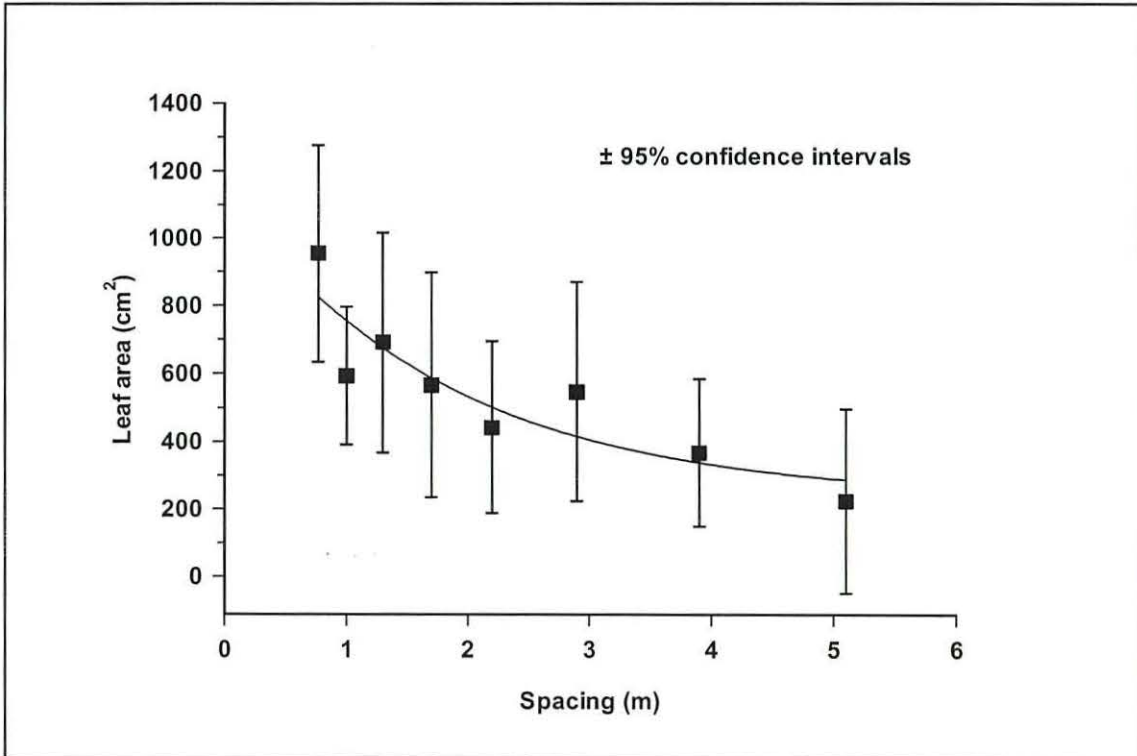
Table 2.11 Coefficients of exponential models of a response variable of leaf area fitted against the explanatory variables spacing and fan for Neroche 46: fan 1

Assessment	Model parameters[1]				Model:% total variance and significance
	α	β	ρ	δ	
July 1997	246.4	30003755	0.177×10^{-6}	-23.58	80.5*
July 1998	233	906	0.576	n/a	71.4*

[1] Form of models shown in equations [2.6] for July 1997 and [2.7] for July 1998; *$P \le 0.05$.

2.3.2   Randomized block experiment

2.3.2.1   Survival and growth

At the end of the first growing season four trees had died in the 2 m spacing treatment, one in the 5 m and 17 in the 10 m spacing treatment. Analysis of survival showed that these differences were significant ($P=0.003$). This was surprising as trees in the 10 m treatment were protected with treeshelters which are often claimed to increase survival (Potter, 1991).

There were three distinct periods of height growth in the spacing treatments (Table 2.12). First, in the three growing seasons up to October 1990, trees in the 10 m and 5 m treatments (wide spaced) were significantly taller than those in the 2 m treatment (close spaced). The most likely explanation for these differences is the fact that trees in the two widely spaced treatments were protected by 1.5 m treeshelters and fertilised, whereas trees in the 2 m spacing treatment had neither of these. In October 1990 the height of the close spaced trees was 65.6 cm less than the lower of the two wide spaced treatments (10 m). Second, for all assessments between October 1990 and November 1995 there were no significant differences between treatments, although at the last of these assessments the close spaced treatment was 101 cm taller than the higher of the two wide spaced treatments (10 m). Third, from September 1996 differences in height were significant and in January 2000 the close spaced treatment was 360.0 cm taller than the higher of the two wide spaced treatments (10 m). At no time during the course of the experiment was there any significant difference between the 10 m and 5 m spacing treatments.

49

Table 2.12 Summary results of analysis of variance of height of ash trees for North Wyke 3

Assessment date	10 m	5 m	2 m	Standard error of difference	Significance
	Mean height (cm)				
April 1988	44.1	39.4	39.4	2.52	ns
Dec 1988	68.0	76.0	50.3	3.26	**
Oct 1989	95.2	124.1	65.0	6.97	**
Oct 1990	178.5	196.3	112.9	11.49	**
Oct 1991	249.6	255.6	205.9	19.73	ns
Oct 1993	345.0	352.0	356.0	25.6	ns
Oct 1994	363.0	361.0	417.0	30.8	ns
Nov 1995	378.0	372.0	479.0	36.0	ns
Sep 1996	407.0	373.4	564.0	38.4	*
Feb 1998	433.1	382.3	623.6	43.7	*
Oct 1998	467.2	415.9	725.4	58.8	*
Jan 2000	495.8	440.7	855.2	63.6	**

Deg.of freedom = 4; Student's t for $P \leq 0.05 = 2.8$;
ns - not significant, * $P \leq 0.05$, ** $P \leq 0.01$

There was no significant difference in stem diameter between the treatments in January 1992 (Table 2.13). However, at each of the four subsequent assessments of dbh, values in the 2 m spacing treatment were significantly greater than in either of the two wide spaced treatments. Throughout the investigation height:stem diameter ratios varied between 6.6 (cm mm^{-1}) and 13.9 (cm mm^{-1}) (Table 2.7, page 40). Initially, trees at the two widest spacings had higher height:diameter ratios, probably due to the influence of the treeshelters, and this resulted in significant differences up to September 1995. For the three assessments after this there was no significant effect of spacing on height:diameter ratio.

Table 2.13 Summary results of analysis of variance of stem diameter of ash trees for North Wyke 3

Assessment date	Stem diameter (mm)			Standard error of difference	Significance
	10 m	5 m	2 m		
Jan 1992[1]	22.4	24.8	29.0	2.13	ns
Sept 1995	32.2	29.9	46.0	3.13	*
Feb 1998	47.1	39.4	68.8	3.75	**
Oct 1998	55.2	44.7	76.7	5.10	**
Jan 2000	59.6	47.7	83.2	5.78	**

Deg. freedom = 4; Student's t for $P \leq 0.05 = 2.8$; ns - not significant, *$P \leq 0.05$, **$P \leq 0.01$
[1]Measured at 20 cm above ground, all other stem diameters at 1.3 m above ground (dbh)

Figure 2.18 Effects of spacing on height at North Wyke 3: results of parallel curve analysis
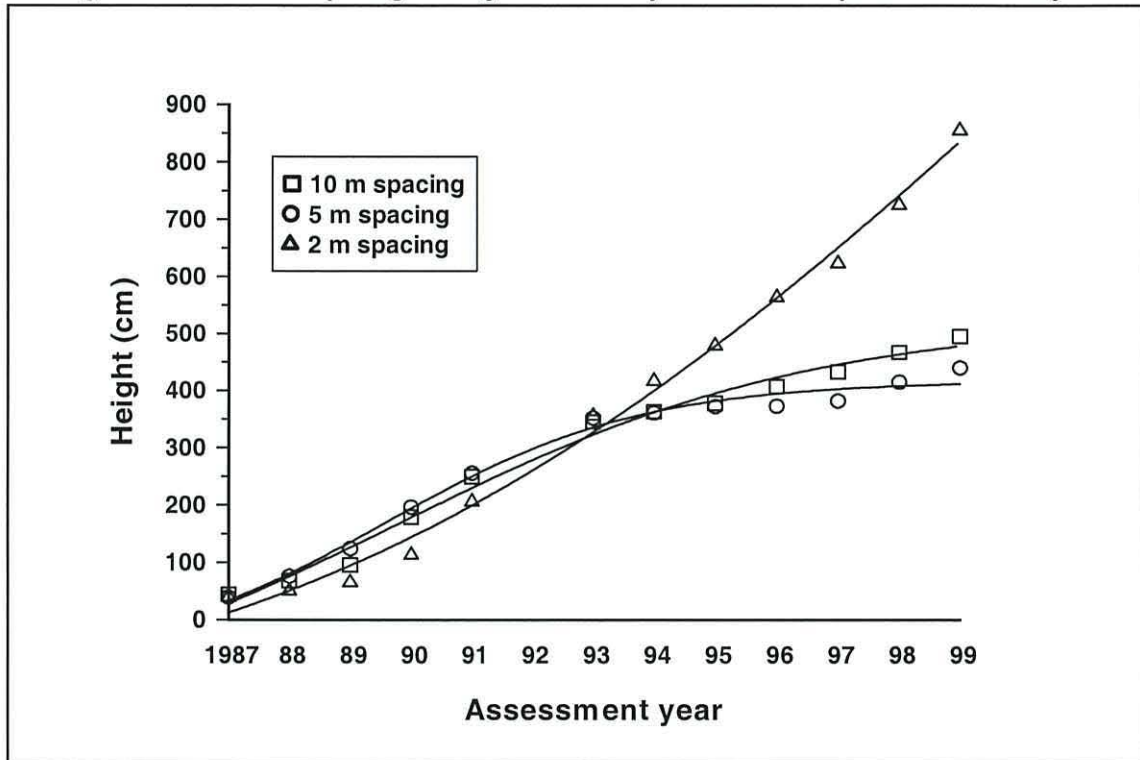
In the parallel curve analysis of height (Figure 2.18) the best model required all non-linear parameters to be estimated separately (Table 2.14). Figure 2.18 tends to hide the differences between the first two stages of growth described above because each of the three treatments were on similar growth trajectories. However, it does emphasize the very large differences after November 1995, when trees in the close spaced treatment were clearly on a different height growth

Table 2.14 Parameter estimates for parallel curve analysis of North Wyke 3

Model parameters	Spacing		
	10 m	5 m	2 m
α	-198	-80	-232
γ	722	497	2282
β	0.289	0.474	0.166
μ	3.71	3.57	13.78

NB α = lower asymptote; β = slope parameter; μ = point of inflexion for explanatory variable; α + γ = upper asymptote (α and γ are the non-linear parameters)

trajectory from the two wider spaced treatments. To emphasize this the parameters in Table 2.14 can be used to estimate the upper asymptote for each of the growth curves, i.e. when it is predicted that height growth will effectively have stopped. For the 10 m and 5 m spacing treatments this would be at 5.24 m and 4.17 m respectively; however, for the 2 m spacing it would be 20.50 m. The very low predictions for the wide spaced treatments confirm observations that height growth has stopped or is very slow. However, this is only a prediction and in reality the effect may be temporary and height growth may resume, for example, when crowns come into contact with each other.

2.4 Discussion

2.4.1 Effects of spacing on survival and growth

Before discussing the results of the investigation it is important to establish their integrity. In both experimental designs a number of possible confounding factors may have influenced the results. In the Nelder experiments, it has been assumed that any possible cultivation effect of the planting operation was nullified by the compaction provided by firming trees into position. It is interesting to note that there has been little or no discussion of these two influences in the literature. Secondly, it has been assumed that the change in weed control specification at Neroche did not bias the results. Evidence that the latter assumption is correct is that the results from Swadlincote, where total weed control was carried out from planting onwards, showed the same trends. In summary, there were relatively few problems with these Nelder experiments compared with other published accounts. For example, Giordano and

Hibbs (1993) describe the use of Nelders to investigate the growth of red alder (*Alnus rubra* Bong.) and admit 'some of these trees (at wide spacing) experienced more deer and elk damage in previous years than did closely planted trees'.

In the randomized block experiment possible confounding factors were not quite as subtle as in the Nelders. For example, the two wide-spaced treatments were different from the 2 m treatment because they had 1.5 m treeshelters, fertilization of the grass sward, sheep grazing during the period of establishment and pruning of every tree (at close spacing the best trees were selected for pruning). These factors are impossible to disentangle with the information available. The early effects of the treeshelters and fertilization were apparent in the height data for the first four growing seasons. Despite these concerns the value of the results from the randomized block experiment is that they support trends from the Nelder experiments at Neroche and Swadlincote. However, in isolation the results would have to be treated with some caution.

It is also important to establish how the sites met the requirements of ash. In general the early growth rate of ash at all three sites was good. However, early growth is not always a reliable indicator of the ability of a site to support the long-term growth of a particular species. Ecological site classification (ESC) provides a more objective framework for making such judgements and all three sites were rated as 'suitable' for ash. Subjective silvicultural judgement would support this for Swadlincote and Neroche but would rank North Wyke lower. The latter is an acid surface water gley which, if it was left for re-colonization, would probably support a W10 woodland (*Quercus robur-Pteridium aqilinum-Rubus fruticosus*) rather than a W8 (*Fraxinus excelsior-Acer campestre-Mercurialis*). Site factors may have been a factor in the relatively poor height growth of the 5 m and 10 m spacing treatments compared with the 2 m spacing. The effects of site variation were also apparent at Neroche where the 'fans' term was included in the model for growth assessments, while at Swadlincote it was not. This reflects the fact that site variation was low at Swadlincote and relatively high at Neroche, where trees in fans 1 and 2 had poorer growth than trees in fan 3. The most likely explanation for this was that fans 1 and 2 occupied a part of the site which was less well drained than fan 3. Hence at Neroche and North Wyke there was evidence for poorer growth of ash where drainage was impaired.

The results from this investigation have consistently shown that the early growth of ash is better at closer spacing in the range 1.0 m × 1.0 m to 5.0 m × 5.0 m. However, the results have not established this effect of spacing as a general principle in the silviculture of ash. This could only be achieved by studying the species' physiology

over a wide range of site conditions. The results must be judged against a background of a dearth of information on the subject of the effects of spacing on the growth of broadleaved trees in Europe. The fact that the results were consistent across two different experiment designs (Nelder fans and randomized block) at three different sites in lowland England adds weight to the argument that better growth at close spacing *may* be a silvicultural characteristic of ash. The growth parameters measured at all sites were height and stem diameter; in addition, stem dry weight, root dry weight and leaf area data from the Nelder at Neroche showed a similar negative relationship with increased spacing.

Only two references on the effects of spacing on the growth and development of *Fraxinus* spp. have been located in the literature. Firstly, data from an 8-year-old Latin square spacing trial of *Fraxinus uhdei* Lingl. in south-western USA showed that spacing did not affect height or diameter (Burgan, 1971). Despite the fact that it was a designed trial, the different species and growing conditions make it difficult to relate the findings of this latter study to conditions in Britain. The second example comes from the Nord-Picardie area of France where Goff and Levy (1984) investigated 50 stands of ash. They reported that dominant height at age 40 decreased as an index of spacing increased, and this seems to support the findings of the present study. The index of spacing used by Goff and Levy (1984) was the crown projection area divided by diameter at breast height, which would reflect past competition within the stand to a much greater extent than initial spacing. Unfortunately, it is not clear from their paper how the distribution of the 50 stands used relates to the relationships (*wrt* their Figure 6) and therefore they should be treated with caution. However, if the findings of Goff and Levy (1984) are accepted this would mean that ash dominant height can only be a good measure of site quality if the past competitive nature of the stand is quantified. This challenges the widely held view that dominant height of trees is relatively insensitive to spacing (Lanner, 1985). It is interesting to note that Claessens *et al.* (1999) did not take this into account in their site index curves for ash growing in Wallonia, Belgium. In summary, there are few, if any, other data in the literature to support the findings of this aspect of the work presented in this thesis.

Examples of studies of the effects of spacing in other species include that of Scott *et al.* (1998), who investigated a series of Douglas fir (*Pseuotsuga menziesii* (Mirb.) Franco) test plantations on similar sites with six initial planting densities from 300 to 2960 trees ha^{-1}. A size-density relationship was apparent after four years and after six years height and diameter at the widest spacing were 75% and 67% respectively of those at the closest spacing. Knowe and Hibbs (1996) examined the red alder Nelder

54

fans initially investigated by Giordano and Hibbs (1993). They produced a height projection function which showed a 'temporal ripple' in maximum height growth that progressed from the high to the lower planting densities over time, although it should be noted that the experiment was affected by browsing damage at the wider spacings.

In terms of the general principles of the relationship between plant growth and density these results are surprising. As described in section 2.1.1, the general relationship is that yield per plant is inversely proportional to total yield within a wide range of densities, i.e. at high densities the mean size will be low and at low densities the mean size will be high. In addition, within this range, the total yield per unit of area is independent of density (the law of constant final yield). However, these general principles are applicable to populations of plants which are competing for resources with each other. A possible explanation for the results of this study is that there was little, or no, competition between the trees at different spacings. The main evidence for this is that in the experiments at Neroche and North Wyke the height:diameter ratios were largely unaffected by spacing. On the two occasions when the height:diameter ratios were significantly different between spacings, for the first two assessments at North Wyke, this could be attributed to the presence of treeshelters on trees at the two wider spacings.

There is a considerable body of evidence to support the use of height:diameter ratios as measures of competition in stands of trees. For example, Hamilton and Christie (1974) present data for 16 year old trees from two randomized block spacing experiments in clonal poplar. Results are only reported after the onset of competition but in both experiments the height:diameter ratios decreased with increased spacing. For example in one experiment ratios decreased 126→98→85 (all cm mm^{-1}) as initial plant spacings changed 2.1×2.1→3.4×3.4→4.6×4.6 (all m). Cole and Newton (1987) showed for Douglas fir five years after planting that height:diameter ratios decreased from 125 to 60 (cm mm^{-1}) with increased spacing. Baldwin *et al.* (2000) showed for beach pine (*Pinus contorta* Dougl. var. *contorta*) aged 38 that height:diameter ratios decreased from 96 to 84 (cm mm^{-1}) as spacing increased from 1.8×1.8 m to 3.7×3.7 m.

The unexpected results must be accounted for. The basic building blocks of plant growth are water, light and nutrients, but the way plants use these resources is a complex of many interacting factors (Landsberg, 1986). To fully appreciate this complexity one has to consider the work of Whitehead *et al.* (1984), who investigated the water budgets of Scots pine trees in an unreplicated Forestry Commission spacing

trial, or the work of Giordano and Hibbs (1993) who attempted to separate the effects of competition for light and moisture in the growth of red alder in three Nelder *1a* spacing experiments. In both cases the experiments were subject to intense measurement but did not fully succeed in explaining the growth differences which occurred. The words of Harper (1977) are sobering in this respect 'there are possibly no examples of plant interactions in the field in which the mechanism has been clearly and unambiguously demonstrated'. To explain the differences observed in this study further work with different objectives and approaches is needed. However, reasons for the differences can be suggested to help develop hypotheses if such work was to take place.

In the work described in this thesis three pieces of evidence have been collected which allow some, albeit rather superficial, insight into how spacing has affected the patterns of plant growth in ash. These were: calculation of a TSI for each of the first three growing seasons, determination of the shoot:root ratio and estimation of the foliage area in the summers of the third and fourth growing season. The TSI analysis showed that in the first year trees at all spacings were recovering from transplant shock; however, in the second year trees at close spacing had recovered from transplant shock whereas those at wide spacing had not. In the third growing season trees at all spacings had recovered from transplant shock. Analysis of the shoot:root ratio suggested that as spacing increased trees partitioned a lower proportion of their dry matter to the root. The pattern of foliage area in the summers of 1997 and 1998 both showed that better growth at close spacing was supported by increased foliage area. It is difficult to fit together three such fragmented pieces of information; however, the TSI analysis indicated that the better growth at close spacing commenced in the second growing season, one year before spacing had a significant effect on either height or diameter growth. Many authorities have demonstrated that recovery from transplant check is mainly related to the ability of the plant to obtain water from the soil (Örlander, 1986; Haase and Rose, 1993; Rose *et al.*, 1993). Considering the importance of water in the growth of ash, discussed in detail in Chapter 1, this must be a possible factor in these spacing experiments and sits comfortably with the finding that trees at close spacing have a greater proportion of their biomass as roots.

It is clear from the above that inadequate information was collected for a detailed physiological explanation of the observed results. However, this does not prevent consideration of hypotheses, provided as 1–4 below, which could explain the better growth of trees at closer spacings.

1.   *Improved microclimate at close spacing*

Trees at close spacing shelter each other more than trees at wide spacing. The main effect of shelter is generally considered to be a reduction in wind velocity (Heiligmann and Schneider, 1975), but a reduction in wind velocity can be accompanied by changes in air temperature, solar radiation, relative humidity, soil moisture and soil temperature, in such a way that better conditions for plant growth are created (Evans, 1984; Hart, 1991; James, 1982; Kerr and Evans, 1993). Work on the effects of shelter on the growth of black walnut (*Juglans nigra* L.) in the USA has shown that barriers which reduce wind velocities by 67% significantly increased stem height and diameter, leaf area and shoot dry weight (Heiligman and Schneider, 1974 and 1975). This result has recently been repeated for ash in an experiment in Thetford for which results have not yet been published (Kerr, 2000).

2.   *Trees at close spacing will close crowns earlier, resulting in reduced interspecific competition for moisture and nutrients*

At close spacings the tree canopy will close more quickly and therefore weed suppression (and use of water by other vegetation) will be reduced (Willoughby and McDonald, 1999). In the Nelder experiments the areas were kept as weed free as possible, so this is unlikely to have had a major influence on tree growth. However, in the randomized block experiment, where trees at all three spacings had 1 m diameter spot weed control, this influence could have been more important.

3.   *Alterations in growth patterns*

The work of Aussenac and Levy (1983), described in section 1.3.1, has shown how quickly ash will stop growing in response to the onset of moisture stress. Other triggers, such as temperature of the stem, may also exist and could affect trees at wide spacing more than at close spacing. Changes may also be induced at close spacing which mean that ash begins to display neoformation, giving greater scope for the growing shoot to elongate. The fact that ash leaves are preformed and the buds are determinate was discussed in section 1.4.1. However, it was also noted that in other species of *Fraxinus* neoformation had been observed; shoots are not entirely preformed in the resting bud and a proportion of the leaves are formed during the growth season. If this occurs in ash and if it is triggered at close spacings this could produce increased shoot growth.

4.   *Early response to competition through alterations in the red–far-red light reflected from foliage*

Leaves of trees contain phytochromes which are photoreceptors and generally absorb red light and reflect far-red light. They can sense changes in the ratio of red to far-red light and any change in the ratio can indicate the presence of neighbouring plants. Using Nelder experiments, Aphalo *et al.* (1999) demonstrated increased height growth of downy birch (*Betula pubescens* Ehrh.) after one year at closer spacing, and suggested this might be associated with the decrease in the red:far-red ratio which also declined as spacing decreased.

2.4.2   Effects of spacing on height and diameter distributions

Height and diameter distributions for the Nelder experiments at Neroche were generally skewed to the right, with a small number of large individuals and a larger number of small ones. This was true in a statistical sense but observation of the distributions in Figures 2.10 and 2.11 do not reveal the strongly skewed populations envisaged in Harper's (1977) 'hierarchy of exploitation'. However, although some of the height and diameter distributions were not normal, and in some cases were bi-modal, there was no clear evidence of any tendency to change from a normal to a bi-modal distribution at any of the spacings. Only height distributions at equivalent spacings to 1.3 m and 4.8 m showed any degree of stability as non-normal distributions and in fact there were many cases where a non-normal distribution became normal in the following year. Hence the bi-modal distributions described by Ford and Newbold (1970) and Ford (1975) were not observed in this study. The lack of bi-modality is further evidence that competition between trees in the spacing studies was minimal or in its very early stages. The populations studied by Ford (1975) and Ford and Newbold (1970) were much older and relatively dense compared to the ash spacing experiments and intraspecific competition had been operating in them for many years.

2.4.3   Effects of spacing on tree form

The fact that the central stem:branch dry weight ratio showed no relationship with spacing suggests that spacing had little effect on tree form. The most likely explanation for this is that branch mortality had not yet commenced and this is further evidence that there was little, or no, competition between trees in the experiment at

Neroche. Spacing will probably only begin to affect tree form when competition begins to cause branch mortality, and this is expected to be earlier at close spacings.

2.4.4   Implications for silvicultural practice

Traditionally silviculturists have always been clear that where timber production is an important objective of management (Kerr and Evans, 1993), or where new woodlands are being created on bare land (Kerr, 1993), spacings of no more than 2.0 m × 2.0 m should be used for most broadleaved tree species.   After the formulation of the Forestry Commission's policy on broadleaved woodland in 1985 large areas of woodland were created or regenerated with spacings of 3.0 m × 3.0 m or wider (Kerr, 1993).   The difference between silvicultural recommendations and practice caused great debate on the effects of spacing on the growth and form of broadleaved trees, but this was carried on with little objective information.   An exception is the paper by Savill and Spillsbury (1991).   An excellent example of the dearth of objective information on the effects of spacing on growth and form is provided by Duncan (1985).   He espoused the planting of broadleaves, mainly sycamore and cherry, at 6 m × 6 m spacings based on his experience in northeast Scotland.   The main motivation for the system was that 'current systems of broadleaved silviculture will not yield a profit'.   It would be interesting to re-visit his woodlands now.

The logic of the silviculturist's argument is that close spacings provide a wider pool of stems from which to select final crop trees, and that the reduced time to canopy closure, compared with wide spacings, would lead to the early onset of branch mortality and, on bare land, the site being captured more quickly to woodland conditions.   The results of the work described here suggests that, for ash, an added benefit will be that trees will grow better and therefore pass through the vulnerable establishment phase more quickly.

A further implication of the finding that height growth of ash is poorer at wide spacing is that the current yield table for ash, which is anyway combined with sycamore and birch in Edwards and Christie (1980), will not be accurate for many recently planted woodlands because the yield table assumes an initial spacing of 1.5 m x 1.5 m.   The comparison of any individual stand of trees against a yield table, which represents average growth over a wide area, is an abuse (Rollinson, 1987).   However, the evidence from this study suggests that the patterns of growth and yield for the cohort of woodlands established at 3 m × 3 m spacings in the late 1980s and early 1990s will be very different from those predicted by the yield table published in Edwards and

Christie (1980). This particular concern, together with an interest in the use of ash in agroforestry, led to a study of free growing ash trees in southern England by Christie (1989).

Christie's study produced yield models for initial stocking densities of 50, 100 and 200 stems per hectare (sph) for three site qualities. For example at 50 sph ($\approx$ 14.1 m x 14.1 m) the models predict mean height to be between 20.4 m and 16.3 m at age 60, depending on site quality. Because there were so few sample plot data, the models were generated using stem analysis from 21 open grown trees sampled throughout southern England. The trees were growing in hedgerows or open fields when felled and an assumption was made that similar conditions had prevailed in the establishment phase. Hedgerow trees are notoriously difficult to age and may originate from a coppice shoot which already has an established root system; this would have a very different pattern of early height growth from a transplant. In addition, trees in open fields may have been part of a woodland in the past; even in the early 1970s grants were available to convert broadleaved woodlands to agriculture. The author admits that '.. it was difficult to tell if they had been isolated all their life. In a number of instances (only 2 would have been 10% of samples)... it was evident that there had been some degree of competition in the past'. Evidence from the study reported here suggests that this 'degree of competition' can have a significant effect on early height and stem diameter growth. Whether this is a short or long-term effect is not really known.

A study by Doyle et al. (1986) investigated the economic effects of intercropping widely spaced ash trees with grassland. The model of tree growth they used assumed a stem diameter increment at breast height of between 0.75 and 1.0 cm year^{-1}. The authors warn that 'given the large number of assumptions necessitated by the limited availability of data and in the absence of any means of validating the model, extreme care is needed in interpreting the results'. Such data have been produced in the randomized block experiment reported here. After 13 years trees in the 10 m spacing treatment had achieved a mean radial increment of only 0.45 cm year^{-1} and, perhaps more significantly, height growth had all but stopped. It is important to emphasize that the site at North Wyke has probably played a part in these results, being mainly an acid clay more suited to oak than ash. However, it does demonstrate the wide bands of confidence required when using models which are not calibrated with good, preferentially experimental data.

There are two other areas for which the results of this study have implications. The first is the deployment of improved genetic material from tree improvement programs, if and when this is available. Results from this study question any assumption that the material could be established at, or near, final crop spacing if rapid establishment of the trees and subsequent good growth are important. The second area is the possibility of using close spacing to reduce herbicide inputs during establishment. Willoughby (1999) reported the effects of a range of alternative ground cover and silvicultural regimes which aim to reduce herbicide input during establishment on fertile lowland ex-agricultural sites. The main conclusion was that close spaced trees (the experiments used ash and Douglas-fir) with a single herbicide application soon after planting was the most practical option. There is a suggestion in the data that height and diameter growth of ash was good at close spacing but the experiments were not established to test this hypothesis. The work described here adds credence to Willoughby's conclusions.

Chapter 3

Effects of other broadleaved tree species on growth and form

3.1 Introduction

Without human influence most of Europe would be covered by forests consisting of mixed species stands (Rackham, 1992). The influence of man has been, firstly, to clear large areas of woodland and convert it to agricultural land and then, secondly, reforestation with even-aged, single species plantations. More recently there has been reaction against single species plantations and a desire to encourage planting of more natural mixed forests (Rodwell and Patterson, 1994). Bartelink and Olsthoorn (1999) state four reasons for increasing the area of mixed forests: (i) they are more resistant to storms and less susceptible to attacks by insects and diseases; (ii) they spread financial risk; (iii) working with natural processes such as natural regeneration should bring cost savings, and (iv) people prefer mixed species stands for amenity and biodiversity. This change of emphasis is a challenge because silvicultural theory and practice has largely been concentrated on single species stands (Kelty, 1992).

3.1.1 Useful models for describing mixtures of species

The study of mixtures of plant species has received a lot of attention in the ecological and agronomic literature and some useful models have been developed which can be used to illustrate the relationships between two or more species when they grow together and their proportions and densities are varied. Some early experiments used an 'additive design' in which species 1 was sown at a standard density and species 2 was sown with it at a range of densities. Although these could be described as ecologically valid, in that they have relevance to many field situations, the main problem with the design was that the effects of proportion of the mixture and density were confounded (Harper, 1977). Many of these problems were eliminated in 'replacement designs' (de Wit, 1960) in which two species are sown together but the proportions are varied while maintaining a constant overall density. Other types of design have also been used (Cousens, 1996) and there has been much debate concerning the validity of some approaches for the study of competition between mixtures of species (DeBenedicts, 1977; Firbank and Watkinson, 1985; Connolly, 1986 and 1987; Law and Watkinson, 1987; Sackville Hamilton, 1994). This debate has generated some useful concepts for understanding the results of mixture experiments.

The use of replacement designs was championed by Harper (1977) as he judged them to be particularly elegant for the study of plant interactions involving two species. He developed a series of models which could be used to understand the results from mixture experiments but which also illustrate some general principles (Figure 3.1). In Model 1 the growth of the two species in mixture results in each contributing to total yield in direct ratio to its original proportion. This type of result can be obtained when the density of both populations is so low that there is little, or no, competition, or when the results of competition between the two species are balanced. In either case the yield of the mixture is predictable from the yield of pure stands. In Model 2 the two species make demands on the same resources but do so differentially. As with Model 1 the yield of the mixture is predictable from the yield of the pure stands. In Model 3 neither species contributes its expected share to the yield of the mixture, which is not predictable from the yield of pure stands; an example could be where there was allelopathy. In Model 4 the two species escape some measure of competition with each other and possess 'ecological combining ability' (Harper, 1977). The mechanisms for this are many and complex and have been usefully reviewed by Man and Lieffers (1999).

**Figure 3.1 Models to describe the results
of mixture experiments**
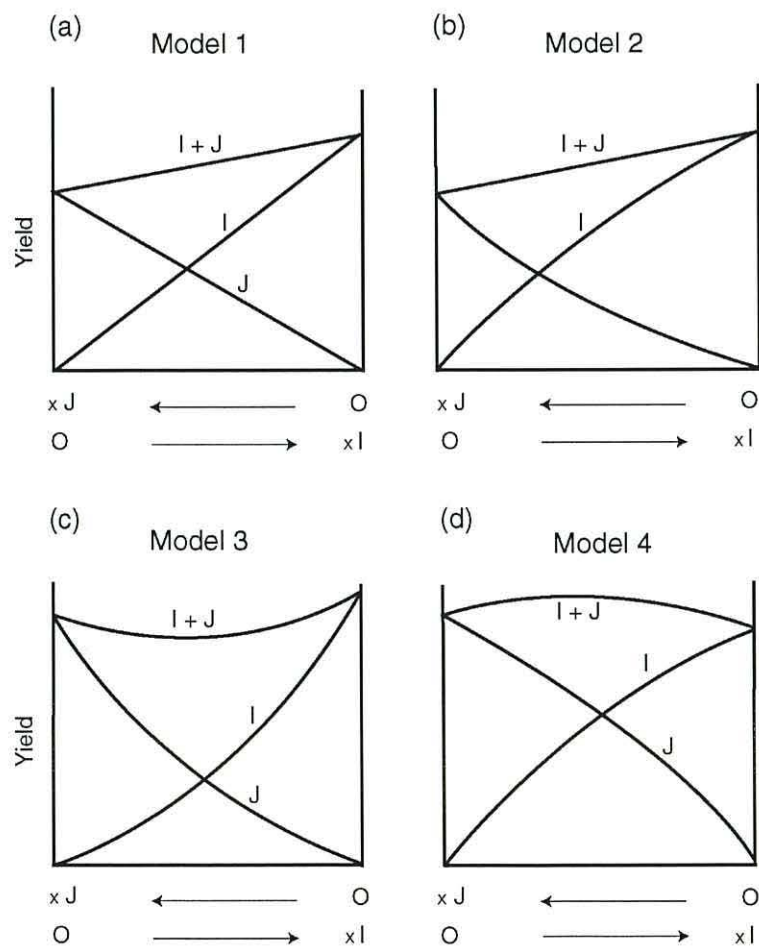
3.1.2 Mixture experiments in forest research

Both Zutter *et al.* (1997) and Man and Lieffers (1999) comment that until recently controlled experiments examining the interaction of two species have been limited. However, those that exist can be classified into one of two categories. Firstly there are experiments which attempt to quantify the effect of the species in mixture with each other. Examples include Bhatnagar *et al.* (1993) who examined the interaction between a non-native species (*Leucaena leucocephala* (Lam.) de Wit) and a native species (*Acacia nilotica* L.) in northern India and von Althen (1988) who investigated the effects of planting arrangement on pure stands and mixtures of sixteen broadleaved species in Canada. Secondly, there are the more detailed studies which aim to investigate the nature of the mechanism of interaction between the species. Examples of this type of investigation include Shainsky and Radosevich (1992) who investigated competition between Douglas fir and red alder and Perry *et al.* (1994) who investigated mixtures of loblolly pine (*Pinus taeda* L.), sweet gum and broomsedge (*Andropogon virginicus* L.). In contrast to the ecological literature, there has been little debate concerning the validity of particular designs; instead each investigator has achieved the aims of the experiment by using an appropriate design and method of analysis (Cousens, 1996; Kelty and Cameron, 1995).

In Britain, the silviculture and yield of mixed species stands has been summarized by Kerr *et al.* (1992). They distinguish between mixtures growing on lowland (< 250 m asl) sites where interactions between species have not been demonstrated, and upland conditions where clear species interactions have been shown. In particular, mixtures of Sitka spruce with pines (*Pinus* spp.) or larches (*Larix* spp.) on oligotrophic soils have been studied by Morgan *et al.* (1992); the main cause of the interaction between species concerns nitrogen availability. The Gisburn experiment in North Yorkshire also included these spruce/pine or larch mixtures but in addition produced data on the growth of two broadleaved species, common alder (*Alnus glutinosa* (L.) Gaertn.) and oak, in mixture with Scots pine and Norway spruce (Brown, 1992). Using the concept of *relative yield total* (RYT) of de Wit and Van den Bergh (1965), Brown (1992) showed that the broadleaves in mixture with Scots pine were more productive than when pure; however, this was not the case when the same species was in mixture with Norway spruce.

Relative yield is a convenient measure of the yield of each species in mixture expressed as a proportion of its yield in monoculture. The mean of these two relative yields is relative yield total and can be calculated using the formula:

$$RYT = 0.5 \ x \left[\frac{\text{yield sp. A in mixture with sp. B}}{\text{yield sp. A pure}} + \frac{\text{yield sp. B in mixture with sp. A}}{\text{yield sp. B pure}} \right]$$

[3.1]

on an equal area basis.

In cases where only competition for resources occurs, the RYT is theoretically unity, even though the mixture yield may exceed the mean yield of the component species. Where resource utilization appears more efficient in the mixture, e.g. where both components are more productive in mixtures than when pure, or where the mixture as a whole outyields the more productive component in monoculture, then RYT > 1.0. With overall growth reduction, and RYT < 1.0, some constraint on the availability of resources may be occurring. This approach has also been used by Malcolm and Mason (1999) to show the growth benefit of planting Scots pine in mixture with silver birch at two upland sites. However, the RYT values range from 0.91 to 1.16 and should be treated with some caution because the authors do not explain their method of estimating standing volume and it is difficult to reconstruct the calculations of RYT from the data presented in their Table 3.3.3.

A novel approach to the study of the influence of neighbours on the growth of silver birch trees has been described by Jones and Harper (1987a; 1987b) which was based on earlier work by Mailette (1982a; 1982b) and Jones (1985). They described the demography of buds and branches on replicates of three birch trees planted 20 cm apart on the corners of an equilateral triangle. Branches were divided into three groups: those entering into the canopy of another tree, those not entering into the canopy of another tree, and an intermediate category. After three years, branches in the canopy of other trees had fewer buds being 'born', a greater proportion that were dying and generally smaller mean branch size than the other two categories of branch. The study produced clear evidence that the behaviour and fate of a bud were affected more by its local environment than by its position on the tree.

The work of Jones and Harper (1987a; 1987b) has important implications for the study of the effects of mixtures on the growth and form of ash. Firstly, by describing the production and development of buds and branches of a tree as a demographic process they suggested a new approach to the assessment of the form of a tree. Secondly, they demonstrated the mechanism by which intraspecific competition in birch trees alters form.

Evans (1984) describes two methods by which a faster growing tree, conifer or broadleaved, can 'nurse' or 'help to grow' a slower growing broadleaved species: (i) by

protecting the broadleaved species from unseasonal frosts, particularly in late spring; and (ii) by providing side shelter, essential to the growing of quality broadleaves, by aiding upward tree growth and better tree form. As mentioned previously Kerr *et al.* (1992) found little evidence for these effects in unreplicated trials in lowland areas, while upland studies mainly focused on growth rather than tree form; a point emphasized by Mason and Baldwin (1995) who discuss tree form of English oak (*Quercus robur* L.) in mixture with European larch and Norway spruce in southern Scotland, but did not measure it.

The objective of the work described here is to examine the effect of mixture design on the growth and form of ash trees planted in mixture with oak, beech and cherry.

3.2. Materials and methods

3.2.1 Site description

Three experiments of ash in mixture with oak, beech and cherry were established on the Perridge Estate, Devon. The site is an ex-pasture area 6.5 km southwest of Exeter (50° 41' N, 3° 36' W). The topography of the area is one of small hills up to 200 m asl with sloping valley sides. The experiment is at 130 m asl on a slope (10°) with a southwest aspect, the only direction from which it is not sheltered by the surrounding land.

The soil is a brown earth classified by Avery (1980) as a typical brown earth which overlies Millstone grit and Culm measures from the Carboniferous period. In terms of Ecological Site Classification for tree growth the site lies within the warm moist zone described by Pyatt *et al.* (2001). Soil samples taken in spring 1998 showed: pH 5.8; P 16 mg kg^{-1}, K 168 mg kg^{-1}, Mg 83 mg kg^{-1}. These were a good level, and balance, of nutrients for ash according to Taylor (1991) and so no foliar samples were taken.

3.2.2 Experiment design and details of establishment

The design used for each of the experiments was a balanced two-component competition experiment using a hexagonal lattice described by Boffey and Veevers (1977) and Veveers and Boffey (1979). The experiment design has a honeycomb of overlapping hexagons, such that within any one row each species is surrounded by zero to six individuals of the same species and conversely by six to zero individuals of the second species as shown in Figure 3.2. In each experiment there are 84 assessment trees, which are numbered, and guard trees, which are not numbered, and are arranged to balance the

experiment. The 84 assessment trees comprise two species for which there are six replicates of seven 'mixture' treatments [2×6×7 = 84]. An example is given in Table 3.1 which describes the treatments where species A = ash and species B = cherry and, importantly, explains the notation for the seven treatments levels from A_6B_0 to A_0B_6. A great strength of the design is that each row (horizontal points in Figure 3.2) has a replicate of each treatment for each species, i.e. 14 trees, which allows it to be used as a blocking factor in the analysis.

Figure 3.2 Experiment design for mixture experiments
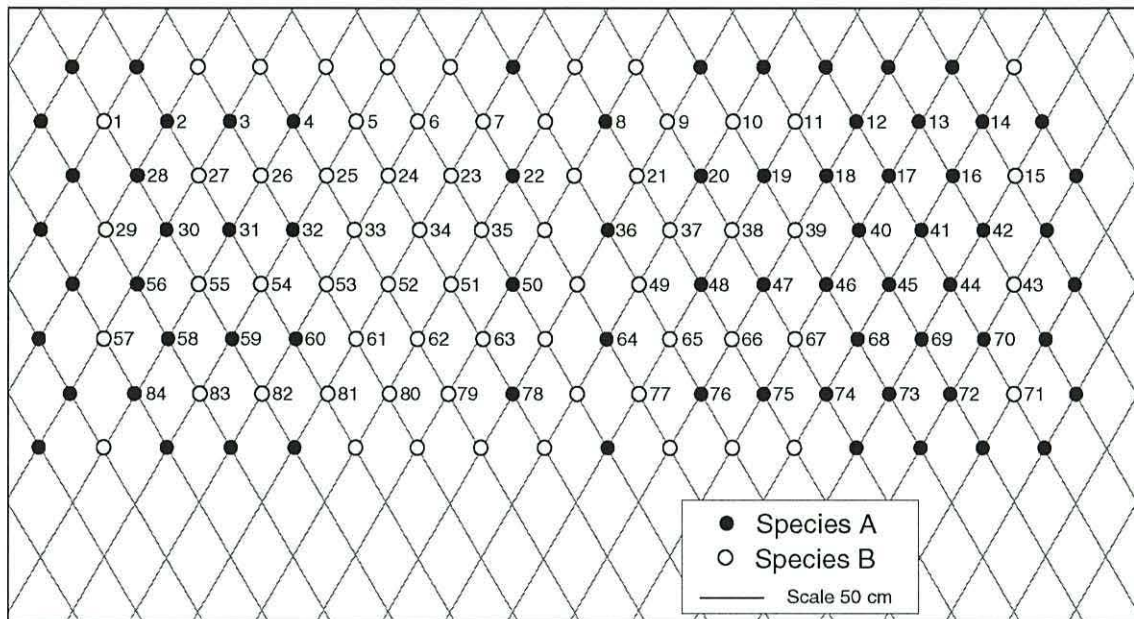
Table 3.1 Description of experimental design using the ash(A):cherry(B) experiment as an example

Treatment code[1]	Treatment description: tree surrounded by:	% balance	Tree numbers in Figure 3.2											
			Ash						Cherry					
$A_6:B_0$	six ash trees	100A	13	17	41	45	69	73	1	15	29	43	57	71
$A_5:B_1$	five ash trees and one cherry	83A-17B	12	16	40	44	68	72	11	27	39	55	67	83
$A_4:B_2$	four ash trees and two cherry	67A-33B	14	18	42	46	70	74	10	26	38	53	66	82
$A_3:B_3$	three ash trees and three cherry	50A-50B	2	28	30	56	58	84	9	21	37	49	65	77
$A_2:B_4$	two ash trees and four cherry	33A-67B	3	19	31	47	59	75	7	25	35	54	63	81
$A_1:B_5$	one ash tree and five cherry	17A-83B	4	20	32	48	60	76	5	23	33	51	61	79
$A_0:B_6$	six cherry trees	100B	8	22	36	50	64	78	6	24	34	52	62	80

[1] Ratios given as numbers of trees (N) of species A_N: species B_N.

Close observation of Figure 3.2 and Table 3.1 reveals that there are generally more of a particular species at one side of the experiment and some treatments are not well distributed, for example all ash trees in treatment A_3B_3 are on the left hand side. To remove any confounding due to site variation two experiments were established side-by-side with species positions reversed; for example in Figure 3.2 tree number 1 is cherry, in the second experiment it was ash. For analysis, data from the two experiments were combined and this increased to 12 the number of replicates of each mixture treatment. Trees were planted at 50 cm spacings in the lines with 50 cm between lines; the effective spacing between trees in different lines was 56 cm due to the hexagonal layout.

Three experiments were planted: ash in mixture with each of cherry, beech and oak. The experiments were planted on 22 January 1996 inside a deer and rabbit proof fence. Planting stock was good quality 1+1s of the sizes shown in Table 3.2. Complete weed control to 50 cm beyond each of the guard trees was practised for the duration of the experiment. This was initially achieved using glyphosate (2 l ha^{-1}) and propyzamide (Kerb flowable at 3.75 l ha^{-1}). Subsequent control in the summer was by glufosinate ammonium (3 l ha^{-1}). The latter is not translocated and therefore safer than glyphosate (Willoughby and Dewar, 1995). In winter, propyzamide was used as described above.

Table 3.2 Initial sizes of trees in the mixture experiments

	Ash : oak		Ash : beech		Ash : cherry	
	Ash	Oak	Ash	Beech	Ash	Cherry
Mean height (cm)	33.4	37.3	32.7	24.6	35.0	36.1
Mean stem diameter (mm)	4.8	5.6	5.7	2.8	5.7	5.6

3.2.3 Growth assessments

After planting the height (nearest 1 cm) and stem diameter (nearest mm at a marked point 5 cm above ground level) of each tree were measured; the initial stem diameter assessment did not take place until early June 1996. Subsequent assessments of height and stem diameter occurred in September 1996, January 1998, March 1999 and February 2000. At the end of each growing season a height:stem diameter ratio was calculated for each tree by dividing height (cm) by stem diameter (mm).

In April 2000 the volume of the central axis of ash trees in four mixture treatments (A_6:B_0, A_4:B_2, A_2:B_4, A_0:B_6) was assessed in each of the three experiments. For each tree the central axis was defined as the stem between the apical bud of the leader, defined as the tallest branch, and the base of the tree. The mid-diameter of 20 cm sections from the

apical bud was measured to the nearest 0.1 mm with a vernier calliper. Where there was a branch or stem deformation, the stem diameter was measured 5 cm below and above this point and a mean calculated. At the bottom of the tree the maximum section length was 30 cm, e.g. if it was 32 cm it was split into two sections of 16 cm. The volume of each tree was estimated using the formula in equation 3.2:

$$\sum_{i=1}^{n} V = \frac{L \times D^2}{4}$$ [3.2]

where: V = volume of section (cm^3); L = length of section (cm); D = mid-diameter of section (cm) and n = number of sections.

3.2.4 Bud assessments

The bud classification used by Gill (1971) for white ash was adapted by observation for ash. This produced the classification for first order buds (i.e. those obviously not enclosed within another bud) shown in Table 3.3.

Table 3.3 Bud classification for ash

Description	Bud classification
Buds apical, not subtended by a leaf scar	Terminal
Buds axillary, subtended by a scar of a foliage leaf:	Axillary
(a) largest bud in axil	(a) Major
(b) smaller bud in axil	(b) Minor
Buds axillary, subtended by a scar of a scale	Scale

For each bud assessment only ash trees in the four mixture treatments (A_6:B_0, A_4:B_2, A_2:B_4 and A_0:B_6) were assessed, i.e. 48 trees. At each assessment the leader was defined as the tallest branch; in most cases this originated from the terminal bud of the previous year's increment. The annual leader growth increments since the time of planting were then determined; the planted tree was two years old but was treated as a single section. On each growth increment (section) the numbers of terminal, major axillary and scale buds were counted and the numbers of live branches were also counted and classified according to bud origin. Observations had also shown that axillary buds on the winter shoot can sometimes be raised off the main stem, and these were noted separately from other buds. In addition, if the tree had forked in the previous growth season this was recorded and the fork marked with a thin ring of paint; this was done to ensure that successive assessments were done on the same section. The first assessment was in December 1996, when two sections were assessed (the planted tree, section 1, and the

1996 increment, section 2), and then subsequently in November 1997 (sections 1,2 and 3), March 1999 (sections 1,2,3 and 4) and March 2000 (sections 1,2,3,4 and 5).

3.2.5   Data analysis

3.2.5.1   Analysis of growth data

After each assessment the data were checked and the distribution of residuals was examined to ensure it was random. Height, stem diameter and height:stem diameter ratios for each of the two species in each mixture were analysed separately using analysis of variance and sums of squares were partitioned as shown in Table 3.4 (column 2). The volume of the central stem of the ash trees was also analysed using analysis of variance, and sums of squares were partitioned as shown in Table 3.4 (column 3).

Table 3.4 Analysis of growth assessments: partitioning of sum of squares

Source of variation	Degrees of freedom: height and diameter	Degrees of freedom: volume
Blocks	11	11
Linear[1]	1	1
Quadratic	1	1
Higher order than x^2	4	1
Residual	66	33
Total	**83**	**47**

[1] The degrees of freedom available for testing the mixture design were partitioned to test the nature of the relationship, i.e. linear, quadratic or a higher order.

Relative yield total was calculated for the three mixtures (using equation 3.1) for each of the assessments between January 1996 and March 2000. Yield was estimated using the formula in equation 3.3:

$$Y = H \; x \; D^2 \qquad\qquad [3.3]$$

where: Y = estimated yield (cm^3), H = mean height (cm), D = mean stem diameter (cm).

Data for the pure species were provided by individuals surrounded by six trees of the same species (treatment A_6:B_0), and data for the species in mixture were provided by individuals surrounded by six of the other species (i.e. treatment A_0:B_6).

Data on the number of forks in each of the years 1996, 1997, 1998 and 1999 were analysed using a general linear model with a binomial error distribution and a logit link

function (see Appendix 3.1 and Crawley, 1993). The response variable was the proportion of trees forked and the explanatory variables were mixture (as a variate) and blocks, fitted in that order in Genstat (Anon., 1993). This has the effect of changing the question from 'are there significant differences between the means?', which would apply if the mixture term was fitted as a factor, to 'is there a significant relationship between the fitted terms and the proportion of the trees forked?'. The dispersion parameter was set to one for the analysis because the binomial total for each observation was one, and hence Genstat cannot estimate the value. To test for significance of the mixture effect the deviance ratio in the accumulated analysis of deviance table was compared with an approximate value from the χ^2 distribution in Genstat (Anon., 1993).

3.2.5.2   Analysis of bud and branch data

Box 3.1 Note on nomenclature
The following nomenclature has been used:
xxyyzq
where: *xx* is either br (branches) or bu (buds); *yy* is the year of assessment; *z* is the classification of buds, i.e. terminal (t), axillary (a) or scale (s); *q* is the section number (1,2,3,4 or 5; the lowest section on each tree is number 1). Where the *z* element is missing, the code refers to the total number of buds or branches on a section.

For example the variate bu97a3 refers to the numbers of axillary buds in 1997 on section 3; or br98t2 is the number of branches originating from a terminal bud on section 2, assessed in 1998 and buyyq is the total number of buds assessed in year *yy* on section *q*.

Analysis of this data was carried out in a number of stages.

Stage 1   Initial investigation involved calculating and tabulating, for each of the four mixture treatments, the total and mean number of buds and branches for each section of the tree according to the nomenclature in Box 3.1.

Stage 2 The results of stage 1 were inspected to determine where there were any obvious trends in the data. Where trends were apparent or there were large differences between means for different mixtures these were analysed using a general linear model with a Poisson error distribution and log link function (Crawley, 1993). The response variable was the number of buds/branches and the explanatory variables were mixture (as a variate) and blocks, fitted in that order in Genstat (Anon., 1993). To test for significance of

the mixture effect the deviance ratio in the accumulated analysis of deviance table was compared with the approximate value from the *F* distribution in Genstat (Anon., 1993).

Stage 3 This attempted to examine the changes in the numbers of buds and branches between years which could affect the form of the tree. Specifically this involved: (a) the mortality of buds and (b) an assumed conversion from buds to branches, both between two successive years. This was done by considering the change as a proportion. For the mortality of buds the proportion was:

$$M_q = \frac{bu\,(yy-1)\,q - buyyq}{bu\,(yy-1)\,q}$$
[3.4]

where:

M_q = proportion of buds lost between two successive years on section *q*

buyyq = the total number of buds assessed in year *yy* on section *q*

bu (yy–1) q = the total number of buds assessed in the year before *yy* on section *q*

For the conversion from buds to branches the proportion was:

$$T_q = \frac{bryyq - br\,(yy-1)\,q}{bu\,(yy-1)\,q}$$
[3.5]

where:

T_q = proportion of buds converted to branches on section *q*

bryyq = the total number of branches in year *yy* on section *q*

br (yy–1) q = the total number of branches in the year before *yy* on section *q*

bu (yy–1) q = the total number of buds in the year before *yy* on section *q*

Initial analysis of T_q revealed a weakness in the data recorded in the field. Dead branches were not recorded and therefore it was possible that there were cases where the difference in branch count between years underestimated the proportion of buds converted into branches. In some instances there were more branch deaths than buds converted and therefore negative values of T_q were obtained. For this reason no results of analysis of T_q have been presented.

If there was a detectable pattern in M_q the data were analysed using a general linear model with a binomial error distribution and a logit link function (Crawley, 1993). The response variable was the proportion of buds lost for *all* trees assessed and the explanatory variable was the mixture (as a variate). To test for significance of the mixture

effect the deviance ratio in the accumulated analysis of deviance table was compared with the approximate value from the *F* distribution in Genstat (Anon., 1993).

In the above analysis the data were combined over all trees and the model does not take into account the fact that buds were located on different trees. A further analysis was carried out in which individual tree data were used and which allowed for the fact that there were four levels of mixture design. This was done by entering the actual values of the mixture (0,2,4,6) as a covariate. The final model was thus a generalized linear mixed model (GLMM) with a random component (rows and mixture) and fixed effect of the variate - mixture. The inclusion of mixture in the random component was to allow for the fact that observations were only made at four distinct levels. Significance was determined by comparing the Wald statistic with the *F* distribution using (1, 1.9) degrees of freedom, where 1 is the number of *df* associated with the Wald statistic and 1.9 is the effective *df* applied to the variances for the mixture. For the effect of mixture to be significant at $P \le 0.05$ the Wald statistic had to be greater than 18.5.

3.3   Results

3.3.1   Growth

Detailed results can be found in Appendix 3.2.

3.3.1.1   Ash and cherry

Survival was excellent with 100% of all trees planted in spring 1996 present in February 2000. The mean height of the cherry at the end of the fourth growing season was 281.8 cm and the ash at the same time was 253.7 cm tall, reflecting the fact that both species had similar height growth trajectories and maintained a presence in the upper canopy (Figure 3.3, page 76). Cherry was consistently taller than ash: after the first growing season the cherry was 80% taller than the ash, but in the subsequent three growing seasons the relative differences in height became progressively smaller (40%, 14% and 11% respectively).

The effect of the mixture on height was significant for two assessments, both for cherry, in September 1996 and January 1998 (Figure 3.3). At the former date the relationship was quadratic with a minimum between A_2B_4 and A_3B_3. One year later in January 1998 the relationship was linear with a direct relationship between the height of cherry and the

numbers of surrounding ash trees, i.e. cherry was taller when surrounded by a higher proportion of ash (Figure 3.4). However, in subsequent assessments in March 1999 and February 2000 the mixture had no effect on the height of cherry. Throughout the four growing seasons the mixture had no significant effect on the height of the ash.

In contrast to the height data, stem diameter development was very different between the two species (Figure 3.5, page 77). At the end of the fourth growing season in February 2000 the mean stem diameter of the ash was 22.3 mm compared with 38.9 mm for the cherry. Also in contrast to the height data, there were many more dates when the effect of the mixture was significant.

In both species, there was a significant effect of mixture on stem diameter at the first assessment in June 1996; in ash the relationship was linear, with larger diameter trees associated with more cherry in the mixture (Figure 3.6). In the subsequent two growing seasons there were no significant relationships for ash. However, in March 1999 and February 2000, it became clear that the largest ash trees were found where there were few or no cherry trees (Figure 3.7, page 78); interestingly this was the reverse of the initial effect in June 1996.

For cherry, the mixture effect was significant at all five assessment dates, and a consistent pattern emerged of a direct relationship between the diameter of the cherry and the number of surrounding ash trees, i.e. larger diameter cherry trees were surrounded by a higher proportion of ash. Initially, in June 1996, there was a significant effect but it was of a higher order than quadratic and therefore showed no clear pattern. In September 1996, the relationship was quadratic and then in the three subsequent assessments from January 1998 (Figure 3.8) to February 2000 the relationship was linear.

These changes in height and diameter were reflected in the results of the analysis of the height:diameter ratio of ash (Table 3.5, page 81) and cherry (Table 3.6, page 82). If it is accepted that significant changes in the shape of a tree are indicative of competition then this started in the 1998 growing season, i.e. this was when significant changes to the shape of both ash and cherry trees occurred. In addition, higher height:stem diameter ratios of ash were associated with higher proportions of cherry in the surrounding mixture and *vice versa*.

Results of the analysis of the central stem volume of ash showed that there were no significant differences between mixtures in April 2000 (Figure 3.9). The RYT consistently increased from 1.25 in January 1996 to 1.78 in March 2000 (Table 3.7, page 83).

Significant differences between mixtures in the number of forks were apparent for the March 1999 and March 2000 assessments (Table 3.8, page 85 and Appendix 3.3). However, the results are contradictory, with more forks in March 1999 associated with high proportions of ash in the mixture while in March 2000 the reverse was true.

3.3.1.2   Ash and oak

Survival in this experiment was good with 100% survival in the first two growing seasons of trees planted in spring 1996. Mortality commenced in the third growing season (1998) during which seven oak trees died (4.2% of assessed trees of both species) and after the subsequent growing season a further two oak trees died (5.4%).

The mean height of the oak at the end of the fourth growing season was 117.8 cm and the ash at the same time was 238.9 cm tall, reflecting the fact that the species had different height growth trajectories and that the mixture developed a two-tier canopy structure (Figure 3.10, page 79). Generally the form of the oak was poor with a minority of trees having a strong central axis. At the end of the first growing season in September 1996 the oak was 1.02 cm taller than the ash; however, at the end of the subsequent growing seasons ash was taller than the oak and the relative difference between them increased from 41% in January 1998, to 78% in March 1999, and then 102% in February 2000. There was only one significant effect of the mixture on the height growth of ash and none on oak. In September 1996 the relationship was quadratic with a maximum at A_3B_3 (Figure 3.11, page 80).

The pattern of development of stem diameter for the two species was similar to that for height (Figure 3.12). Mean stem diameter of the oak at the end of the fourth growing season was 17.8 mm and for the ash at the same time was 29.7 mm, reflecting the species' different growth trajectories. However, in contrast to height a clear relationship developed between the stem diameter of ash and the balance of species in the mixture. In January 1998 there was a significant mixture effect but it was of a higher order than quadratic and therefore showed no clear pattern. However, after subsequent growing seasons, in March 1999 and February 2000 (Figure 3.13, page 84), there was a linear relationship between ash stem diameter and the number of oak trees in the mixture, i.e. larger diameter ash were associated with more oak trees in the surrounding positions.

Figure 3.3 Height development of ash and cherry in mixture

↓ indicates where the mixture had a significant effect
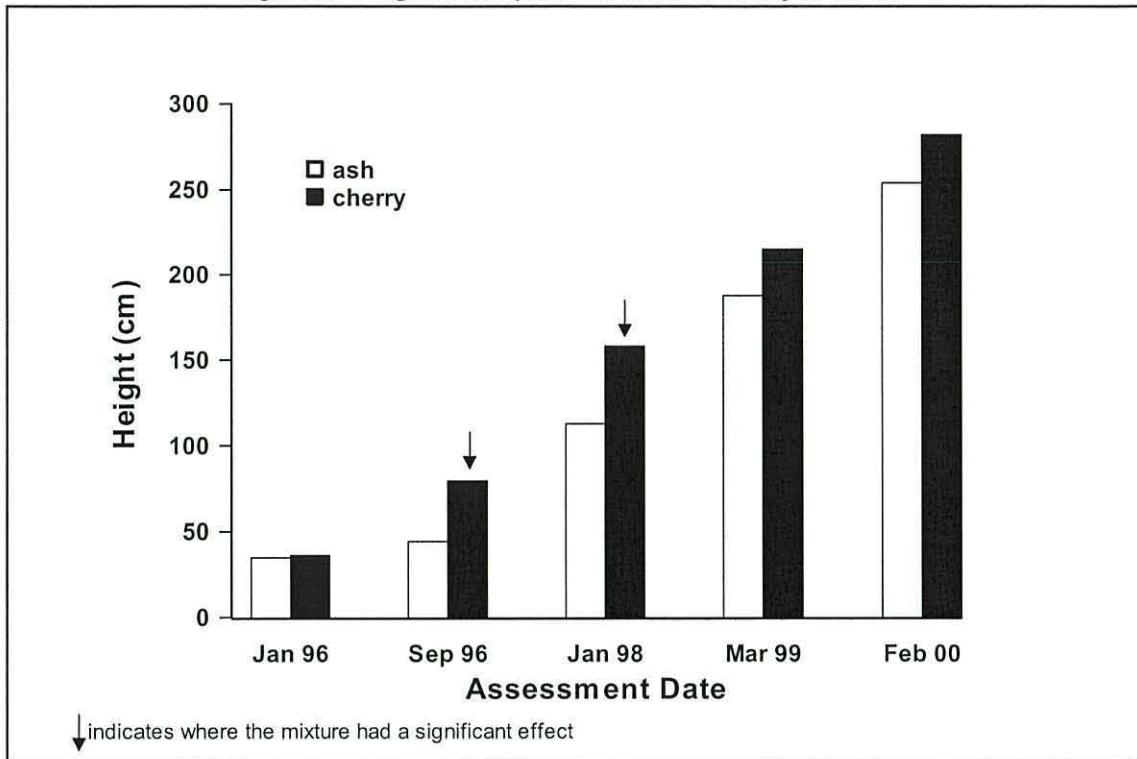
Figure 3.4 Height of cherry in mixture with ash in January 1998
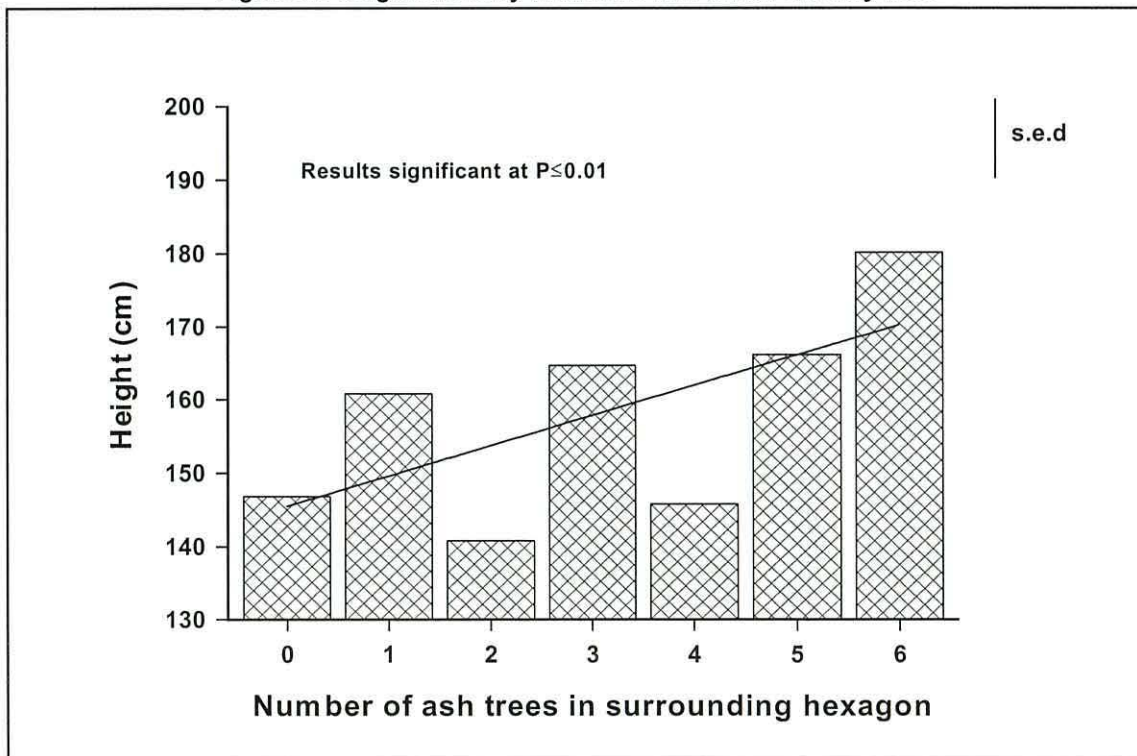
Figure 3.5 Stem diameter development of ash and cherry in mixture

↓indicates where mixture had a significant effect
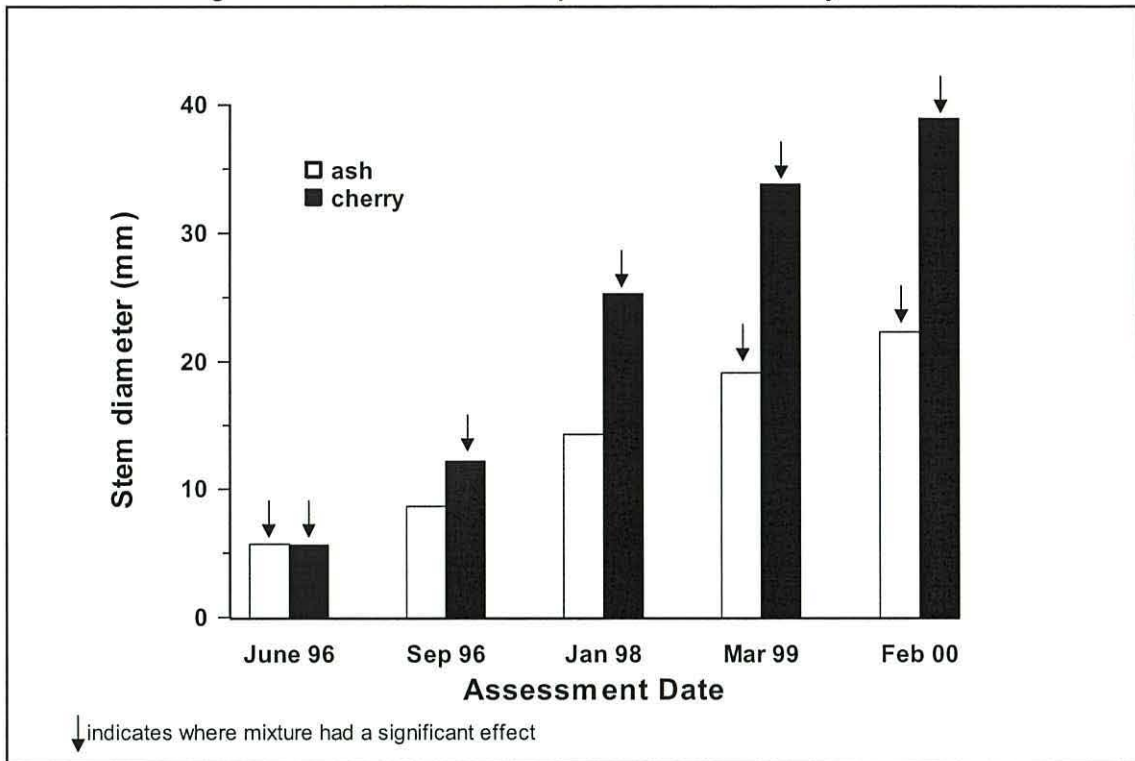
Figure 3.6 Stem diameter of ash in mixture with cherry in June 1996
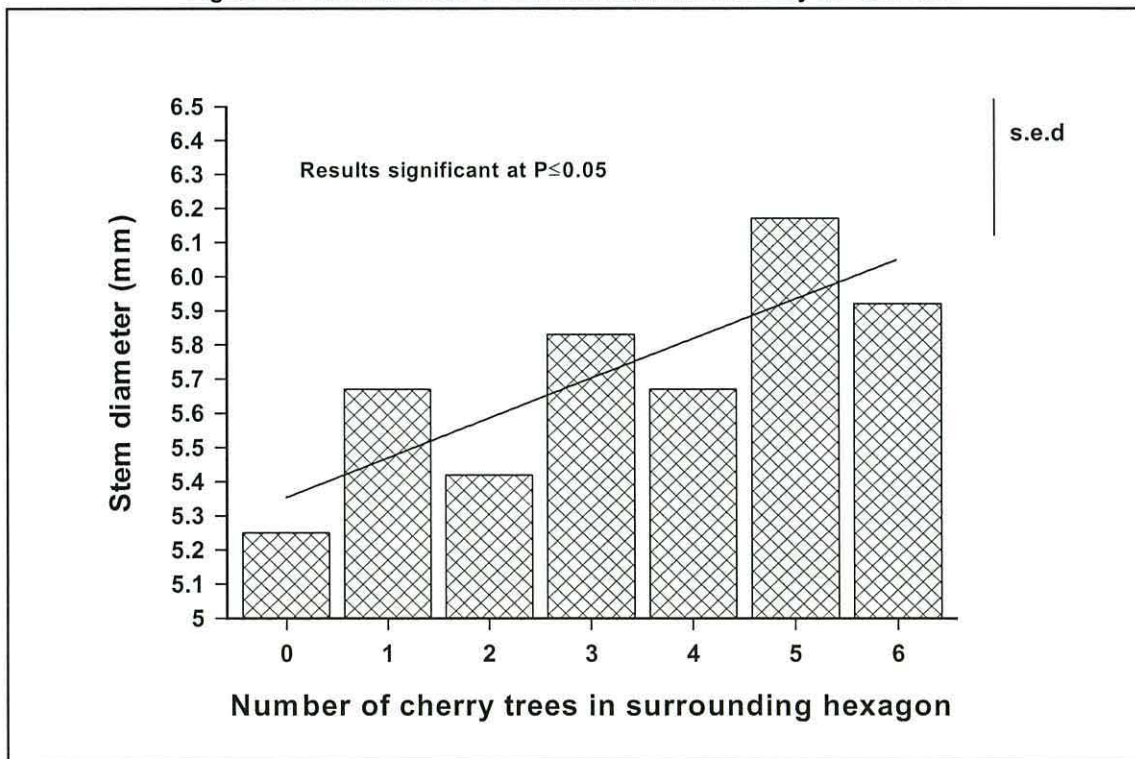
Figure 3.7 Stem diameter of ash in mixture with cherry in February 2000
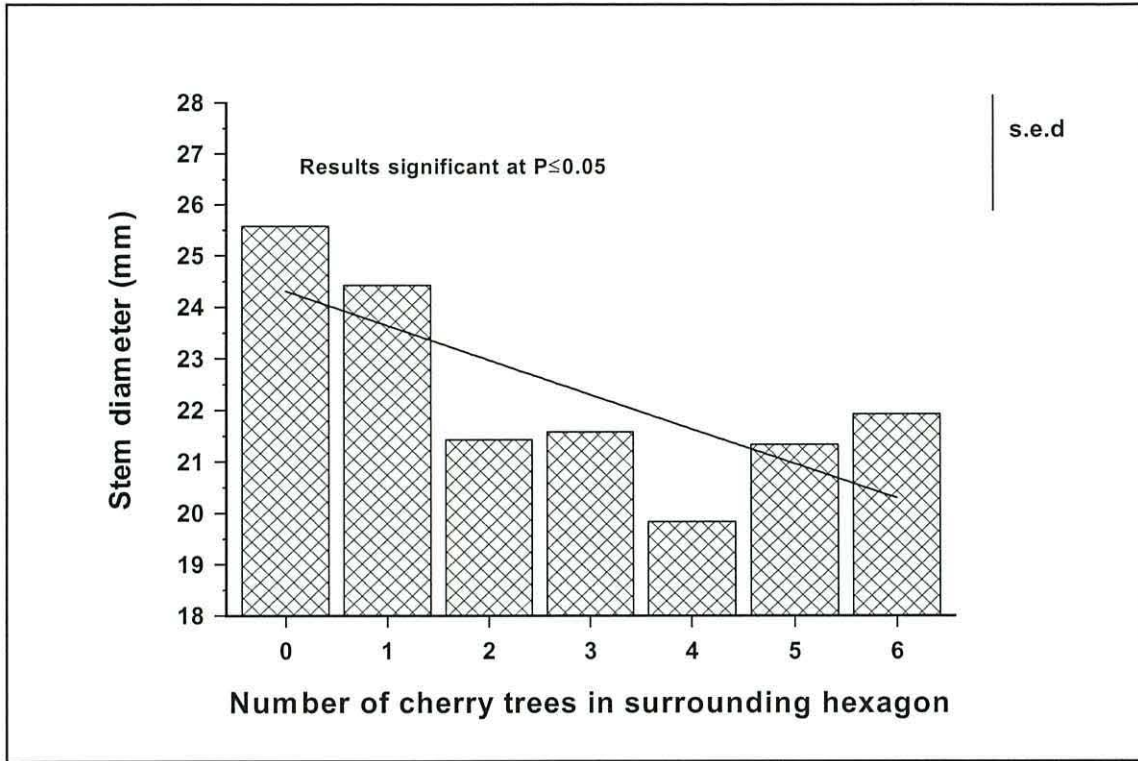
Figure 3.8 Stem diameter of cherry in mixture with ash in January 1998
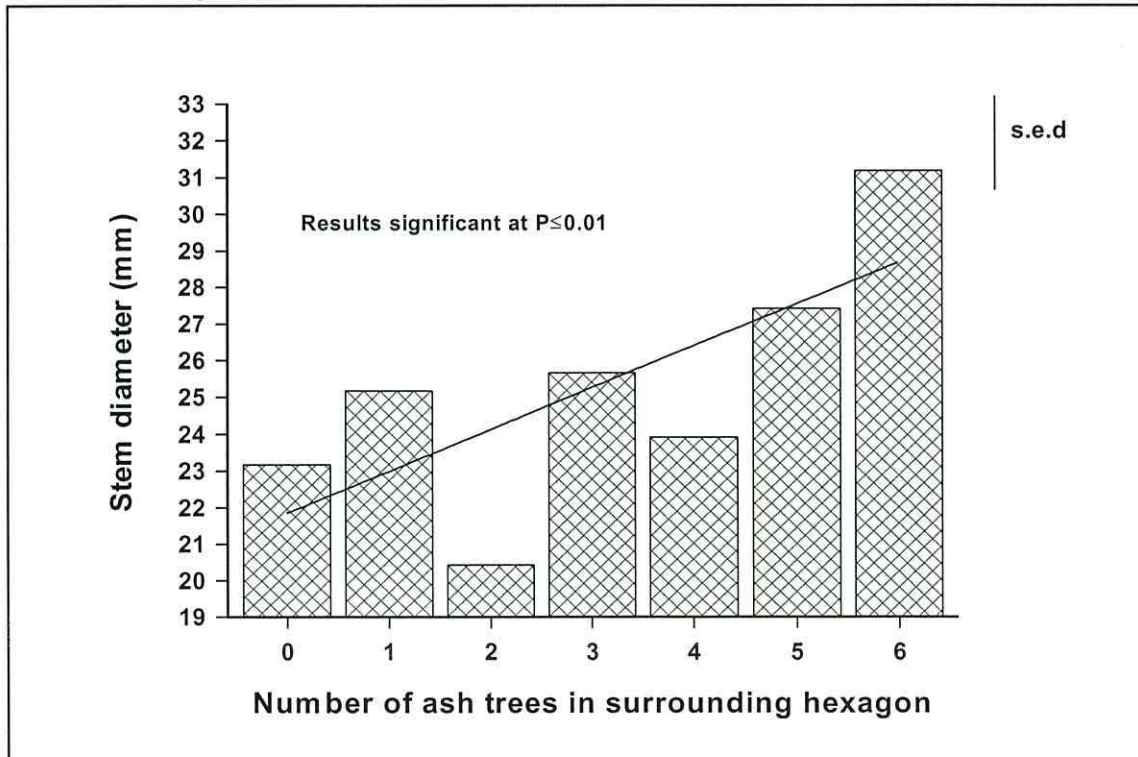
Figure 3.9 Volume of central stem of ash in mixture with cherry in April 2000

Differences not significant

s.e.d

Volume (cm³) — vertical axis: 0, 50, 100, 150, 200, 250, 300, 350, 400

Number of cherry trees in surrounding hexagon — horizontal axis: 0, 2, 4, 6
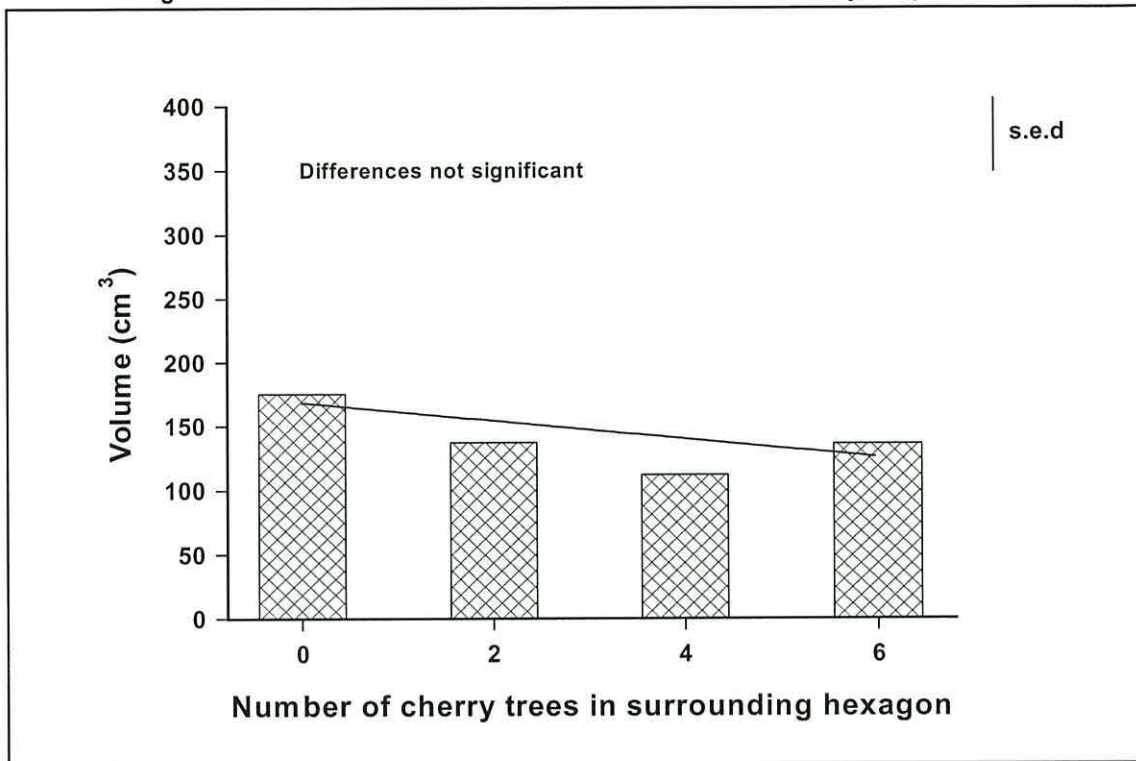
Figure 3.10 Height development of ash and oak in mixture

☐ ash
■ oak

Height (cm) — vertical axis: 0, 50, 100, 150, 200, 250, 300

Assessment Date — horizontal axis: Jan 96, Sep 96, Jan 98, Mar 99, Feb 00

↓ indicates where mixture had a significant effect
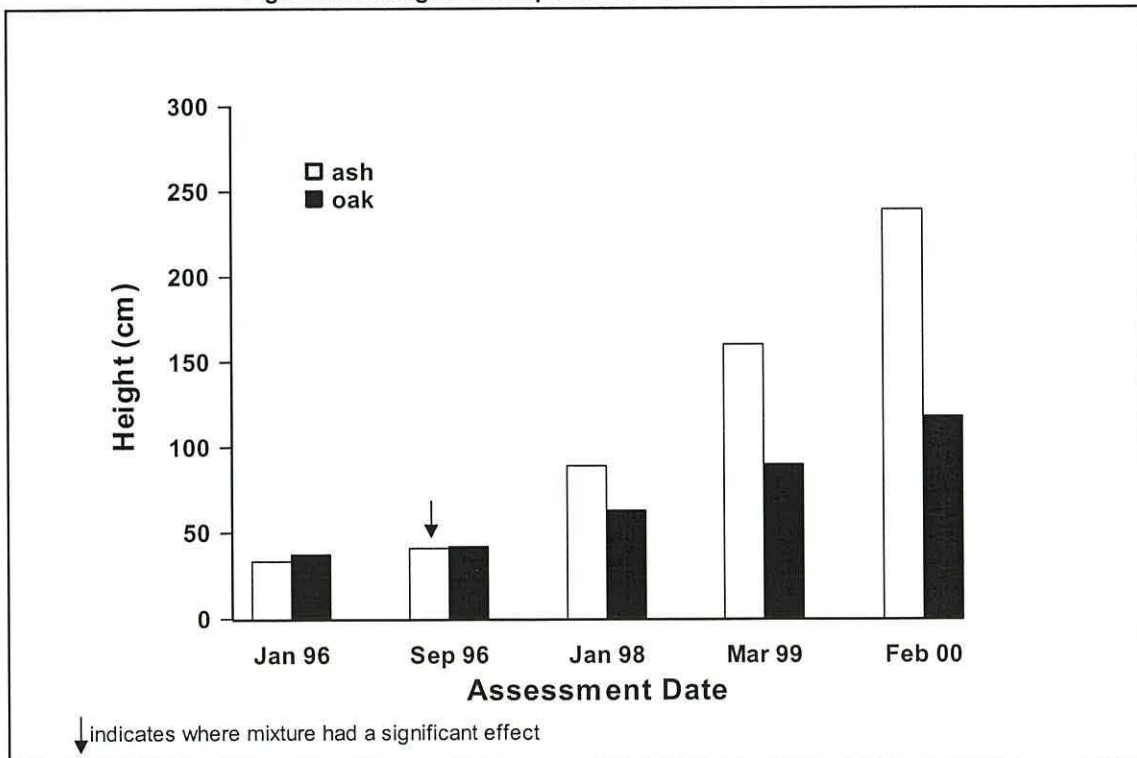
Figure 3.11 Height of ash in mixture with oak in September 1996

Results significant at P≤0.05

s.e.d

Height (cm)

Number of oak trees in surrounding hexagon
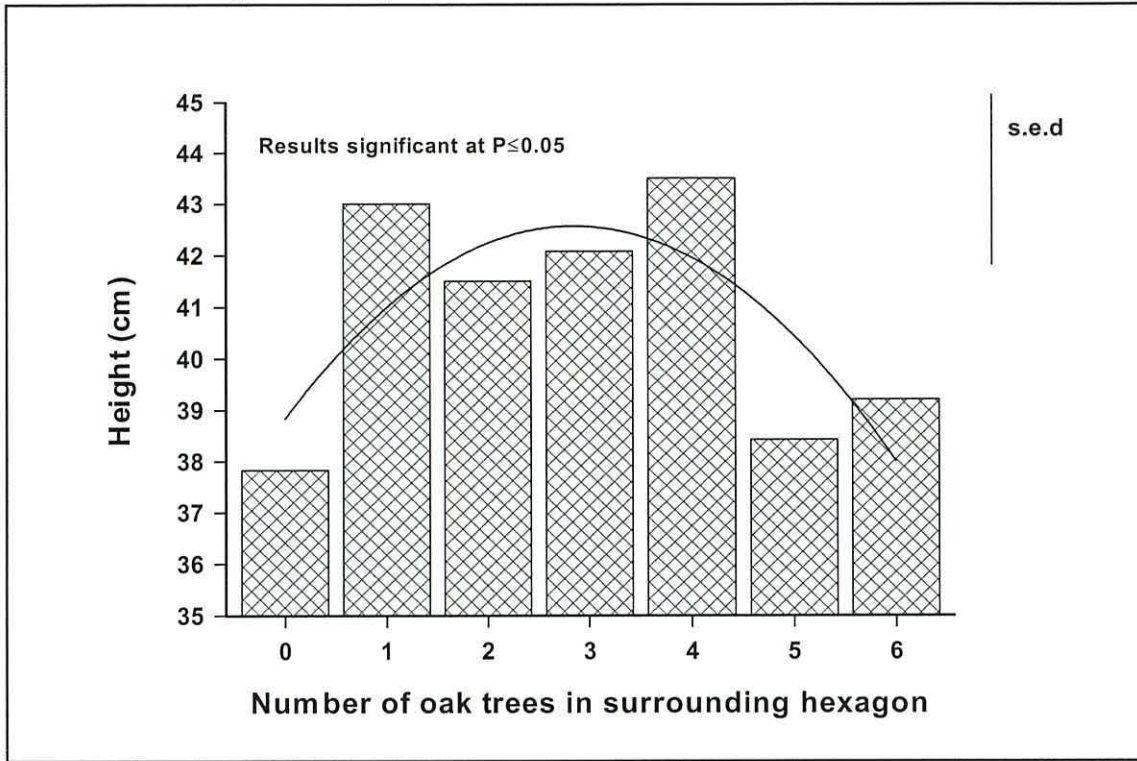
Figure 3.12 Stem diameter development of ash and oak in mixture

□ ash
■ oak

Stem diameter (mm)

June 96   Sep 96   Jan 98   Mar 99   Feb 00

Assessment Date

↓ indicates where the mixture had a significant effect

80
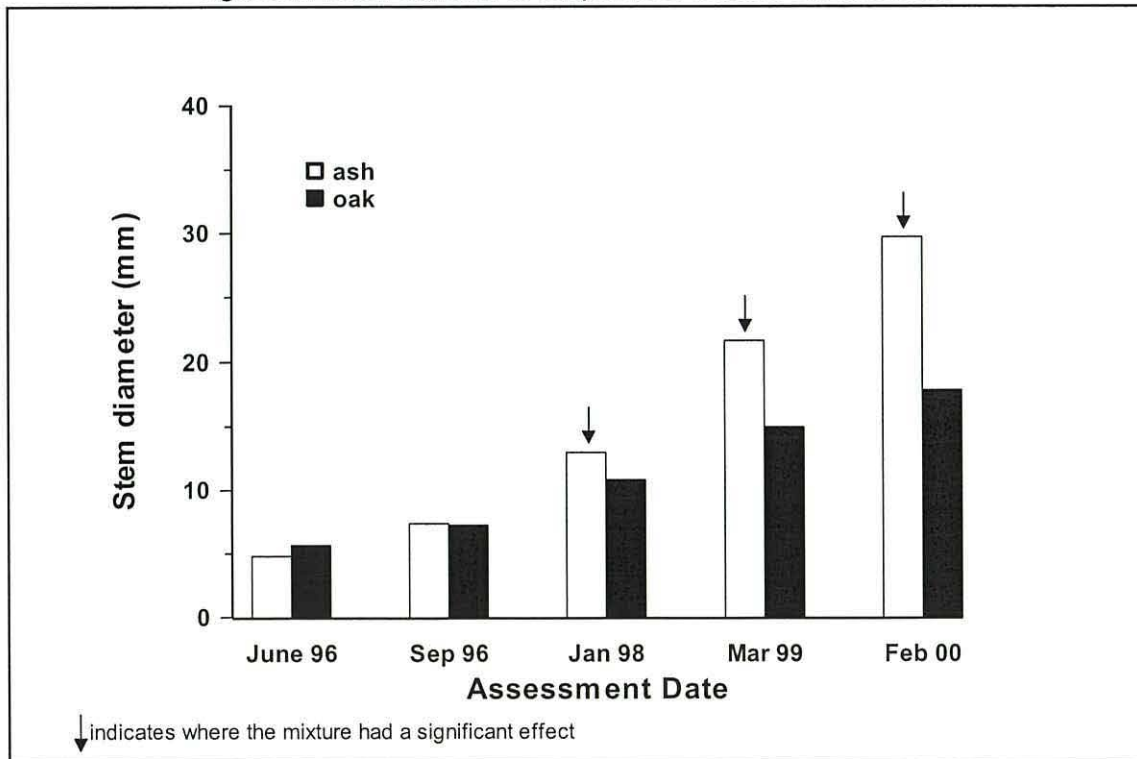
Table 3.5 Results of the analysis of variance of height:diameter ratios for ash

Expt.	Assessment date	Mixture treatment[1] (Height:diameter ratio for ash cm mm^{-1})							Standard error of difference	Signif.
		$A_6{:}B_0$	$A_5{:}B_1$	$A_4{:}B_2$	$A_3{:}B_3$	$A_2{:}B_4$	$A_1{:}B_5$	$A_0{:}B_6$		
Ash: cherry	Sep 96	5.24	5.13	5.33	5.05	5.32	5.25	5.39	0.32	ns
	Jan 98	7.86	8.17	8.06	7.35	7.94	8.27	8.23	0.64	ns
	Mar 99	9.26	9.84	10.28	9.69	10.18	10.63	10.69	0.67	* linear
	Feb 00	10.63	11.14	12.69	11.38	12.07	12.63	12.13	0.84	* linear
Ash: oak	Sep 96	6.11	6.35	5.49	6.06	5.48	5.65	4.91	0.53	* linear
	Jan 98	7.25	6.17	6.52	6.89	6.62	6.48	7.15	0.70	ns
	Mar 99	7.99	7.18	7.67	7.45	7.22	7.63	6.61	0.54	ns
	Feb 00	9.25	7.87	9.04	8.37	8.34	7.9	7.02	0.60	** linear
Ash: beech	Sep 96	5.65	6.45	6.69	5.38	5.84	6.64	6.01	0.49	* higher order
	Jan 98	6.7	6.37	7.55	6.77	6.87	7.04	6.66	0.66	ns
	Mar 99	7.54	7.12	7.43	6.95	7.15	6.22	6.81	0.51	* linear
	Feb 00	8.68	8.26	8.03	7.62	7.30	6.65	6.62	0.56	*** linear

Degrees of freedom = 66; Student's t for $P \leq 0.05$ = 2.00;
ns - not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$; subscripts describe the relationship between ratio and mixture.
[1] Ratios given as numbers of trees (N) of ash A_N: other species B_N.

Table 3.6 Results of the analysis of variance of height:diameter ratios for cherry, oak and beech

Expt.	Assessment date	Mixture treatment[1] (Height:diameter ratio cm mm^{-1} for cherry, oak and beech)							Standard error of difference	Signif.
		$A_6:B_0$	$A_5:B_1$	$A_4:B_2$	$A_3:B_3$	$A_2:B_4$	$A_1:B_5$	$A_0:B_6$		
Cherry:ash	Sep 96	6.50	6.82	6.75	6.83	6.43	6.10	6.72	0.48	ns
	Jan 98	6.49	6.61	7.03	6.52	6.18	6.21	6.10	0.44	ns
	Mar 99	7.42	7.14	7.68	6.73	6.49	5.99	5.45	0.50	*** linear
	Feb 00	8.73	8.22	8.86	7.78	7.44	6.60	6.22	0.54	*** linear
Oak:ash	Sep 96	6.36	5.95	5.46	6.19	6.33	6.07	5.75	0.61	ns
	Jan 98	5.83	5.75	5.32	5.97	6.57	6.23	5.60	0.47	ns
	Mar 99	6.00	5.45	5.62	5.56	6.48	6.39	7.10	0.58	** linear
	Feb 00	6.37	6.06	6.15	6.34	7.16	7.51	7.07	0.52	** linear
Beech:ash	Sep 96	9.42	7.90	6.75	9.32	9.01	8.14	8.45	0.86	* higher order
	Jan 98	6.83	6.16	5.36	7.33	5.96	5.90	6.51	0.78	ns
	Mar 99	6.45	5.89	5.52	5.96	5.15	6.51	6.36	0.80	ns
	Feb 00	6.00	6.65	5.45	5.39	6.09	6.96	6.38	0.53	* higher order

Degrees of freedom = 66; Student's t for $P \le 0.05 = 2.00$;
ns - not significant, * $P \le 0.05$, ** $P \le 0.01$, *** $P \le 0.001$; subscripts are the relationship between ratio and mixture;
[1] ratios given as numbers of trees (N) of ash A_N : cherry/oak/beech B_N.

Table 3.7 Estimation of relative yield total (RYT) for the three mixture experiments

Experiment	Assessment date	Relative yield total
Ash:cherry	January 96	1.25
	December 96	1.41
	November 97	1.55
	March 99	1.55
	March 00	1.78
Ash:oak	January 96	1.09
	December 96	1.36
	November 97	1.65
	March 99	1.48
	March 00	1.77
Ash:beech	January 96	1.09
	December 96	1.13
	November 97	1.16
	March 99	1.48
	March 00	1.29

Height:stem diameter ratios of ash were greater when there was more ash in the surrounding mixture in September 1996 and February 2000, (Table 3.5, page 81). If it is accepted that significant changes in the shape of a tree are indicative of competition then there would appear to have been an early and late phase of competition in the experiment. In contrast, competition commenced during the 1998 growing season on the oak, and larger height:stem diameter ratios were associated with higher proportions of oak in the surrounding mixture (Table 3.6, page 82). Interestingly, in both March 1999 and February 2000 there were no significant differences between mixtures in oak height or stem diameter considered separately; differences were only apparent in the ratio between them.

Results of the analysis of data on the central stem volume of ash showed that there was a significant linear relationship between mixture design and the volume of the central stem of ash in April 2000 (Figure 3.14). Larger ash trees were associated with more oak in the surrounding mixture. The RYT for the mixture increased from 1.09 in January 1996 to 1.77 in March 2000 (Table 3.7). Significant differences in the number of forks were apparent for the March 2000 assessment. However, the mean number of forks for the four treatments were 2,1,0,0 (Table 3.8, page 85) and because the data were under-dispersed and $P=0.049$ this result must be treated with considerable caution (Appendix 3.3).

Figure 3.13 Stem diameter of ash in mixture with oak in February 2000

Results significant at P≤0.05

s.e.d

Stem diameter (mm)

Number of oak trees in surrounding hexagon
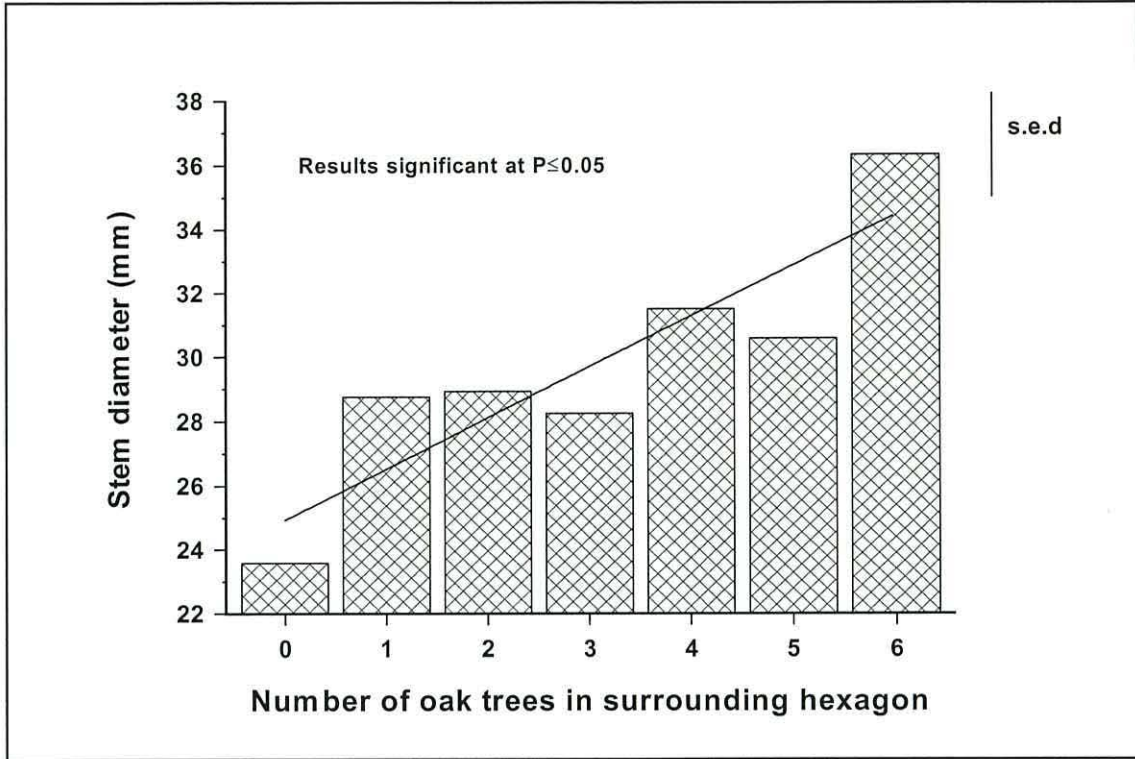
Figure 3.14 Volume of central stem of ash in mixture with oak in April 2000

Results significant at P≤.05

s.e.d

Volume (cm^3)

Number of oak trees in surrounding hexagon
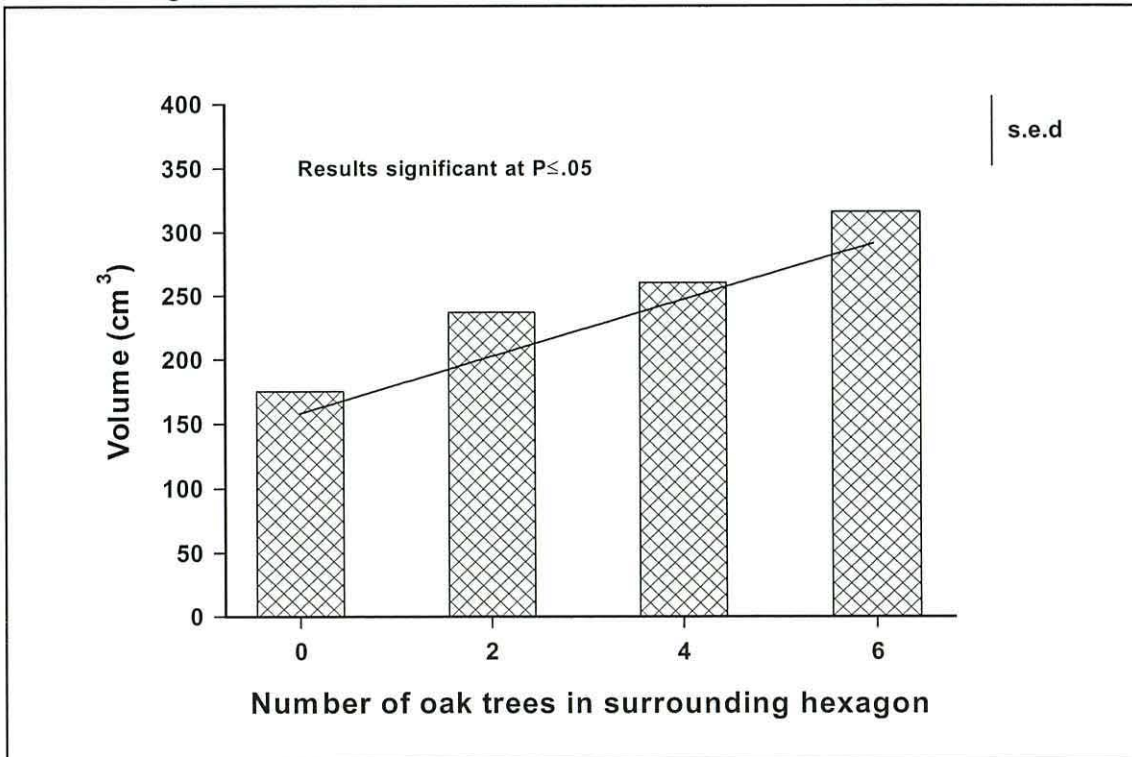
Table 3.8 Results of the analysis of ash forking

Expt.	Assessment date	Mixture treatment[1] (Number of new forks in each year on ash)				Significance[2]
		$A_6:B_0$	$A_4:B_2$	$A_2:B_4$	$A_0:B_6$	
Ash:cherry	Dec 96	1	0	2	1	ns
	Nov 97	6	5	4	4	ns
	Mar 99	5	3	0	1	**
	Mar 00	3	2	5	7	*
Ash:oak	Dec 96	0	1	2	2	ns
	Nov 97	2	1	3	3	ns
	Mar 99	2	1	3	2	ns
	Mar 00	2	1	0	0	*
Ash:beech	Dec 96	2	0	1	0	ns
	Nov 97	6	4	3	3	ns
	Mar 99	0	0	2	1	ns
	Mar 00	2	2	2	4	ns

[1] Ratios given as numbers of trees (N) of ash A_N : cherry/oak/beech B_N.
[2] From accumulated analysis of deviance table, for significant results see Appendix 3.3.

3.3.1.3 Ash and beech

Survival in this study was lower than in the other two experiments. One ash and 13 beech died during 1997; a beat-up reserve of eight beech trees of the same genotype had been established on-site and these were planted into randomly selected beat-up positions in March 1998. During 1998 two beech died and in 1999 nine beech died. The number of live trees at each assessment is summarized in Table 3.9.

Table 3.9 Number of trees in the ash:beech experiment at each assessment

Assessment date	Number of ash	Number of beech
September 1996	84	84
January 1998	83	71
March 1999	83	77
February 2000	83	68

The mean height of the beech at the end of the fourth growing season was 97.8 cm and the ash at the same time was 230.5 cm, reflecting the fact that the species had different growth trajectories and that the mixture, similar to that in the

ash:oak experiment, developed a two-tier canopy structure (Figure 3.15). The beech were initially smaller than the ash, in contrast to the other two experiments where the initial sizes of the two species were well matched. At the start of the experiment the ash were 7.2 cm taller and 2.9 mm greater in diameter than the beech. At the end of the first growing season ash maintained its height difference compared with the beech; in September 1996 ash was 37% taller than the beech and the relative difference between them varied from 122% in January 1998 to 171% in March 1999, and then 136% in February 2000. There were two significant effects of the mixture design on the height of ash. In September 1996 the relationship was quadratic with a maximum between A_3B_3 and A_2B_4 (Figure 3.16). In February 2000 a significant effect was also observed but the relationship was of a higher order than quadratic and showed no clear pattern. In February 2000 there was a linear relationship between height of beech and the number of ash trees in the lattice, with taller beech trees being associated with lower proportions of ash in the mixture (Figure 3.17).

The pattern of development of stem diameter for the two species was very similar to that for height (Figure 3.18). Mean stem diameter of the beech at the end of the fourth growing season was 16.0 mm and the ash at the same time was 31.1 mm in diameter, reflecting the fact that the species had different stem diameter growth trajectories. In total there were seven instances where the mixture design had a significant effect on the stem diameter of ash and beech. Four of these occurred up to and including the January 1998 assessment; however, three were of a higher order than quadratic and showed no clear pattern. In March 1999 and February 2000 (Figure 3.19) there was a linear relationship between ash stem diameter and the number of beech trees in the surrounding hexagonal lattice, i.e. larger diameter ash trees were associated with more beech in the surrounding mixture. A clear negative relationship was also apparent in February 2000 between beech stem diameter and the number of ash trees in the surrounding mixture (Figure 3.20), i.e. larger diameter beech trees were associated with low numbers of ash in the mixture.

Analysis of the height:stem diameter ratio indicated that there was an early and late phase of competition between ash and beech, similar to the phases observed in the ash:oak experiment. There were significant mixture effects on both ash and beech in September 1996, but they were of a higher order than quadratic and showed no clear pattern (Tables 3.5 and 3.6, pages 81 and 82). This was also the case with the beech in February 2000. A clear linear relationship was apparent in March 1999 and February 2000 for ash; larger height:stem diameter ratios were associated with higher proportions of ash in the surrounding mixture. The main reason for this latter result was the significant effect of the mixture on ash stem diameter.

Figure 3.15 Height development of ash and beech in mixture

↓indicates where the mixture had a significant effect
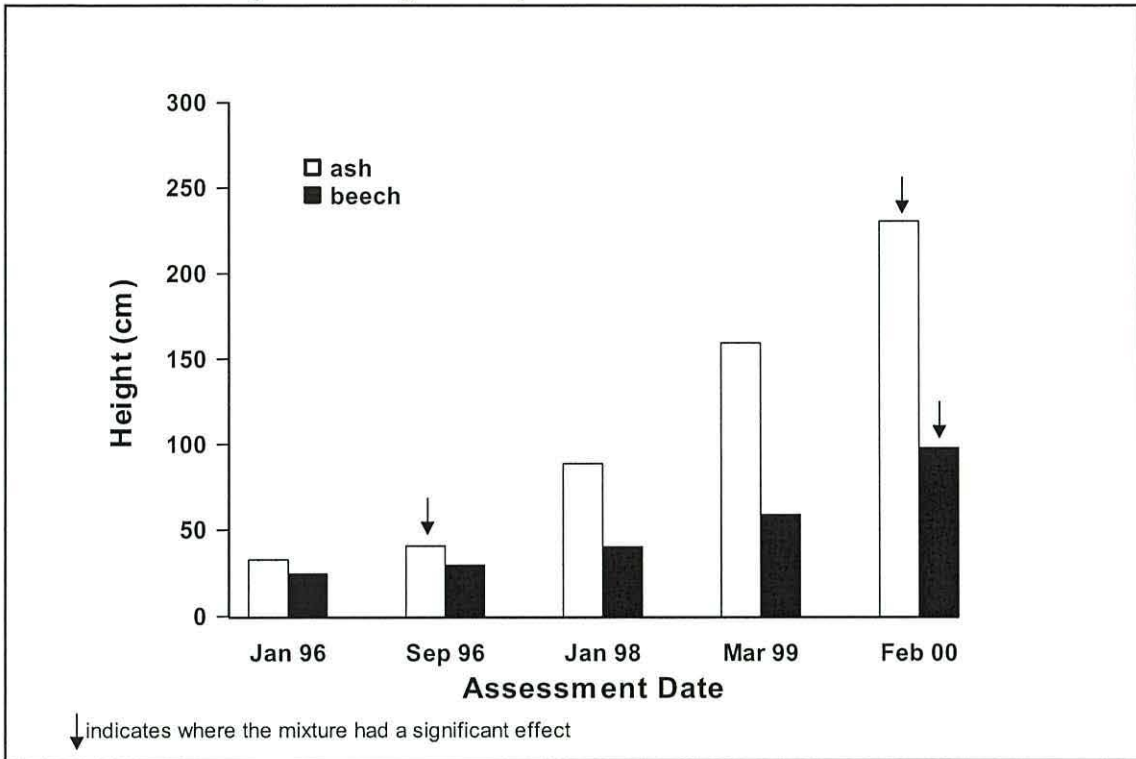
Figure 3.16 Height of ash in mixture with beech in September 1996
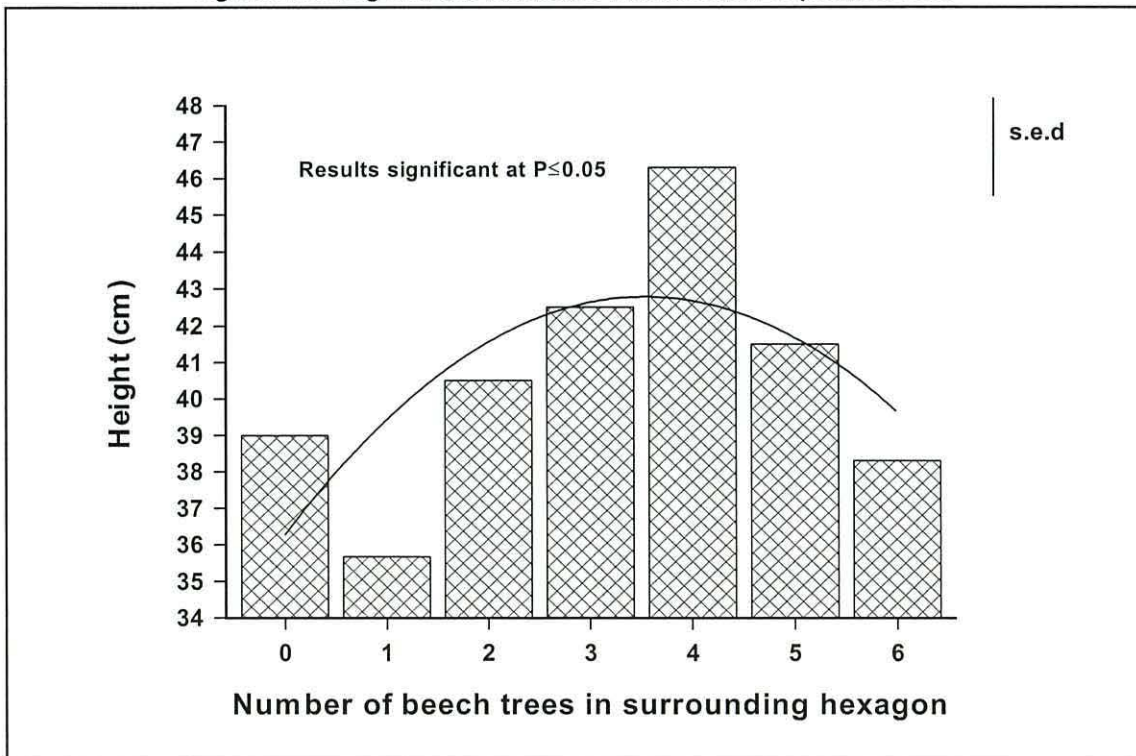
Figure 3.17 Height of beech in mixture with ash in February 2000

s.e.d

Results significant at P≤0.05

Height (cm)

Number of ash trees in surrounding hexagon
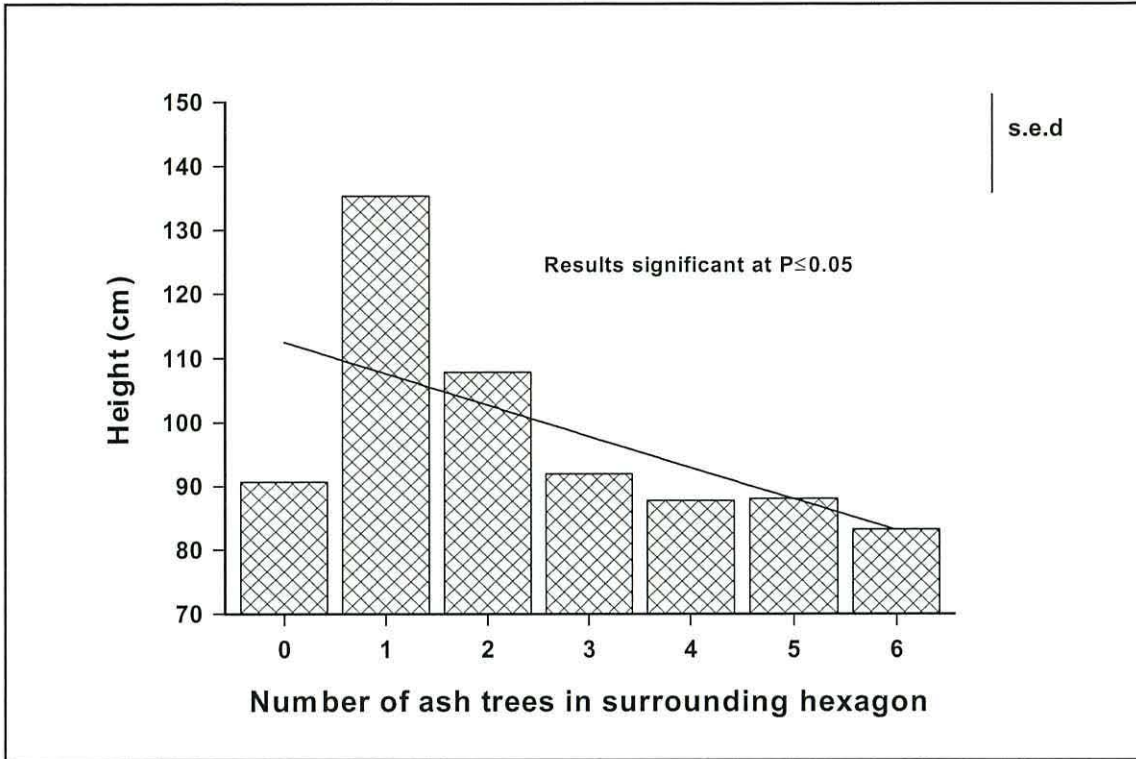
Figure 3.18 Stem diameter development of ash and beech in mixture

□ ash
■ beech

Stem diameter (mm)

June 96   Sep 96   Jan 98   Mar 99   Feb 00

Assessment Date

↓indicates where the mixture had a significant effect
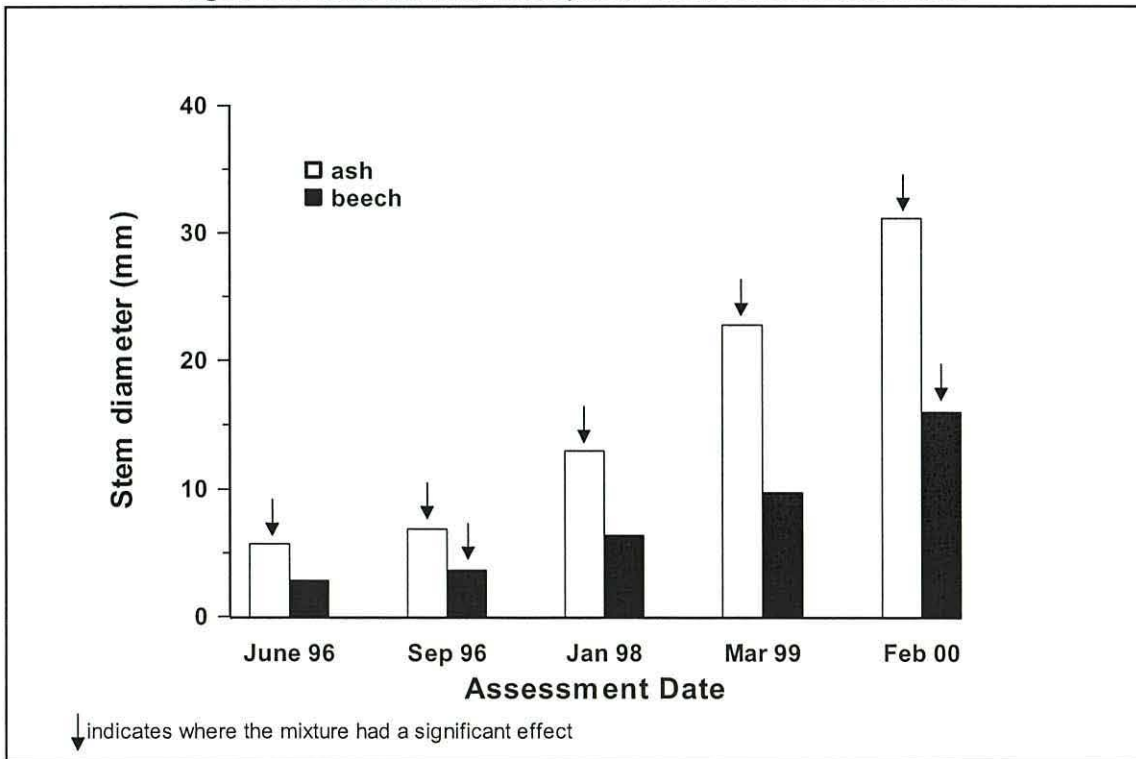
Figure 3.19 Stem diameter of ash in mixture with beech in February 2000

Results significant at P≤0.001
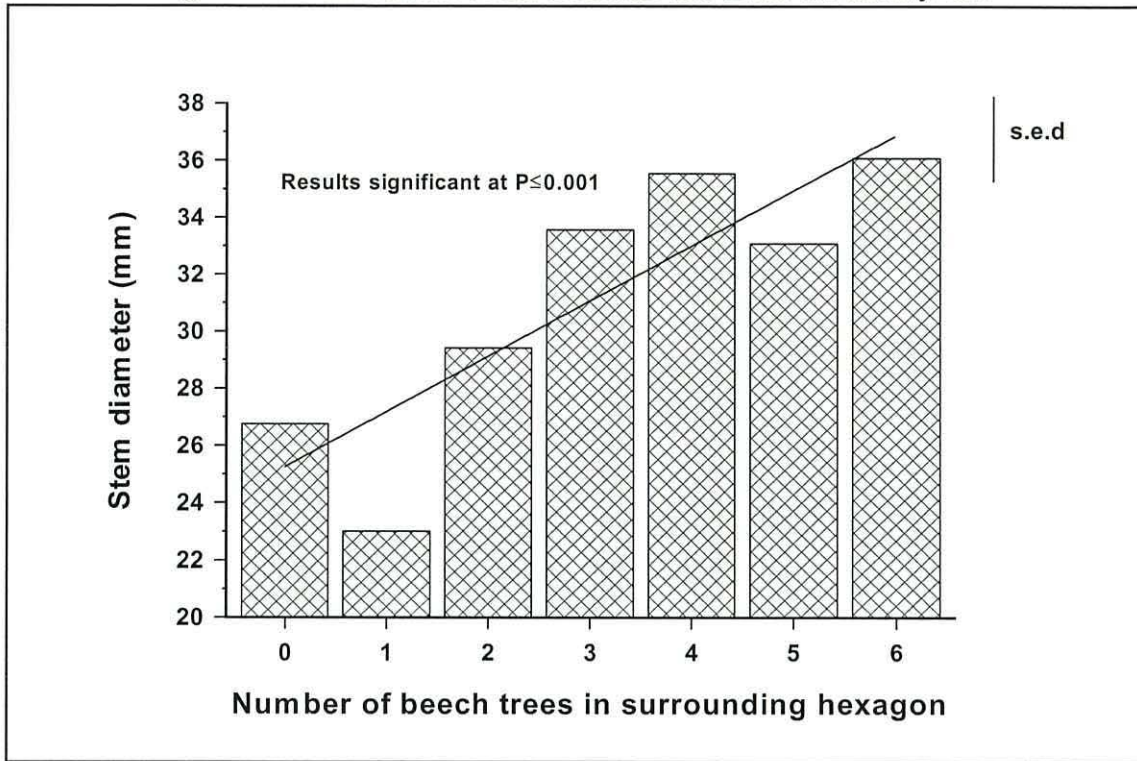
Figure 3.20 Stem diameter of beech in mixture with ash in February 2000

Results significant at P≤0.001
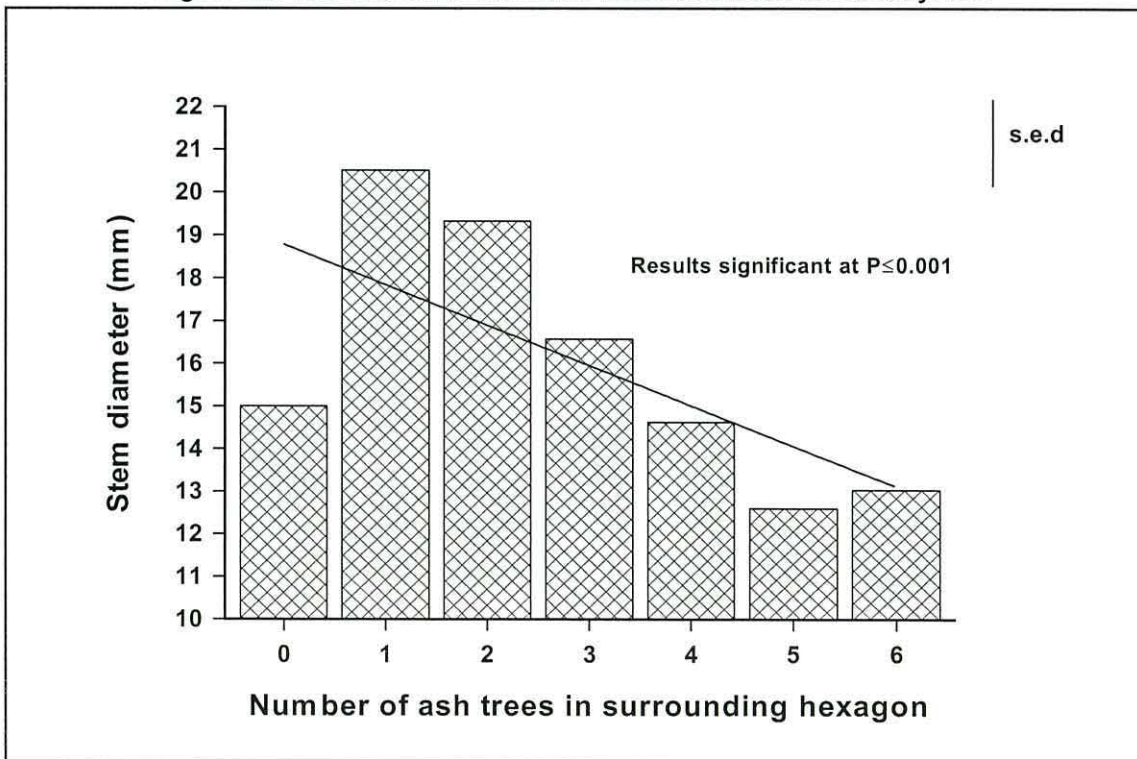
Figure 3.21 Volume of central stem of ash in mixture with beech in April 2000
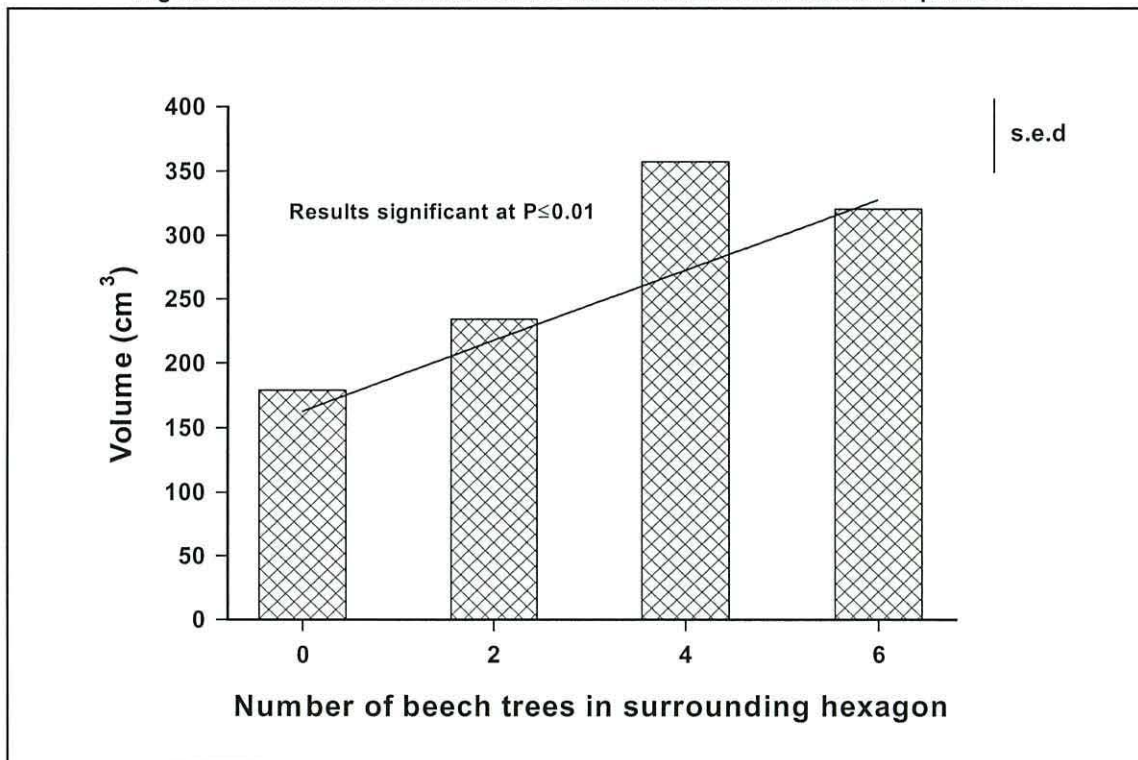
Results of the analysis of data on the central stem volume of ash showed that there was a significant mixture effect in April 2000 (Figure 3.21). Larger trees were associated with higher proportions of beech in the mixture. The RYT for the mixture increased from 1.09 in January 1996, peaked at 1.48 in March 1999 and was 1.29 in March 2000 (Table 3.7, page 83). There were no significant differences in the number of forks in the ash for any of the four years assessed (Table 3.8, page 85).

3.3.2. Bud and branch demography

3.3.2.1 Stage 1 analysis

General patterns in the mean number of buds and branches for the three experiments are shown in Figures 3.22 to 3.27. For buds (Figures 3.22 to 3.24, pages 94-95) the patterns were very similar for the three experiments. At the first assessment the mean number of buds on section 1 was between 12 and 16 and there was a similar number (10-12) on section 2. At later assessment dates, after the initial period of transplant shock, the number of buds on sections 3 and 4 was much higher (between 23 and 26). However, it was also noticeable that the subsequent rate of bud loss on sections 3 and 4 was higher than on sections 1 and 2. The patterns in the total number of branches were also similar in the three experiments (Figures 3.25 to 3.27, pages 95-96). At the first assessment some branches already existed on section 1, but not on section 2. Subsequently, the mean number of branches increased, as dormant buds produced branches, and then either remained stable or gradually declined. On sections 3 and 4 there was a very different pattern of branch production and loss; larger numbers of branches were produced in the second year of growth and, on section 3, the number decreased very quickly the year after.

More details of the mean numbers of buds and branches classified according to bud origin/section of tree and assessment year are shown in Appendix 3.4. The following summarizes the main patterns. The first assessment in December 1996 involved section 1 of the tree, which was the part of the central axis of the two-year-old tree planted in April 1996, and section 2 which was the growth increment of that year. This explains why there are no terminal buds on section 1 in any of the three experiments. At the first assessment of any particular section the mean number of terminal buds varied between 0.9 and 1.0 reflecting the fact that there were instances where this bud was lost or damaged. It is also apparent from the data that by the time of the second and third assessment on any section a small number of branches had been produced from terminal buds. In these cases growth of the shoot from the terminal bud had been overtaken by that of branches from

axillary buds; one of the latter branches was then designated as the leader and formed part of the central axis of the tree.

Generally the number of scale buds was small with the mean number per tree varying between 0 and 2.2. The change from production of scale buds to that of axillary buds is controlled by differentiation in the growing shoot and differences between the two types of bud were sometimes difficult to see on the winter shoot of a tree. Where there was any doubt about their origin they were classified as axillary, and this perhaps accounts in part for the small number of scale buds observed. There were very few occasions where scale buds produced branches, and it was noticed that the small number of trees in which this happened were generally smaller than average and under intense competition.

The mean number of axillary buds on sections 2–5 at the time they were first assessed (i.e. the winter shoot) varied between 7.7 and 26.3. Generally the axillary buds were in opposite pairs on the winter shoot; however, on one particularly vigorous tree they were observed to be in groups of three around the stem. Another interesting observation was that occasionally there would be a group of 4 to 8 axillary buds very close together (spanning 2–3 cm of the shoot length) near the top of the winter shoot. Minor axillary buds were difficult to see at the start of the study and neither they nor any branches which originated from them were counted; this convention was continued throughout the study. In common with branches from scale buds, branches from minor axillary buds were observed to occur on trees which were small and seemed to be under competition stress. There were also occasional instances where new buds on the winter shoot were on protrusions of between 4 and 7 mm in length from the main axis of the stem. It was clear that the majority of true branches (shoots originating from a single bud) originated from axillary buds.

3.3.2.2   Stage 2 analysis

There were seven cases of significant mixture effects, three in the ash:cherry experiment, four in the ash:beech experiment and none in the ash:oak experiment (Table 3.10). More details of each of these, including data and results of the analysis of deviance, can be found in Appendix 3.5. The number of significant effects was small, seven from 258 possible combinations of species, section of tree, class of bud and year of assessment. However, as can be seen from Table 3.10 the results were consistent in showing that more buds and branches were associated with higher proportions of cherry and beech in the mixture. It was also apparent that all significant effects were on axillary buds, but were well distributed between sections 1–5 and assessments from November 1997 to March

1999. The results for br99a5 in the ash:cherry experiment were of interest as these were the raised buds which were noticed on the winter shoot. The analysis indicated that their appearance was related to mixture, with more being produced when the ash was surrounded by higher proportions of cherry.

Table 3.10 Results of the analysis of the numbers of buds and branches

Experiment	Assessment	Relationship between assessment and mixture
Ash:cherry	bu98a2	More buds when surrounded by higher % of cherry
	bu98a4	More buds when surrounded by higher % of cherry
	br99a5	More branches when surrounded by higher % cherry
Ash:beech	bu97a2	More buds when surrounded by higher % of beech
	bu98a4	More buds when surrounded by higher % of beech
	br98a1	More branches when surrounded by higher % of beech
	br99a4	More branches when surrounded by higher % of beech

3.3.2.3   Stage 3 analysis

Figure 3.28 (page 97) illustrates the results of bud mortality (M_q) in the three experiments. The proportion of buds lost between successive years ranged between 0.24 and 1.00 and generally increased with time, as the number of buds on each section declined. Section 1 was a little different as this was the initial planted tree and was two years old; it showed higher mortality rates than section 2 in the first year.

The results of the analysis of M_q using the initial general linear model and the general linear mixed model are summarized in Table 3.11 (page 99). Considering all the experiments, results from the general linear model showed there was only one significant mixture effect at $P \leq 0.05$ and a further two at $P \leq 0.10$. However, results from the general linear mixed model (one with a more appropriate error structure) showed that none of the mixture effects were significant. The one significant result (for ash:beech mixture on bud mortality 1996-97 section 2) from the initial analysis is shown in Figure 3.29 (page 98) and the one with the highest Wald statistic (for ash:cherry mixture on bud mortality 1997-98 section 2) is shown in Figure 3.30. Both results show a negative relationship, i.e. the proportion of buds lost increases as the proportion of cherry or beech in the mixture increases.

Figure 3.22 Numbers of buds on ash trees in mixture with cherry
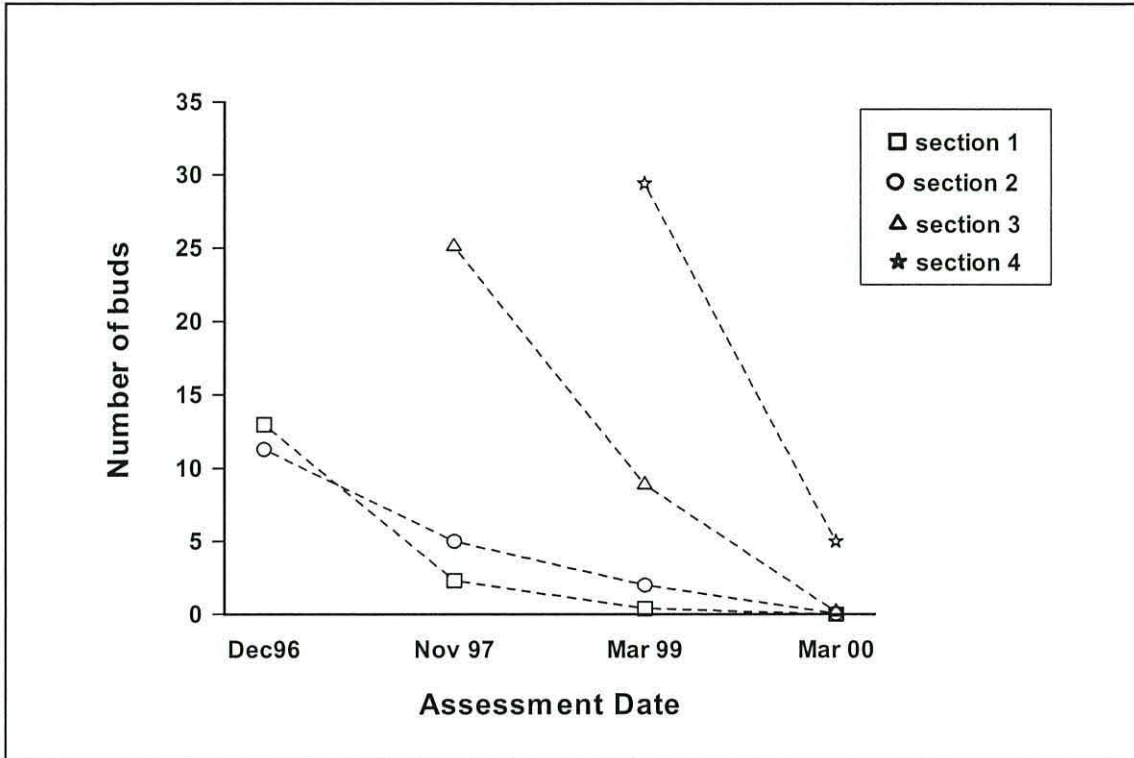
Figure 3.23 Numbers of buds on ash trees in mixture with oak
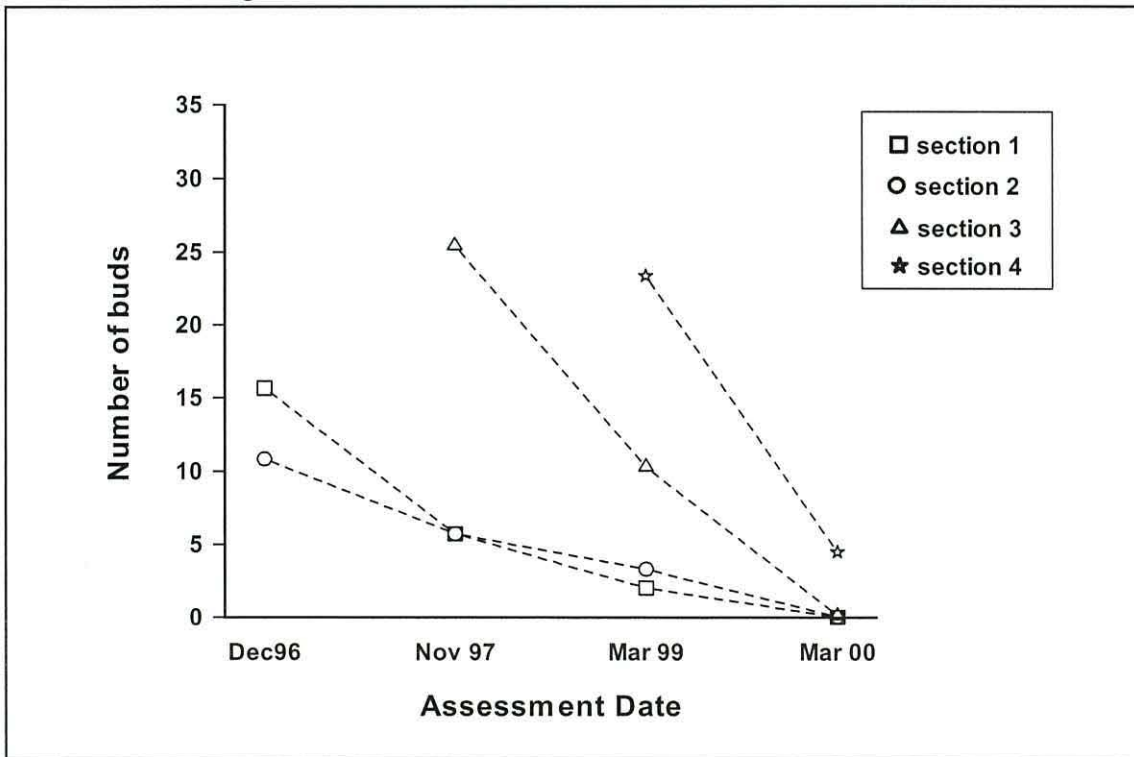
Figure 3.24 Numbers of buds on ash trees in mixture with beech
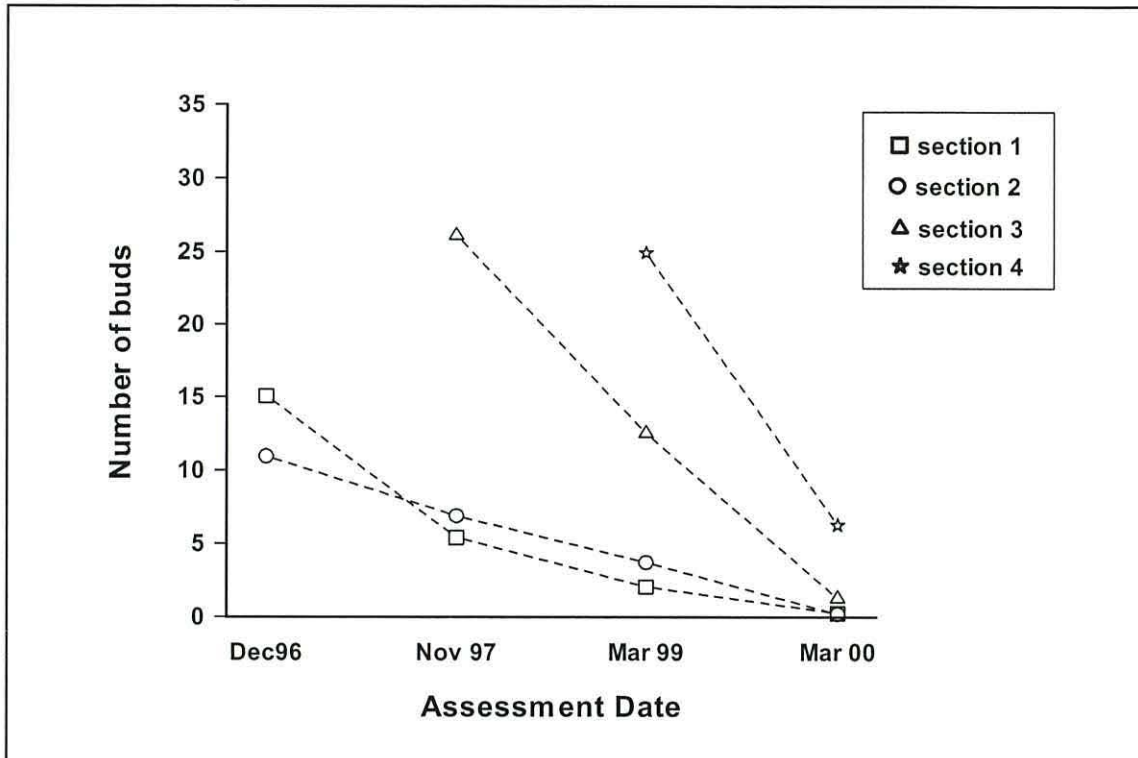
Figure 3.25 Numbers of branches on ash trees in mixture with cherry
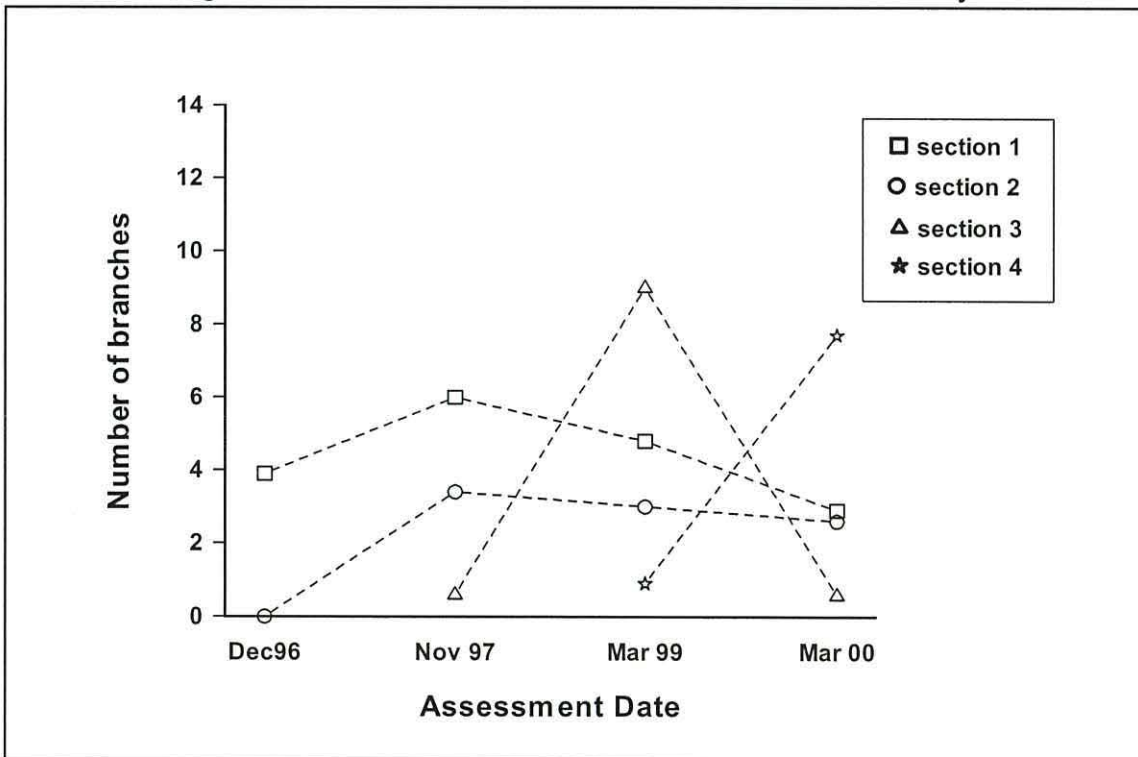
Figure 3.26 Numbers of branches on ash trees in mixture with oak
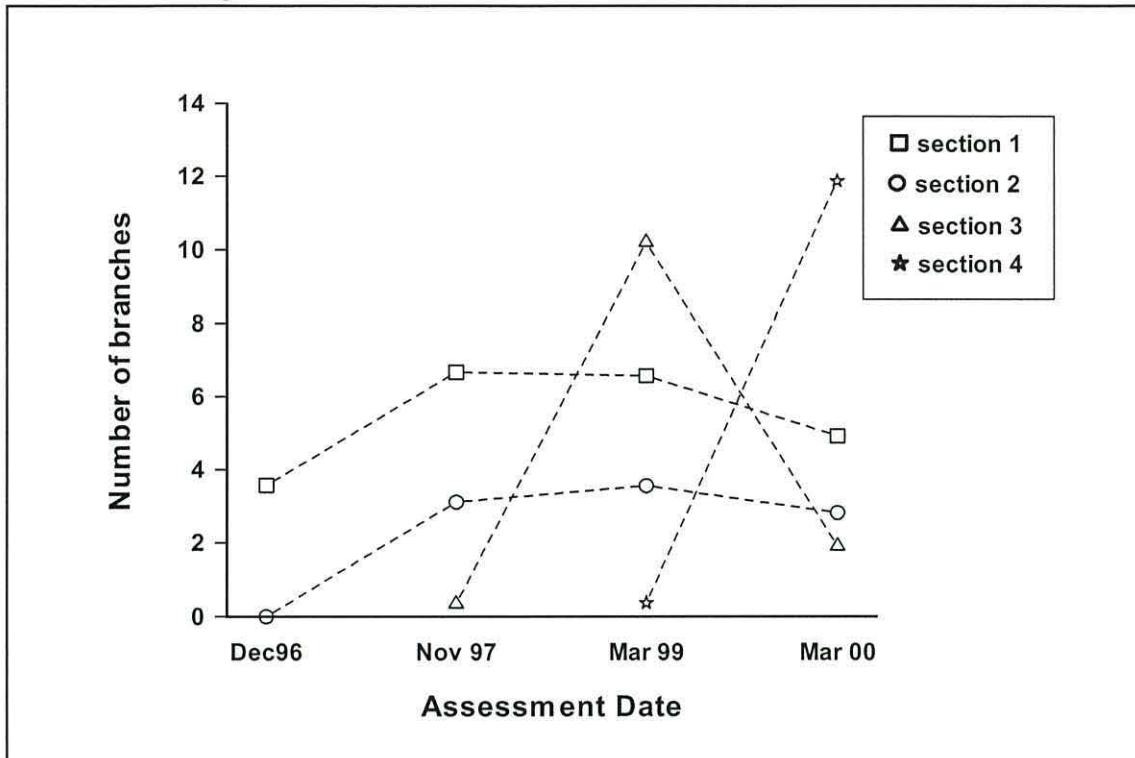
Figure 3.27 Numbers of branches on ash trees in mixture with beech
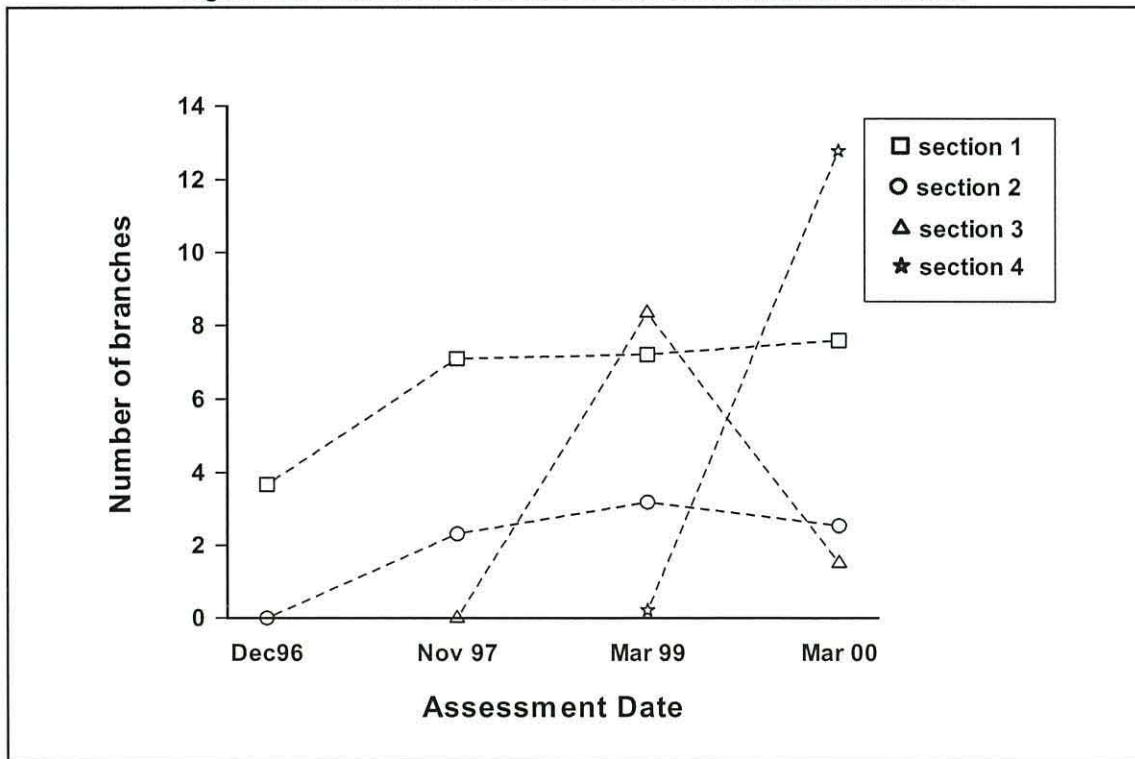
Figure 3.28 Ash bud mortality in the mixture experiments

Ash bud mortality proportions in mixture with cherry

Ash bud mortality proportions in mixture with oak

Ash bud mortality proportions in mixture with beech
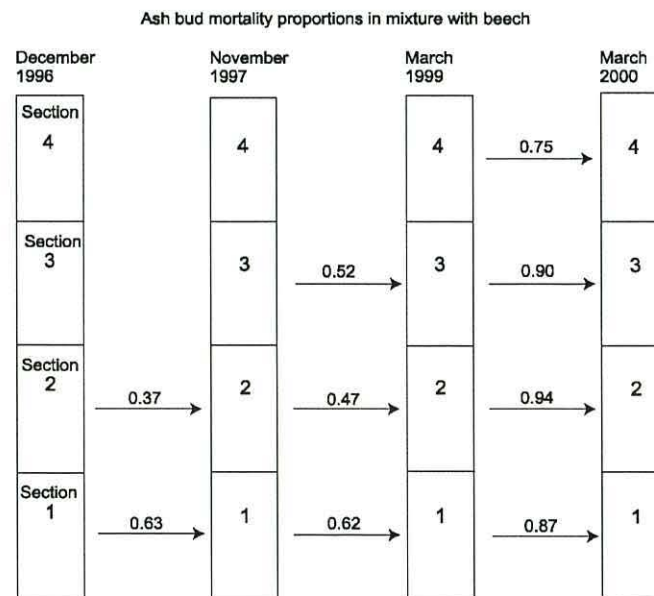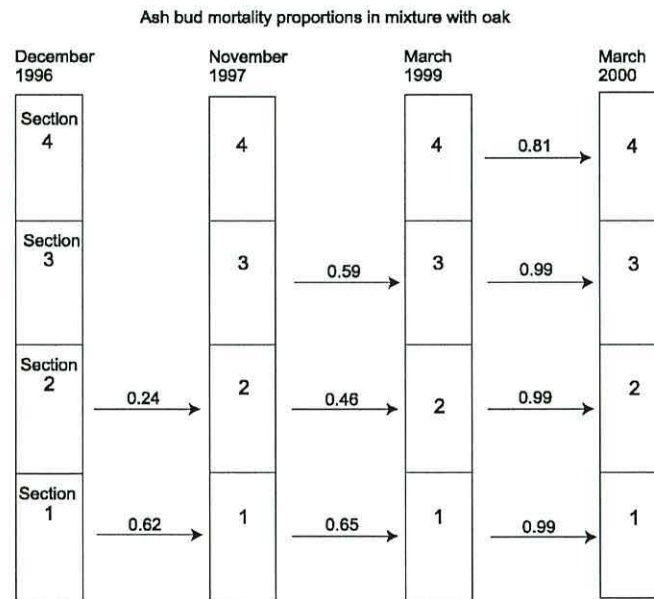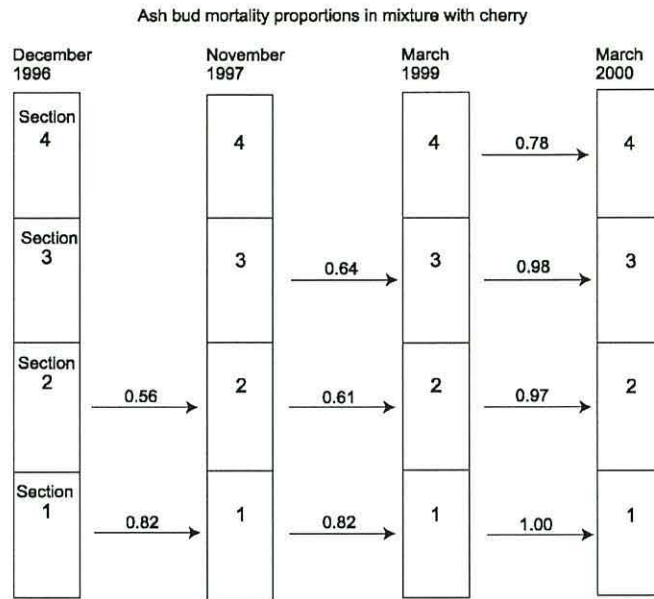
Figure 3.29 Ash bud mortality on section 2 between 1996-97 in mixture with beech
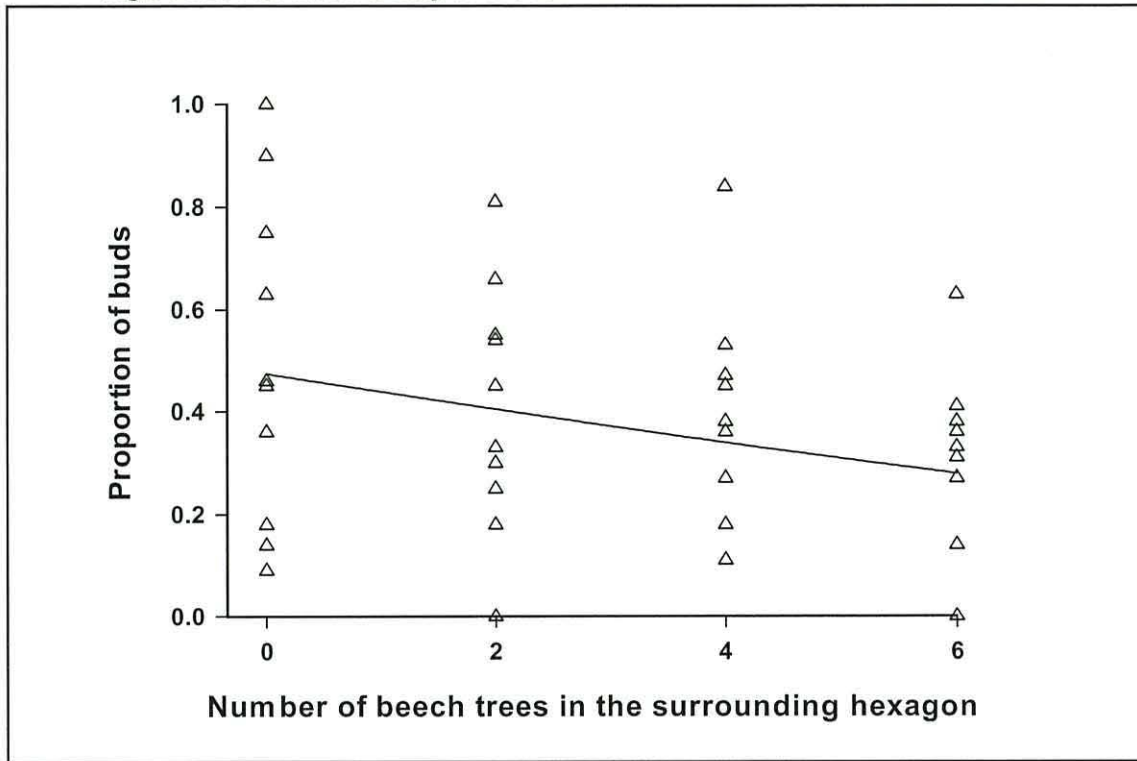
Figure 3.30 Ash bud mortality on section 2 between 1997-98 in mixture with cherry
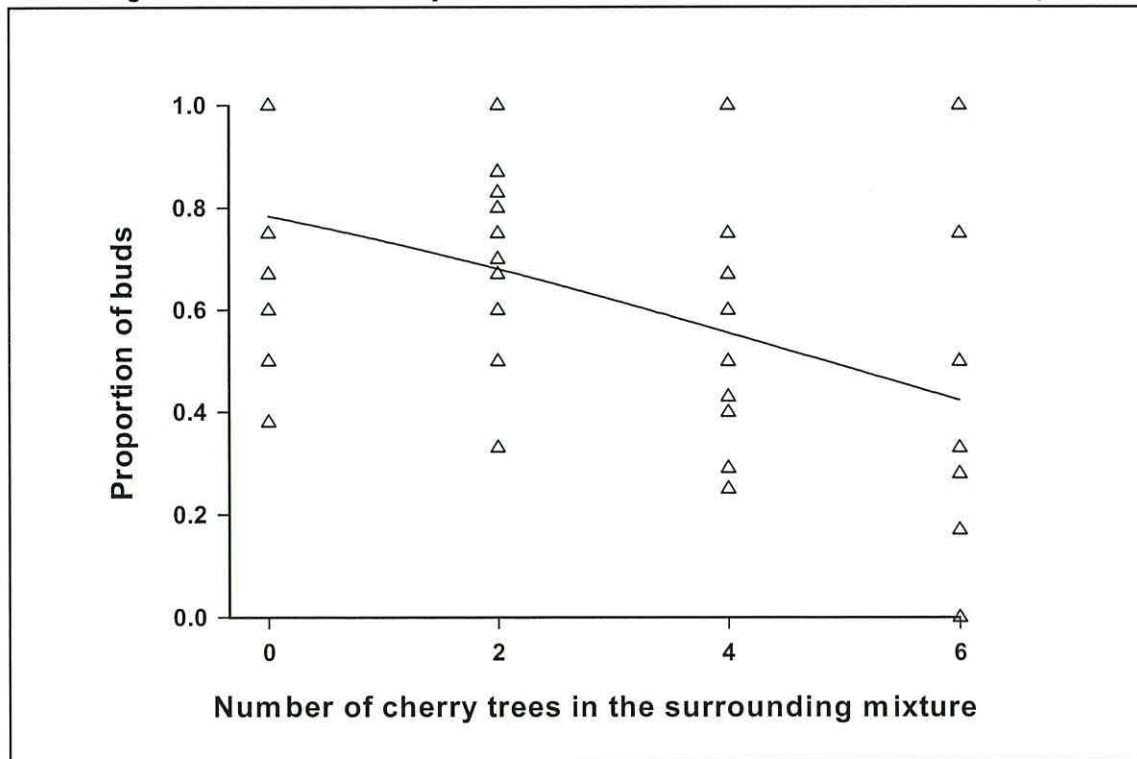
Table 3.11 Results of stage 3 analysis of bud mortality

Years	Section	Ash : oak		Ash : beech		Ash : cherry	
		[1][1]	[2][2]	[1][1]	[2][2]	[1][1]	[2][2]
1996-97	1	0.664	0.0	0.682	1.3	0.1412	1.6
1997-98	1	0.574	0.6	0.981	1.0	0.977	0.0
1996-97	2	0.854	0.1	**0.027**	**3.6**	0.537	0.1
1997-98	2	0.798	0.0	0.962	0.1	**0.063**	**17.6**
1997-98	3	0.569	0.4	**0.072**	**2.7**	0.141	2.8
1998-99	4	0.492	0.1	0.482	0.6	0.840	0.0

[1]The probability of GLIM model being significantly different to horizontal from the first analysis described in 3.2.5.2; i.e. if $P \leq 0.05$ then the model is significant and there may be an effect of mixture.
[2]The Wald statistic from the second analysis described in 3.2.5.2; ≥ 18.5 is required for a significant effect of mixture at $P \leq 0.05$.
Bold figures are those which were significant or nearly so.

3.4 Discussion

In the ash:cherry mixture the initial heights and stem diameters of species were similar and both species grew well throughout the period of the experiment. Effects on height were restricted to cherry and were short-lived; however, effects on stem diameter were evident for both species in most years. Analysis of the height:diameter data indicated that competition between the two species commenced in the 1999 growing season after which the growth of the two species was clearly linked. When ash was surrounded by more cherry, ash stem diameter was reduced and when cherry was surrounded by more ash, cherry stem diameter was reduced. Because the volume of ash trees showed no significant differences between different mixture designs this suggests that ash was reacting to interspecific competition by sacrificing stem diameter increment to maintain height growth and keep its position in the canopy. This is a good example of the way a plant, when under competition stress, can alter the allocation of assimilates among different parts of the tree (Harper, 1977). Plant height is one of the most potent influences governing competitive relationships (Ford, 1975; White, 1980) and in February 2000 the outcome of competition is not as clear as the effect of species on each other (Gibson *et al.*, 1999).

In the ash:oak experiment the initial heights and stem diameters of plants of the two species were similar but the form of the oak was poor. The site was good for tree growth and other areas of oak planted on the Perridge Estate have been successful; the poor form may have been a result of the planting stock not being adapted to the site. There were few effects of the mixture on height growth although the one for ash in September 96 could be

interpreted as a classic 'nursing' effect as described by Evans (1984), Darrah and Dodds (1967) and Gabriel (1986), in which one species encourages better growth or improved form in another. The difference between ash growing pure and in mixture was 5 cm at most and although small, this difference does demonstrate ash growing better in mixture than in a pure stand. There have only been a few examples in the literature where such a nursing effect has been shown and generally this has been by calculating a RYT > 1.0 (Cote and Camire, 1987; Brown 1992; Binkley, 1992; Wei and Kimmins, 1996; Debell *et al.*, 1997). Results for stem diameter clearly showed that ash trees were larger where there was more oak in the mixture. This effect requires careful interpretation because of the two-tier canopy structure. For example, it may not be due to interspecific competition but a lack of intraspecific competition, or another effect such as ash trees having more freedom for movement in the canopy, which has been demonstrated in other studies to encourage stem diameter development (Heiligmann and Schneider, 1974 and 1975). The structure of the ash:oak mixture resembles that of *Leucaena leucocephala* and *Acacia nilotica* mixtures studied by Bhatnagar *et al.* (1993) using a similar hexagonal design first described by Martin (1973). In this mixture the *L. leucocephala* was the faster growing component and developed longer branches with dense foliage above the *A. nilotica* to gain competitive advantage. The fact that ash was in a similarly good position to fix carbon was evidenced by the fact that it had greater volume when surrounded by higher proportions of oak. Analysis of the height:stem diameter data supported the hypothesis that there was an early phase of competition, when the nursing effect was observed, and a later phase when the ash was beginning to dominate the oak.

Unlike the other two species combinations the initial heights and stem diameters of the ash and beech plants were not well matched. The beech did not meet the standards recommended in British Standards Institution (1984) and this may partly explain its poor survival and growth. As with the oak:ash experiment a two-tier canopy developed and analysis of the height:diameter ratios indicated that there was an early and late phase of competition between the species. Again one of the contributory factors to the early phase of competition was a nursing effect of the beech on ash, shown by the greater height of the latter in September 1996. In the latter phase of competition, and also in common with the ash:oak experiment, the stem diameter of ash was generally greater where there was more beech in the surrounding mixture and similar logic could be applied to the interpretation of the results in terms of interspecific and intraspecific competition. One difference from the ash:oak experiment was that at the last assessment in February 2000 both height and stem diameter of beech began to show significant mixture effects, with taller, stouter trees associated with higher proportions of beech in the mixture. Beech is considerably more shade tolerant than oak and this may partly explain the different results

from the two experiments. Conditions in mixtures A_1B_5 and A_2B_4 were clearly favourable for 'drawing-up' beech height growth although the effect was not as clear for A_0B_6 (see discussion on data anomalies below). Of all the critical attempts to explain mixture effects in terms of physiological response, the most successful have been those based on the shading of one component by another; for example, Stern and Donald (1962) examined the interaction between grass and clover in mixture in this way. However, little work has been reported for woody plant species.

In general, two patterns of growth were observed in the experiments. The first, in the ash:cherry experiment, was of two rapidly growing species altering the allocation of assimilates to different parts of the plant and showing a plastic response to interspecific competition. The second, in the ash:oak and ash:beech experiments, was the formation of a two-tier canopy. In both the latter experiments interspecific competition resulted in an early nursing effect on the ash and the final outcome of the competition was clear, with ash being the dominant species. In both patterns of growth, competition affected mainly stem diameter and the shape of the tree with few, and only short-lived effects, on height.

The main advantages of the experimental design were that it enabled the interactions of two species to be studied over a relatively short time scale and it was sensitive enough to detect different stages of competition between the species. The short time scale of study was undoubtedly aided by the close initial spacing adopted in the establishment of the experiments. Study of such a high density planting over a short timescale may make the particular results of the study more applicable to dense natural regeneration than to conventional tree planting. The different stages of competition were apparent in the response of the measured variable to the mixture; initially there was a significant effect but no clear relationship, sometimes an intermediate stage where a quadratic relationship was apparent, and finally a linear relationship. The best examples of this were the stem diameter of cherry, and ash stem diameter in mixture with beech, both between January 1996 and February 2000, and ash stem diameter in mixture with oak between January 1998 and February 2000. However, not all the cases where a higher order effect was detected went on to develop into a clear (quadratic or linear) relationship and in other instances a clear linear relationship was immediately obvious. These results confirm other reports that the onset of competition between two species is gradual with both species adapting their physiology, shape and form to the new competitive situation over a number of growing seasons (Farmer *et al.*, 1988; Shainsky *et al.*, 1992; Fredricksen *et al.*, 1993).

The other advantage of the experimental design is its efficient use of space relative to other designs (Antonovics and Fowler, 1985). It is also worth noting that the basic design

of Boffey and Veveers (1977) used here has been extended to incorporate, in addition to different neighbour frequencies, a range of planting densities within a hexagonal design. For example, Schmid and Harper (1985) used one such design to show that interspecific interactions change in varying ways with different densities. It would be surprising if this was not the case for woody plant species but as yet this has not been studied.

The main disadvantages of hexagonal designs are associated with their statistical analysis and the interpretation of results. Gibson *et al.* (1999) cite Mead (1979) and Antonovics and Fowler (1985) in describing three main disadvantages:(i) they are not randomized and results may be biased by underlying site trends; (ii) the analysis often assumes that 'non-nearest neighbour' effects are insignificant, and (iii) bias may arise if initial size differences are not discounted. In the present study the first of these was dealt with by increasing the number of replicates to 12 and reversing species positions in the two parts of each experiment; this ensured the design was robust. The second of the objections has required some careful interpretation of data, particularly when extrapolating results from single tree plots to pure and mixed stands of trees (see below). The third point was not a problem in the ash:cherry or ash:oak experiments as initial sizes of trees were well matched; however, it could have been a factor in the ash:beech experiment.

One of the main hypotheses investigated, and a question often asked by forest managers, was whether species mixtures are more, less or equally productive than pure stands of component species (Man and Lieffers, 1999). The standard experimental approach for this type of investigation are the 'additive' and 'replacement' designs, described in section 3.1.1, which produce data from which RYT can be calculated. Other British studies of the effects of mixtures on RYT have been those by Brown (1992), and Malcolm and Mason (1999); both used a limited replacement design. In this study, calculation of RYT indicated that all three mixtures were more productive than pure stands of the component species. The results were very clear for the ash:cherry and ash:oak mixtures and clear but less dramatic for the ash:beech. However, as discussed above, this assumes that 'non-nearest neighbour effects' were insignificant. In the ash:cherry experiment the trees in February 2000 were nearly all more than 200 cm tall but only 50 cm apart and on a sloping site with a south-westerly aspect; the assumption of insignificant non-nearest neighbour effects is questionable. Despite this, with results from the ash:cherry and ash:oak suggesting that mixtures could be up to 75% more productive than pure stands, the findings are certainly of interest.

The growth data also gave some interesting results which should be examined. Firstly, on three occasions, there was a significant effect of mixture on stem diameter at the first

assessment after planting in June 1996. It was surprising that any effects were apparent so soon after planting and this emphasizes how quickly the trees began to interact at the spacings used. This adds credence to the observation of 'nursing' after only one growing season in the ash:oak and ash:beech experiments. Secondly, when there were significant linear relationships between growth variables and mixture parameters, occasional mean growth data were indicating a different trend to the general one. Good examples are the height and stem diameter of beech in position A_0B_6 in February 2000 (Figures 3.17 and 3.20, pages 88-89). Lastly, no clear pattern emerged from assessment and analysis of the forking data. This was not one of the main objectives of the experiment but the opportunity to collect the data was taken based on the hypothesis that any possible nursing effect may be detected in the form of the trees and/or growth (Evans, 1984). Below ground effects were not considered in any of the experiments but as shown by Morgan *et al.* (1992) these can be very important in mixtures of tree species.

General patterns of the production and subsequent mortality of buds and branches were similar for ash in the three experiments. On sections 1 and 2 a relatively small number of buds and branches were formed and their rate of loss was slow. This was in contrast to the larger numbers of buds and branches on sections 3 and 4 and the subsequent higher rate of loss observed on section 3. These differences may be related to transplant shock and/or developmental changes within the tree caused by changes in competition.

The study has provided useful data on the bud and branch demography of young ash trees and made some observations which, as far as it is possible to tell from literature, have not been made before. These include the groups of 4–8 axillary buds very close together on the winter shoot of ash. This is not a normal shoot development pattern for ash and may be an indication of neoformation as discussed in 1.4.1 and 2.4.1. In addition, the raised buds on the winter shoot may be a reaction to high levels of competition. The fact that there were significantly more of them with increasing proportions of cherry in the mixture adds credence to this argument.

From the analysis of the growth data it was clear that the ash:cherry mixture and the ash:beech mixtures had developed differently. One consistent result from the bud and branch work was that in both of these experiments the numbers of buds and branches of ash, on some sections at certain assessment dates, increased with higher proportions of cherry or beech in the mixture. The fact that the structure of the mixtures was different probably implies that this happened for different reasons. For example, in the ash:cherry experiment the production of more buds and branches with higher proportions of cherry may be a response to high levels of interspecific competition as trees attempt to maximise

opportunities to increase foliage area. In the ash:beech experiment the increase in buds and branches may have been a result of lower levels of intraspecific competition. However, in all seven instances where there were significant relationships, none lasted for more than one year. The fact that there was no discernible change in bud demography in response to the mixture design was confirmed by the negative results from the analysis of M_q. Not for the first time the wise words of Harper (1977) are appropriate 'it proves very difficult in practice to discover, when groups of plants are clearly interfering with each other's growth, the precise nature of the mechanism involved'.

In summary, results from this study have demonstrated that the stem of ash exhibits a plastic response to competition and have suggested that the mixtures of species studied may be more productive in the early phase of growth than equivalent areas of pure species.

Chapter 4

The influence of spring frosts, ash bud moth (*Prays fraxinella* Bjerk.) and site factors on forking

4.1   Introduction

Forking is one of the major stem deformities in ash. Ash is prone to such damage because the terminal bud is flanked by a pair of lateral buds in the axils of the uppermost leaves of the shoot. If the terminal bud is lost or damaged and fails to elongate in the spring there are two possible successors which, if both develop, will form a fork.

If production of quality timber is an important objective of management, forking is tolerable above 6 m in height as most of the timber value is in the lower part of the stem; below 6 m it is a major defect. Silviculturists have traditionally aimed to reduce the effects of forking on the final crop by planting many more trees than required and removing forked and other poorer trees by thinning. In some species, e.g. beech, production of forks is part of natural morphological development (Ningre, 1997). However, this is not the case with ash even though up to 70% of trees have been reported to be forked in a 13-year-old stand of ash planted at 2500 stems per hectare (sph) at Reichstett near Strasbourg, France (Ningre *et al.*, 1992). With a move in some parts of Europe to low initial planting densities (2500 sph and below) to reduce costs, factors which affect stem form of broadleaves have become increasingly important. Further downward pressure on planting densities may also be exerted in future if genetically improved trees are developed.

The main causes of forking in ash are thought to be unseasonal frosts, ash bud moth (*Prays fraxinella* Bjerk.), genotype, wind damage, mammal damage and bird damage, including feeding by bullfinches on ash buds (Newton, 1964), and hornets (Poulain and van der Stegen, 1997). Many foresters have assumed that the most important of these is unseasonal frosts because the newly emerging leaves of ash are very susceptible to damage (Kerr and Evans, 1993). However, there is little information on the relative importance of each of these factors.

4.1.1 Frost damage

Frost damage to ash and silvicultural measures to avoid it are widely reported (Kerr, 1995). Jones (1950) suggests ash is particularly prone to damage because the cambium resumes activity at least three weeks before leaf emergence and reports annual damage from unseasonal frosts to young ash trees from 1934 to 1941 in Bishop Wood, near Selby, Yorkshire. Generally ash is late flushing compared with other species but its foliage can be killed by prolonged exposure to temperatures as low as only -3 °C (Wardle, 1961). Kerr (1995) described an example of the difficulties of establishing ash in a frosty valley dip. After a number of years in which the trees were frosted back the owner decided to stump them back: an operation which removed the top of the tree leaving about 10 cm of stem and a number of buds above ground. The result of the stumping back was the production of one strong shoot which grew so well in the first season that the tips were above the zone of very cold air: the resulting stand is now rated one of the best ash woodlands in Britain.

4.1.2 Ash bud moth

The potential importance of ash bud moth as a cause of forking was first described by Gent (1955), and more recently by Foggo (1992, 1996a, 1996b). The latter work, which was prompted by a possible link between presence of the moth and die-back of isolated ash trees (Hull, 1991), provided a sound basis for understanding the life cycle and habit of the moth. The larvae of the moth damage ash buds by mining into them for food and shelter. In Britain this part of the life cycle lasts from October to the end of March, after which the larvae leave the bud to escape drowning in the rising sap. During warmer weather in winter the larvae can move from bud to bud and increase damage levels. Foggo and Speight (1995) showed that the moth exhibits a preference based more strongly on bud size than bud position for branch tips collected from mature trees. Based on this they suggested that observations, such as those by Gent (1955), that the moth usually attacks the terminal buds of small trees, could be explained by the fact that small trees have only a few large buds, with the most prominent being the terminal buds. However, perhaps of most interest to the silviculturist was the observation by Foggo (1996b) that 25% of all buds on a sample of 100 saplings had been attacked and of these 71% were dead. If this type of damage was replicated on a wider scale, damage by the moth could be a serious problem for the silviculture of ash.

4.1.3. Genotype

Evidence for a genetic influence on forking in ash comes from observational studies and provenance and progeny trials. Kerr (1995) recorded two types of forking habit, one with persistent forking up the main stem and one with occasional forks. He concluded that the former was more likely to be under genetic control whereas the latter was more likely to be caused by frost or ash bud moth. The importance of correct choice of provenance when planting is shown by Smintina (1995) and Kleinschmit *et al.* (1996) for ash and by Steiner *et al.* (1988) for green ash. In all three cases, examples of provenances from more southerly latitudes than the planting site were less cold hardy or flushed too early, resulting in forking. Marinov (1979) investigated the heritability of stem form in ash and concluded that it is largely inherited from the maternal parent.

4.1.4 Mammal, bird and wind damage

Other types of damage result from mammal damage when trees are not adequately protected in the years after planting. Bird damage and wind damage to the young green leader of ash, which is tender and quite weak in May and June, are also thought to be problems. However, these latter types of damage have been little studied.

The work reported here describes a survey of recently planted ash trees in southern Britain which aimed to (i) quantify the level of forking present; (ii) investigate population levels of ash bud moth and (iii) examine the relationship between forking, incidence of frosts and other site factors.

4.2 Materials and methods

4.2.1 Collection of field data

4.2.1.1 Sampling

The survey involved assessment of three main characteristics at each site: forking, ash bud moth population and number of days frost at the site. First it was necessary to determine: (i) the number of trees per site and (ii) the number of sites to sample.

In the absence of information on previous surveys on similar populations, estimation of the population variance (s^2) can be made using the formula in Freese (1984):

$$s^2 \approx (\frac{R}{4})^2 \qquad\qquad [4.1]$$

where R = range of values expected.

In a pilot survey four plantations of ash (aged 3-7 years) in Hampshire were assessed. The range of forking was between 22% and 74%: thus R = 52, and s^2 = 169 in equation 4.1. To estimate the population mean to within E units with only a 1 in 20 chance that the estimate will be more than E units from the true mean, equation 4.2 describes the minimum sample size (Freese, 1984):

$$n = \frac{1}{\dfrac{E^2}{t^2 s^2} + \dfrac{1}{N}} \qquad\qquad [4.2]$$

where N = the number of units in the population; s^2 = the estimated value of the population variance; t = Student's t value of 1.96 (degrees of freedom=∞; $P \le 0.05$); E = defined as 3 for the survey (i.e. $\bar{x} \pm 3$ would be acceptable).

Number of trees per site Sites were selected which had at least 0.5 ha of ash which was less than six years old. It was assumed that the average stocking was 1000 trees per hectare and thus the minimum value of N was 500. Substituting these values in equation 4.2 gives a minimum sample size of 63 trees per site. However, because little was known about how populations of bud moth would vary and the fixed costs of visiting each site were much higher than the marginal costs of increasing the sample size per site, it was decided to assess 100 trees per site.

Number of sites. The population being studied was defined as ash stands, less than six years old, and planted in schemes which were grant aided by the Forestry Commission in the administrative areas South East England, the West Country and Wye and Avon. The Forestry Commission provided a list of all planting schemes in the population by searching their database to produce a 'master list' of 1100 sites. Hence in equation 4.2 N was 1100, and with this many units in the population the minimum sample size was 68. However, because there was a fixed survey budget of 100 man days in the field and it was judged that each site would take two man days, a practical target of 50 sites was set.

4.2.1.2   Survey procedure

From the 'master list' 20 schemes in each of the three areas were chosen at random as potential survey sites. Each site was visited to ensure it was suitable for the survey: i.e. ash had actually been planted and other factors such as mammal damage were minimal. This initial screening resulted in 18 sites being rejected.

Surveyors were trained using a mock assessment exercise to standardize assessments and reduce measurement error. The number of ash trees present per site was estimated (area $\times$ % ash planted) and a list of 100 random numbers generated, between one and the maximum number per site, using a Genstat program (Anon., 1993). At each site the ash trees present were counted as they were passed by the surveyor, and if the count number was on the list of random numbers then the tree was assessed. Each of the 100 trees was numbered and assessed for:

(i)   Total height (to 0.1 m).

(ii)   Presence/absence of a fork in the central axis of the tree in each year since planting. The definition used for a fork was: where the leader [the tallest branch] for that year's growth did not originate from the terminal bud of the previous year's growth and hence a branch from an axillary bud formed the leader. In some cases a treeshelter made it difficult to assess forking because it was not possible to view the tree in its entirety.

(iii)   Presence of ash bud moth; a terminal bud was removed from the branch which would, in the judgement of the surveyor, assume dominance if the leader was lost.

Other details recorded for each site were: whether the stand was formed by restocking or new planting*; main vegetation type[5]; soil type (using the classification of Soil Survey of England and Wales, (1983); area planted and percentage of ash; presence of mature (seed-producing) ash within 50 m of the planting site; use of treeshelters*; presence of effective weed control*; year planted and a judgement on the anticipated frostiness* using the categories frost hollow, flat land, gentle slope ($\leq$5°) or steep slope (>5°). (For an explanation of asterisks see section 4.2.4.5, page 114.)

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[5] Percent cover in 10% classes of grasses, herbaceous and broadleaved, heather, woody shrubs, gorse and broom, rhododendron, bare and other (specified).

In total, 42 sites were assessed (Figure 4.1) during March to mid-April 1997 to ensure that buds had not started to swell and ash bud moth larvae were still present (Foggo, 1992). Of these 42 sites, five were selected at random and visited again in March 1998 and March 1999 to collect 100 buds from a random sample of trees, sampling a bud from each tree using the procedure outlined in (iii) above.

4.2.2 Bud dissections

Collected buds were sealed in a polythene bag and frozen at -18 °C. Once defrosted, each bud was examined for external signs of ash bud moth attack and the maximum bud diameter was measured to the nearest 0.1 mm. During dissection, the bud was investigated to determine if it was live when removed and if it contained a larva of ash bud moth or other Lepidoptera species; up to nine species have been found in the buds of ash (Foggo, 1992).

4.2.3 Meteorological data

The location of the closest Meteorological Stations (MS) to each of the survey sites was determined and daily minimum air temperatures were obtained for the period April to June for each year when forking data had been recorded on the nearest site. Minimum air temperature can be used as an indicator of plant tissue temperature: for example, Cannell and Smith (1986) used air temperature minus 2 °C as an estimate of tissue temperature, on the basis that tissue temperatures can be 1–3 °C lower than screen air temperatures on still, clear nights.

To obtain daily minimum temperatures at each site the meteorological data were interpolated. For each site the MSs which were within a search radius of 25 km were determined. The figure of 25 km was selected as it was the lowest search radius which would include all 42 sites in the analysis (Table 4.1). If only one MS was present the site was assigned the values for that MS. If there was more than one

Table 4.1 Numbers of sites selected using different search radii

Search radius (km)	No. of sites selected
5	6
10	19
15	32
20	40
25	42
30	42

MS within the search radius a weighted mean minimum air temperature was calculated. The weights were inversely proportional to the squares of distances between the site and the MS (i.e. $1/d^2$, where d = distance between site and MS in km).

Figure 4.1 Location of survey sites and meteorological stations
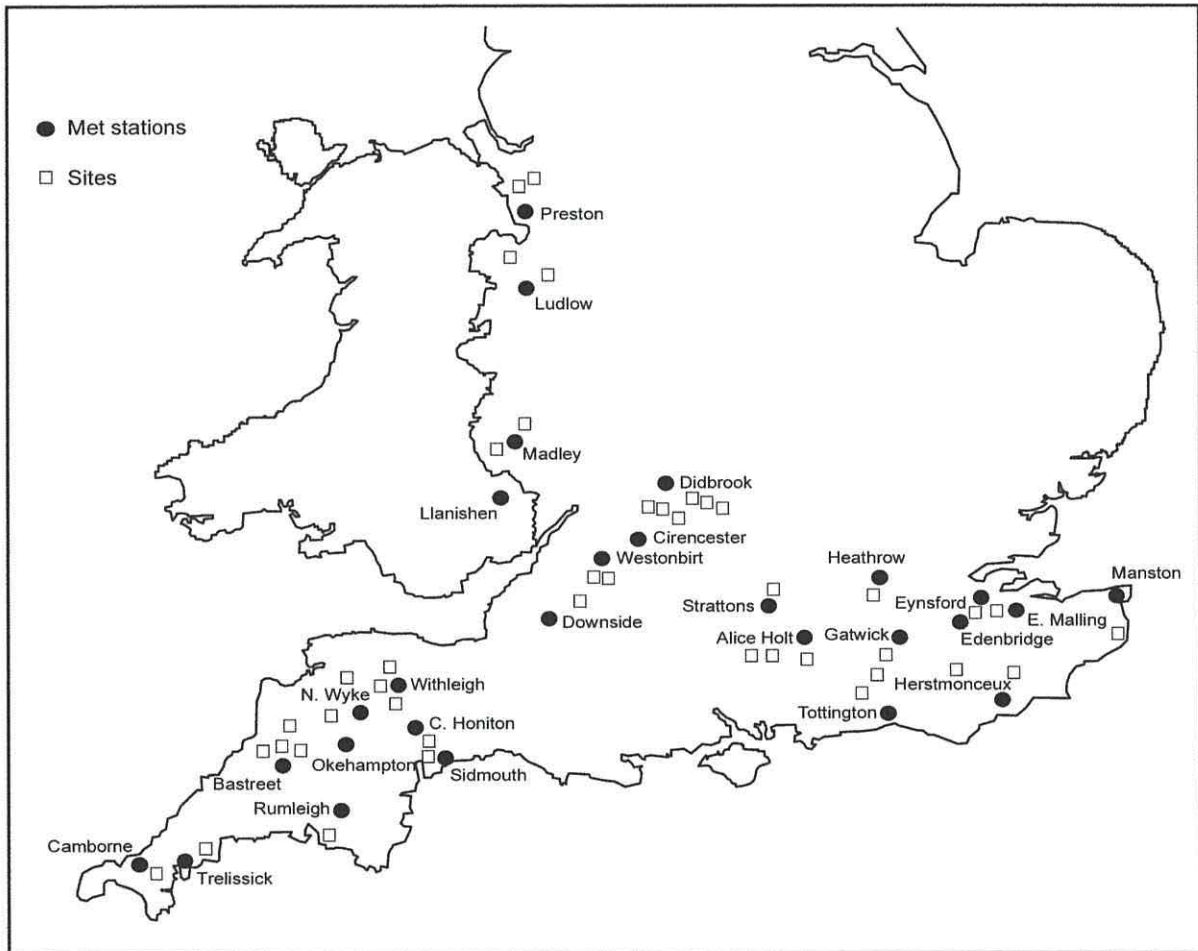
The square of the distance was used to give a large weight to data from MSs close to a site when there were two or more within the search radius.   For example, minimum air temperature on 1 April 1996 from the site 'Gattertop' was calculated using data from the two MSs within 25 km of the site, as shown below.

MS	Distance (d) in km	$1/d^2$	T_{min}
Madley	16.16	0.00383	1.0 °C
Ludlow	20.86	0.00230	-3.2 °C

$$Mean \ \ T_{min} = \frac{(0.00383 \times 1.0) + (0.00230 \times -3.2)}{0.00383 + 0.00230} = -0.6 \ ^\circ C$$

Each mean was adjusted for altitude using an adiabatic lapse rate of 5 °C km^{-1} (Grace, 1983). The result produced daily minimum air temperatures for the period April to June for each of the years 1993 to 1996 for each of the 42 sites. In addition, a frostiness factor for each year from 1993 to 1996 was calculated as the mean number of days with a minimum temperature of –2 °C or lower during the 30 days between 20 April and 19 May for all 42 sites.

4.2.4 Data analysis

4.2.4.1   Meteorological data

The minimum adjusted air temperatures for each survey site between 1 April and 30 June, for the years 1993 to 1996, were plotted to give an overall picture of air temperatures in southern England.

4.2.4.2   Forking

The percentage of trees which forked in each year between 1991 and 1996 was calculated for all sites and, in addition, the proportion of forked trees was calculated for each site in each year.

4.2.4.3   Relationship between meteorological data and forking

Initial investigation of the data involved plotting: (i) the location of each site showing the proportion of trees forked in that year and (ii) the proportion of trees forked against the number of days with minimum temperatures less than thresholds of -3 °C, -2 °C, -1 °C,

0 °C , 1 °C and 2 °C for April, May and June of each year. Using this information, and the fact that ash usually breaks bud in May, it was decided to target May in further analysis.

Analysis of data attempted to explain the proportion of forked trees by fitting a general linear model with a binomial error distribution and a logit link function. The explanatory variables in the models were: (i) the number of days in May with minimum temperatures less than or equal to 2°C or (ii) the number of occasions when two consecutive days in May had minimum temperatures of less than or equal to 2°C, in each case followed by tree age and the interaction of the two main terms. The general form of the model used was:

$$y_i = \alpha + \beta x_{1i} + \delta x_{2i} + \gamma x_{1i} x_{2i} + \varepsilon_i \qquad [4.3]$$

where y = proportion of trees forked; x_1 = (i) or (ii) as described above; x_2 = tree age; α, β, δ and γ are model parameters and ε = errors.

In the analyses it was noted that the residual mean deviancies were much greater than 1.0, the value expected if the residuals were binomially distributed. This means that differences between sites were greater than that expected from random variation. Because of this, tests (such as χ^2) based on changes in deviance, were inappropriate and therefore the final analyses calculated probabilities using an approximate F-test.

4.2.4.4   Relationship between tree height and forking

Since there were differences in the overall number of forked trees at each site, data from each site were analysed separately. The number of times a tree forked was expressed as a proportion of the number of years for which forking was assessed. This proportion was then used as the response variable in a general linear model (with a binomial error distribution and a logit link function) with individual tree height as the explanatory variable; the model was:

$$y_i = \alpha + \beta x_{1i} + \varepsilon_i \qquad [4.4]$$

where y = the number of times a tree forked / number of years assessed, x_1 = individual tree height, α and β are model parameters and ε = errors.

The test of significance of terms in the model was to compare the deviance with values of χ^2; with one degree of freedom, deviance had to be greater than 3.84 to be significant at $P \leq 0.05$.

4.2.4.5   Relationship between site factors and forking

After initial investigation, it was decided that only four of the site factors were considered to be represented in the data in such a way that they were amenable to further analysis (marked with an asterisk in section 4.2.1.2). To consider interactions between factors, at least one of the 42 sites would have to represent each level of each of the site factors, i.e. $2^4 = 16$. Because the sites were randomly sampled no such distribution was apparent and therefore interactions could not be analysed.

For each year the data were combined over all sites (>4000 trees) and the proportion of forked trees at each level of individual site factors was used as the response variable in a general linear model.   The general form of the model used was:

$$y_i = \alpha + \beta x_{1i} + \varepsilon_i$$

[4.5]

where y = the proportion of trees forked, x = the site factor, α and β are model parameters and ε = errors.

The test of significance of terms in the model was to compare the change in deviance with values in χ^2; with one degree of freedom, deviance had to be greater than 3.84 to be significant at $P<0.05$.

4.2.4.6   Bud data

The diameters of buds which contained larvae were compared with the diameters of buds which did not contain larvae using a two-tail Student's t-test assuming unequal variances.

4.3 Results

4.3.1 Meteorological data

In 1995 and 1996 there were prolonged periods in May when temperatures were below freezing; a short period of very cold temperatures also occurred in late April 1995 (Figures 4.2–4.5). In contrast, in 1994 most cold weather occurred before the end of April with few instances of freezing temperatures in May. In 1993 the weather was generally milder with one cold period in early May. Thus the frostiness factor for 1995 and 1996 was higher than for 1993 and 1994, and the period mid-April to mid-May had more frosts in 1995 and 1996 (Table 4.2). Data for 1991 and 1992 were only from two and seven MSs respectively and were not considered.

Table 4.2 Frostiness and variation in forking for the years 1991 to 1996

Year	Frostiness factor[1]	No. sites	No. trees	Trees forked		Incidence of forking per site (%)[2]	
				No.	%	Min.	Max.
1991	-	2	200	30	15.0	9	21
1992	-	11	641	80	12.4	0	30
1993	0.04	26	1969	337	17.1	0	47
1994	0.00	38	3595	764	21.3	0	49
1995	1.29	42	4135	1774	42.9	5	84
1996	0.60	42	4147	1434	34.6	4	84

[1] Defined as the mean number of days with minimum temperatures less than -2°C during the 30 days between 20 April and 19 May for all sites.
[2] Excludes sites where there were ≤ 20 trees.

4.3.2 Forking

The percentage of all trees which were forked varied between 12.4% in 1992 and 42.9% in 1995 (Table 4.2). It is apparent that the percentage of trees which forked in 1995 and 1996 was much higher than in the preceding four years. This increase was also reflected in the range of forking per site which increased from 12% in 1991 to 80% in 1996 (Table 4.2). It is also noticeable that in most years there were sites with little, or no, forking. A large percentage (69%) of trees examined had at least one fork and many (29%) had more than one fork (Table 4.3, page 120).

Figure 4.2 Minimum adjusted temperatures for each survey site from April 1 to June 30 1993

1993 Site Min Temps

Days from 1st April
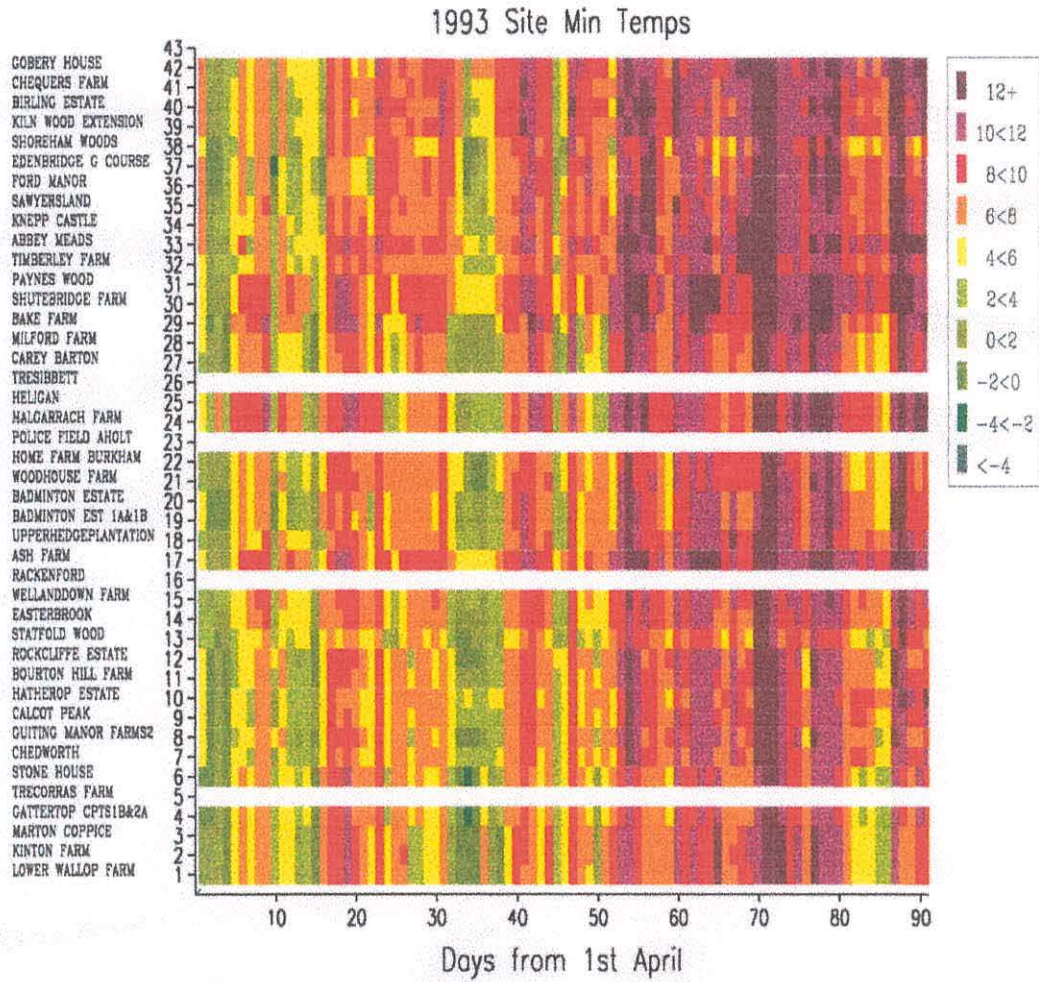
Figure 4.3 Minimum adjusted temperatures for each survey site from April 1 to June 30 1994

1994 Site Min Temps

Days from 1st April
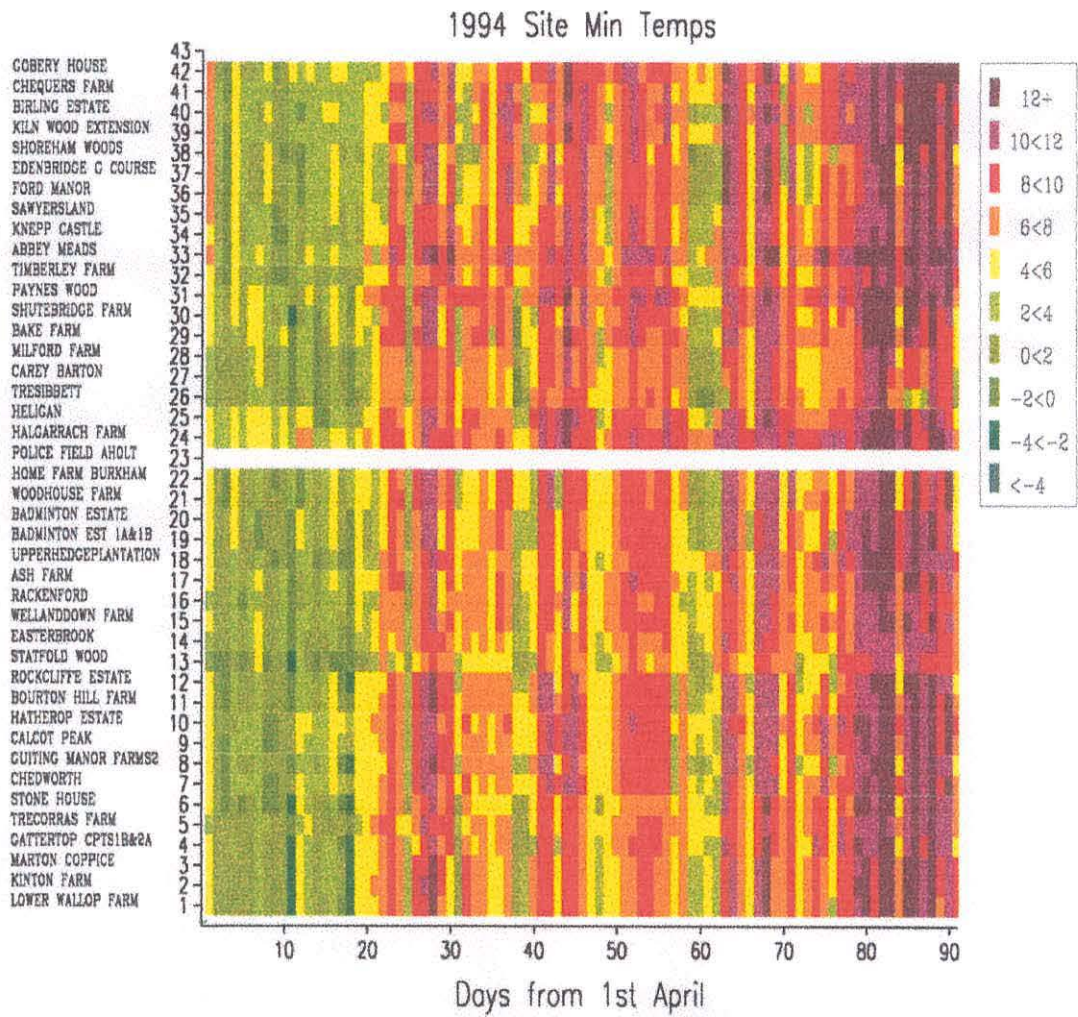
Figure 4.4 Minimum adjusted temperatures for each survey site from April 1 to June 30 1995

1995 Site Min Temps

Days from 1st April
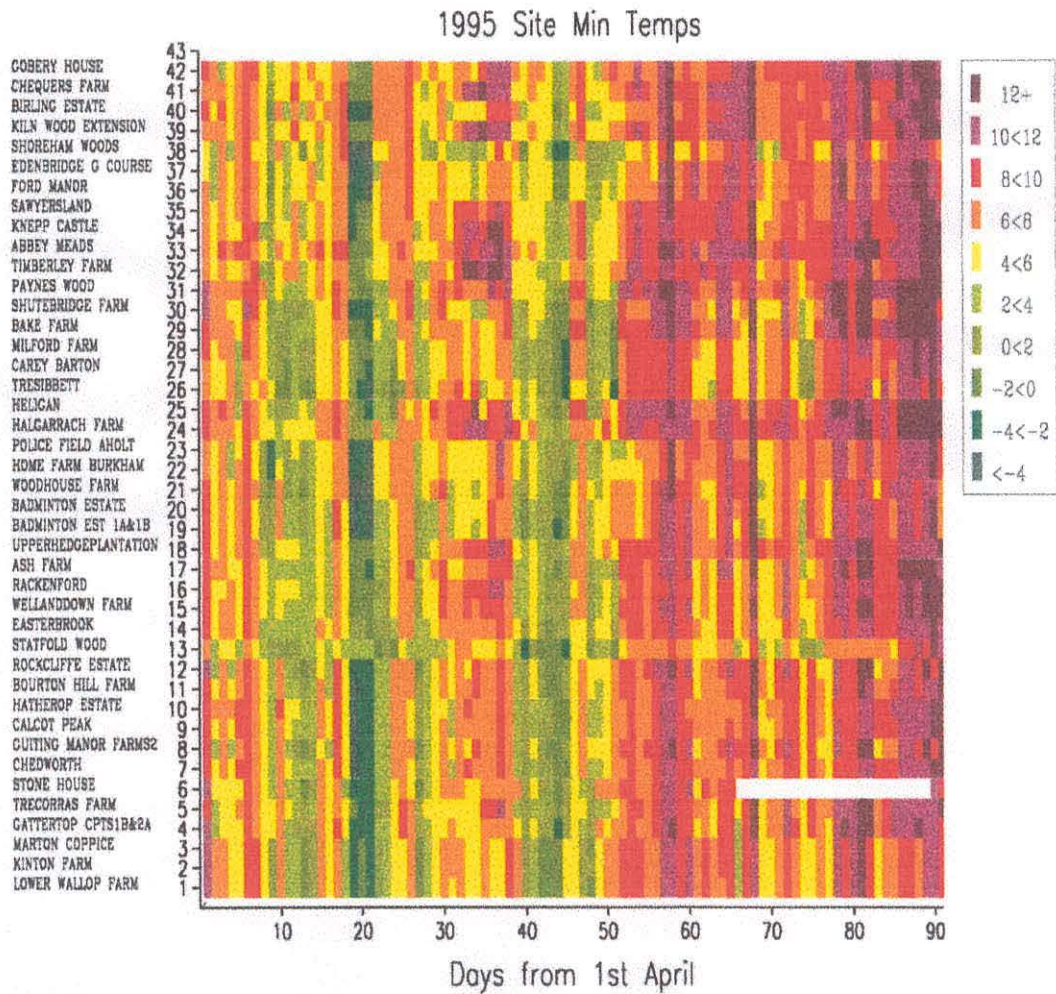
Figure 4.5 Minimum adjusted temperatures for each survey site from April 1 to June 30 1996

1996 Site Min Temps

Days from 1st April
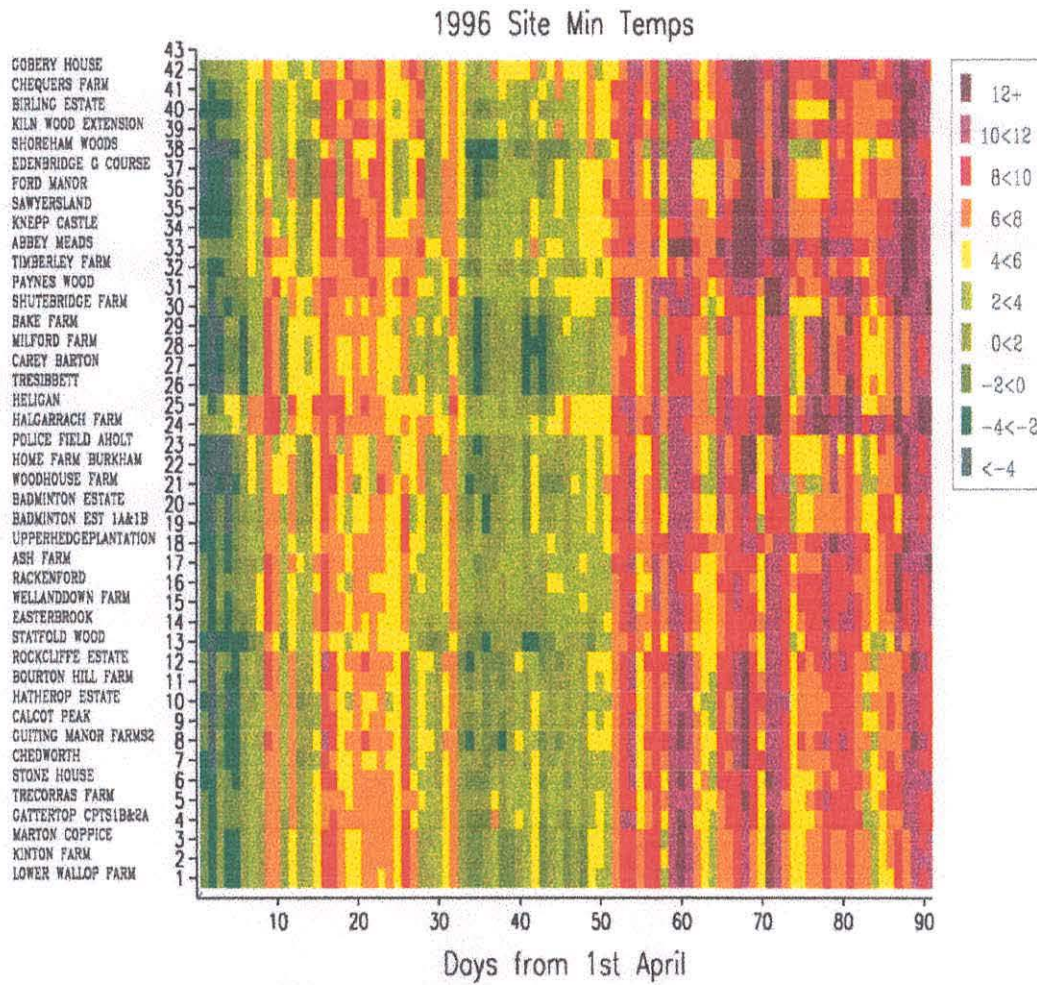
Table 4.3 Occurrence of multiple forks (combined data for all trees)

	Number of forks per tree						Total
	0	1	2	3	4	5	
No. trees	1271	1664	922	246	41	3	4147
%	31	40	22	6	1	0.07	100

4.3.3 Air temperature and forking

Figures 4.6–4.9 (pages 123-126) show that the percentage of forked trees varied between years and also that there were often large differences in the percentage of forked trees between sites in the same region. For example, in 1995 forking at a cluster of six sites in the Midlands varied from 20%–30% to 90%+ (Figure 4.8) and in 1996 forking in a group of 11 sites in south west England varied between 10%-20% and 70%-80% (Figure 4.9). The interpolated temperatures for each site were based on records from one, two or more MSs located at distances between 0 and 25 km from the site. Calculations for nearby sites were likely to have used data from the same MSs so that interpolated values would have been very similar, varying only because of the weighting factor ($1/d^2$) and altitude.

Scatter plots showing the proportion of trees forked in relation to the number of days with minimum temperatures less than 2°C for one day (Figure 4.10, page 127) or two or more consecutive days (Figure 4.11, page 128) indicated that the relationship in May was weak. Analysis of these data showed no significant relationship between May temperature, tree age or the interaction of the two terms, and the proportion of forked trees.

4.3.4 Tree height and forking

Forty two analyses (one per site) were carried out and three have been selected to show the different forms of relationships found. In each case the relationship between forking (number of forks / number of years assessed) and tree height is shown. For 27 of the 42 sites no relationship was found between forking and tree height, as exemplified by results from site 2 (Figure 4.12a, page 129). The plots show the data in 'n' distinct bands (where n = number of years assessed); however, at site 2 not all trees were assessed for the same period, usually because it was not possible to trace internodes back, when a treeshelter blocked the view of the stem. This caused some 'intermediate' horizontal bands to form between the four main ones (Figure 4.12a). At only one site, site 5, was a significant ($P \leq 0.01$) positive relationship between tree height and number of forks found (Figure 4.12b). At the remaining 14 sites a significant negative relationship (four at

$P\leq0.05$, six at $P\leq0.01$ and five at $P\leq0.001$) was found between tree height and number of forks: i.e. smaller trees tended to have more forks, as exemplified by data from site 6 (Figure 4.12c)

4.3.5 Site factors and forking

The site factors included in the analysis were: restocking or new planting; main vegetation type; weeding and the anticipated frostiness of the site. The only significant relationships were between the anticipated frostiness for each site and the proportion of trees forked in the four years 1993 to 1996 (Table 4.4). For each year the results were significant ($P\leq0.001$) although the amount of variation accounted for by the model was fairly low (between 6.6% and 38.1%).

Table 4.4 Model predictions of percentage forking from a general linear model with anticipated frostiness score as an explanatory variable

Anticipated frostiness	No. of sites	Percentage of forked trees[1]			
		1993	1994	1995	1996
Frost hollow	4	22 (2.3)	30 (2.3)	68 (2.3)	39 (2.4)
Flat land	14	29 (1.8)	24 (1.3)	52 (1.3)	41 (1.3)
Gentle slope	13	13 (1.5)	17 (1.1)	34 (1.3)	29 (1.3)
Steep slope	11	4 (0.8)	20 (1.2)	34 (1.4)	31(1.4)
Deviance (df=1)		154.3 [38.1%]	36.5 [6.6%]	231.1 [26.2%]	54.1 [6.8%]
Res. deviance(df=40)		251.0	517.8	649.6	736.8
Tot. deviance(df=41)		405.3	554.3	880.7	790.9
Approximate χ^2 probability		≤0.001	≤0.001	≤0.001	≤0.001

[1] Figures in ( ) are standard errors.

4.3.6 Bud dissections

The proportions of buds containing an ash bud moth or having external signs of damage were very low (Table 4.5); in addition, there was little year-to-year variation in the amounts of damage. No other lepidoptera were found during the bud dissections. Buds which contained a larva were significantly larger than buds where no larva was present (Table

4.6). The mean diameter of the 4106 buds was 4.7 mm ($\sigma = \pm 1.6$ mm); assuming a normal distribution this would mean that approximately 84% of buds were above the minimum diameter for bud exploitation (2–3 mm) determined by Foggo (1992). There was no significant difference between the diameter of buds which showed signs of attack but did not contain a larva, and those buds where no signs of attack were apparent (Table 4.6).

Table 4.5 Results of bud dissections

Year	No. of buds dissected	Dead Buds		Signs of attack by moth: no larva present		Buds containing a larva	
		No.	%	No.	%	No.	%
1997	4106	44 (5)[1]	1.1	6 (2)	0.14	10 (4)	0.24
1997[2]	498	10 (5)	2.0	2 (2)	0.40	0 (0)	0
1998	500	21 (8)	4.2	14 (5)	2.8	1 (1)	0.2
1999	500	6 (2)	1.2	7 (4)	1.4	0 (0)	0

[1] Figures in ( ) show the maximum number per site.
[2] Subset of the 4106 buds for comparison with 1998 and 1999 data

Table 4.6 Comparison of bud size data for 1997-1999

	1997			1998			1999		
	No.	Mean diam. (mm)	Prob.	No.	Mean diam. (mm)	Prob.	No.	Mean diam. (mm)	Prob.
Larva present in bud	10	6.9 ($\pm$1.9)	0.003	1	6.4	-	0	-	-
No larva present in bud	4096	4.7 ($\pm$1.6)		499	5.9 ($\pm$1.5)		500	5.72 ($\pm$1.5)	
Signs of attack: no larva present	6	6.0 ($\pm$2.5)	0.284	14	5.7 ($\pm$2.0)	0.767	7	5.4 ($\pm$0.6)	0.164
No signs of attack	4090	4.7 ($\pm$1.6)		485	5.9 ($\pm$1.5)		493	5.7 ($\pm$1.5)	

Figures in ( ) are standard deviations.
Comparisons were using a two-tail Student's *t*- test assuming unequal

Figure 4.6 Proportion of forked trees at survey sites in 1993

ASH SURVEY

Proportion forking 1993

	0.9+
	0.8<0.9
	0.7<0.8
	0.6<0.7
	0.5<0.6
	0.4<0.5
	0.3<0.4
	0.2<0.3
	0.1<0.2
	<0.1
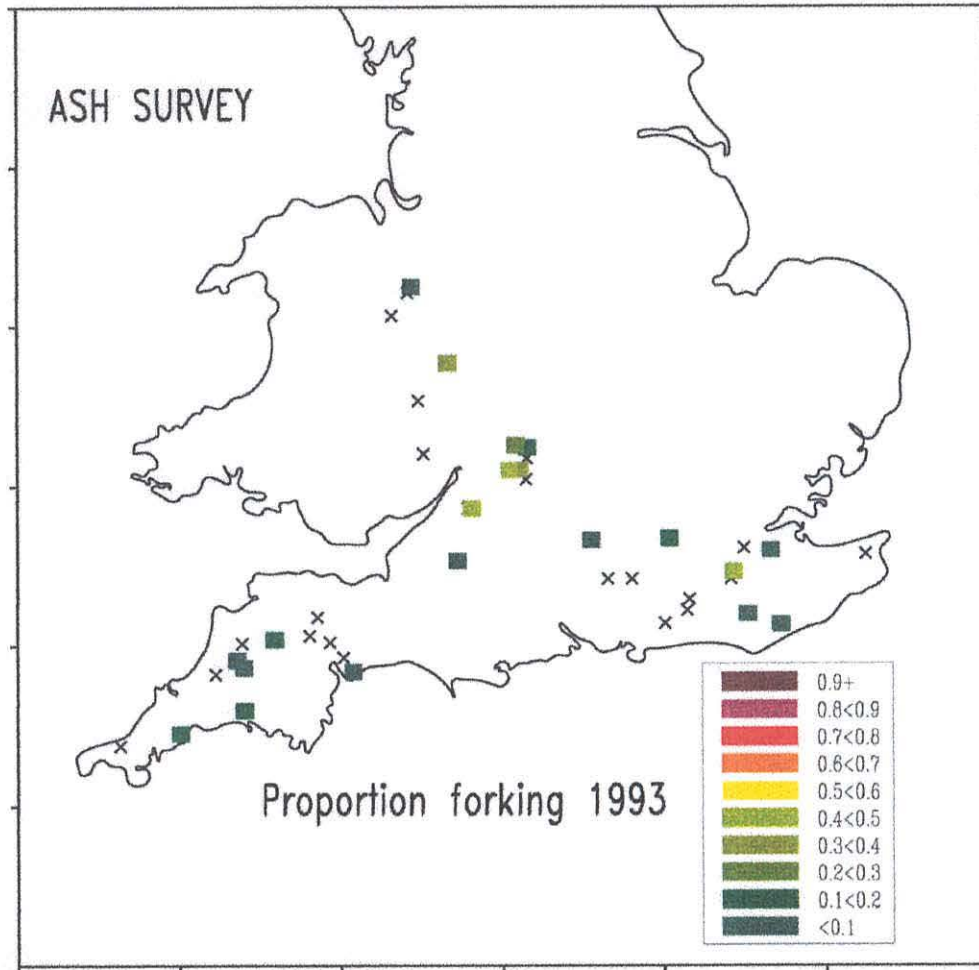
Figure 4.7 Proportion of forked trees at survey sites in 1994

124
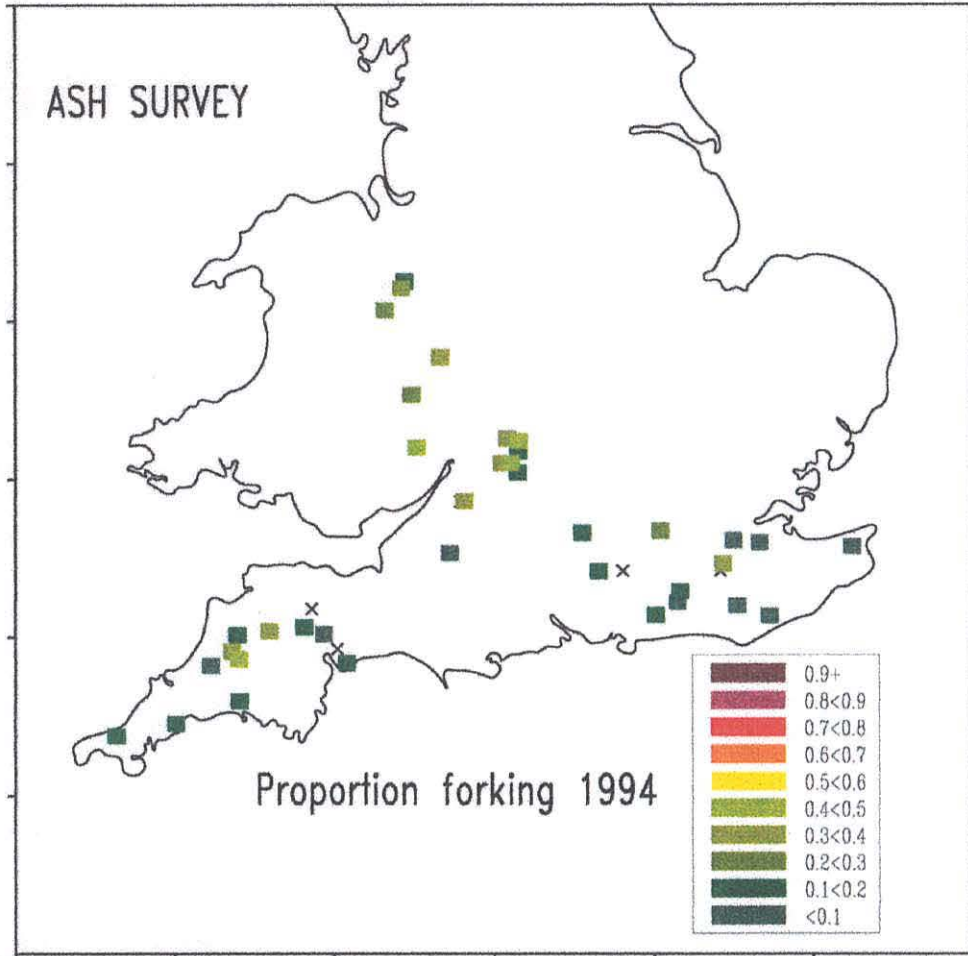
Figure 4.8 Proportion of forked trees at survey sites in 1995
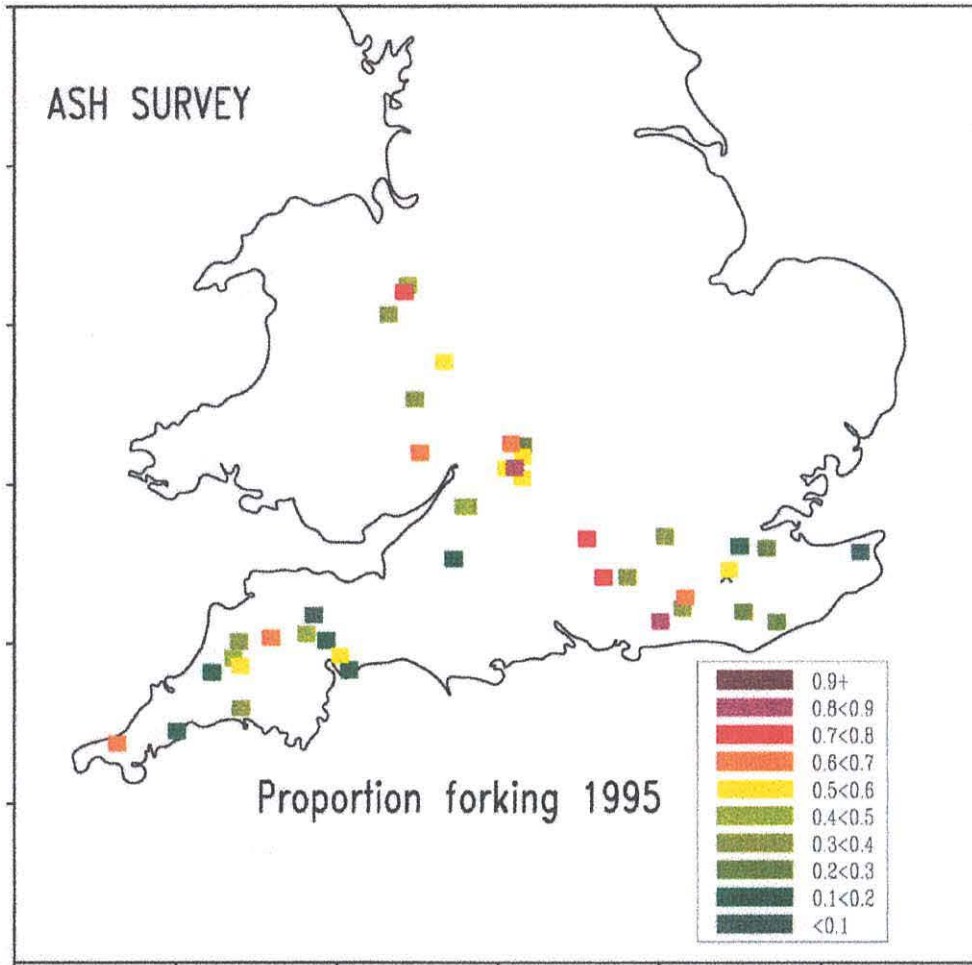
Figure 4.9 Proportion of forked trees at survey sites in 1996

ASH SURVEY

Proportion forking 1996

	0.9+
	0.8<0.9
	0.7<0.8
	0.6<0.7
	0.5<0.6
	0.4<0.5
	0.3<0.4
	0.2<0.3
	0.1<0.2
	<0.1
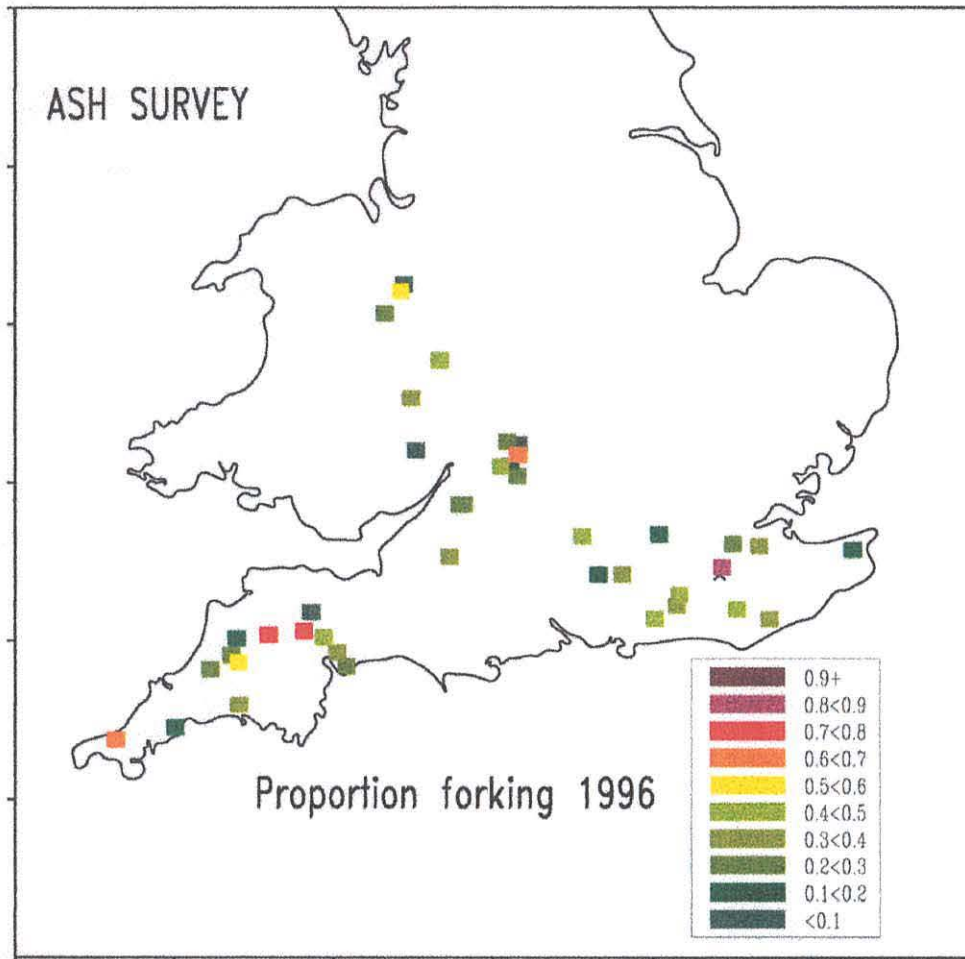
Figure 4.10 Relationship between proportion of trees forked and number of days in May with adjusted minimum air temperature below 2 °C
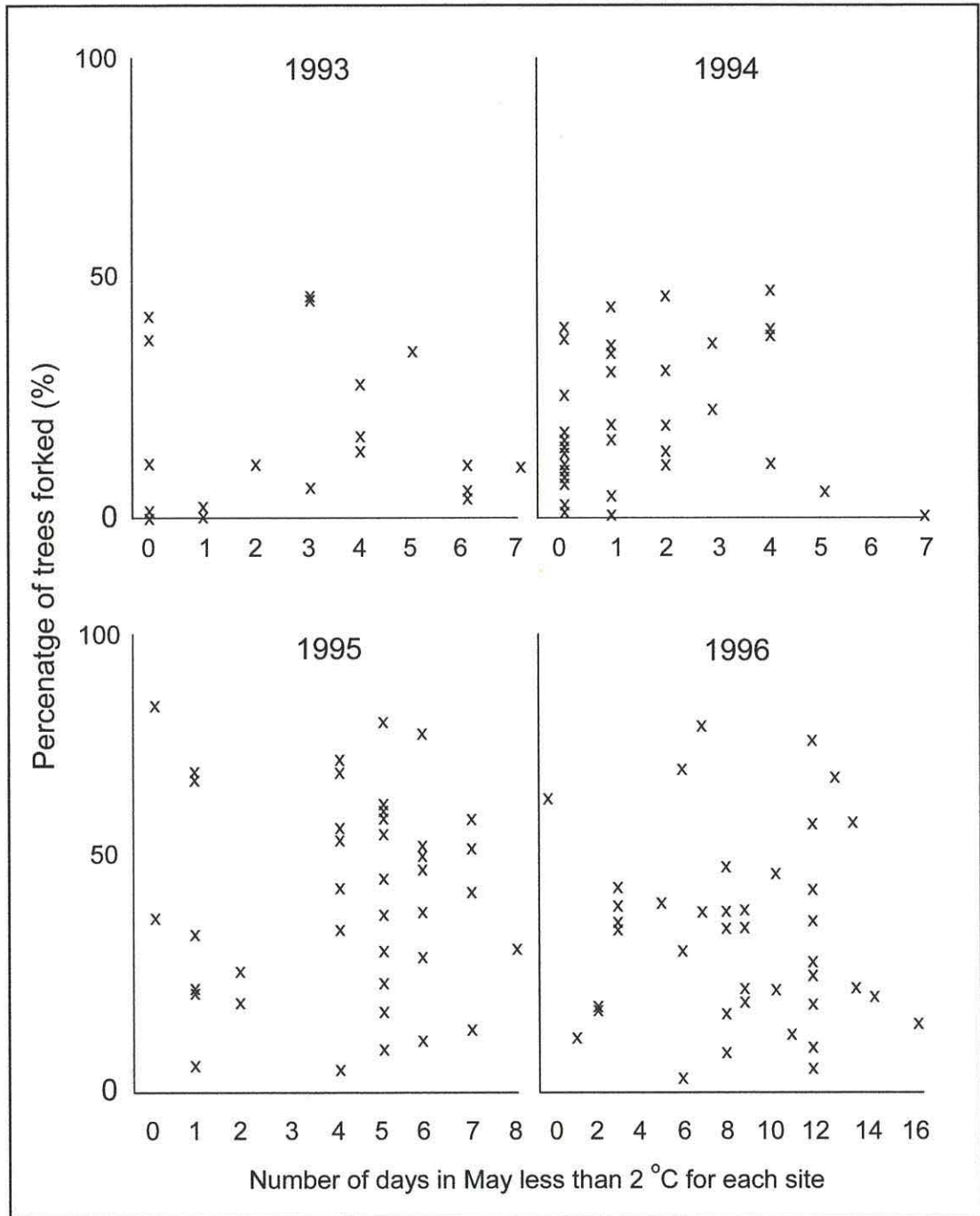
Figure 4.11   Relationship between proportion of forked trees and number of occasions with two consecutive days in May with adjusted minimum air temperature below 2 $^{\circ}$C
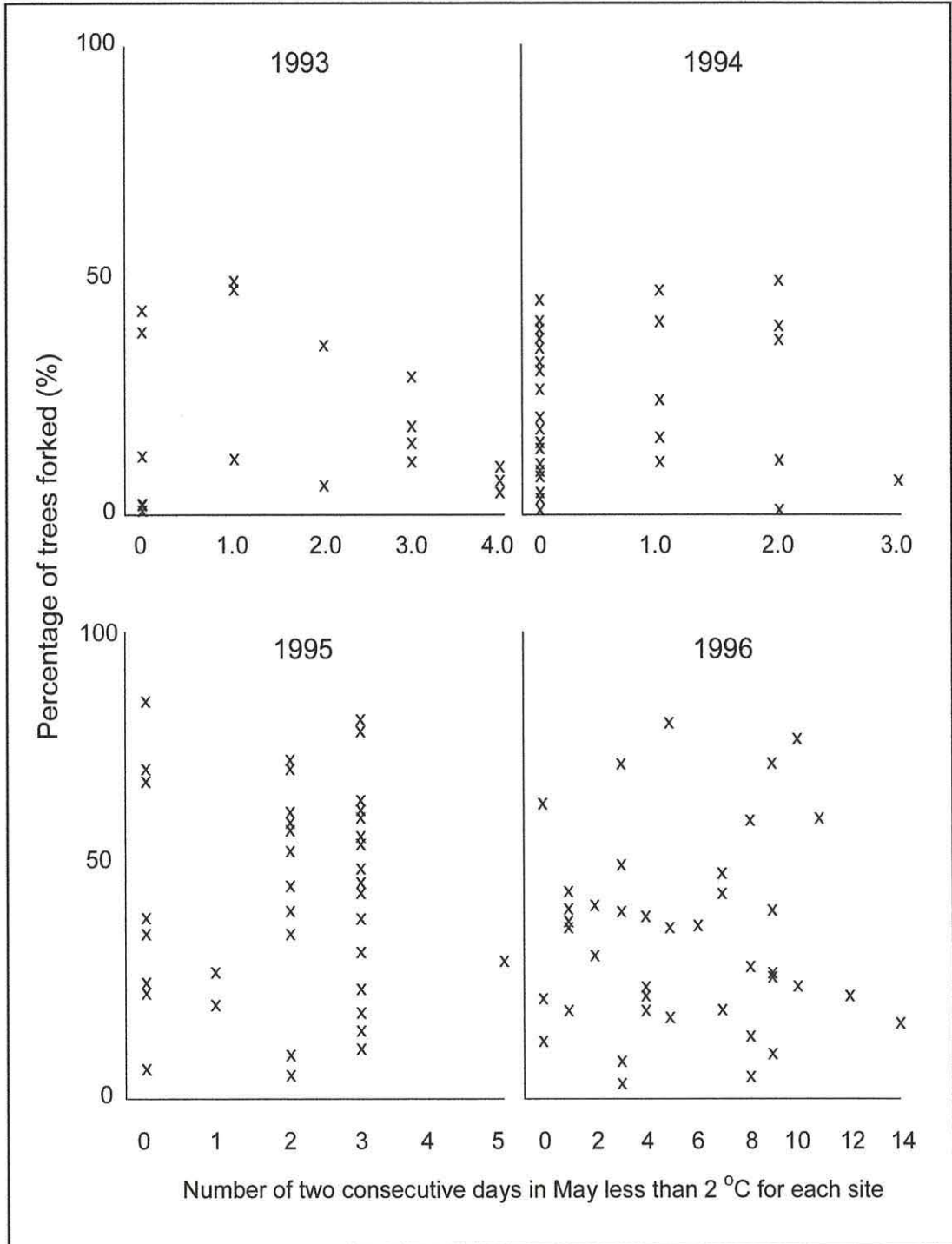
Figure 4.12   Relationships between tree height and forking at (a) site 2, (b) site 5 and (c) site 6
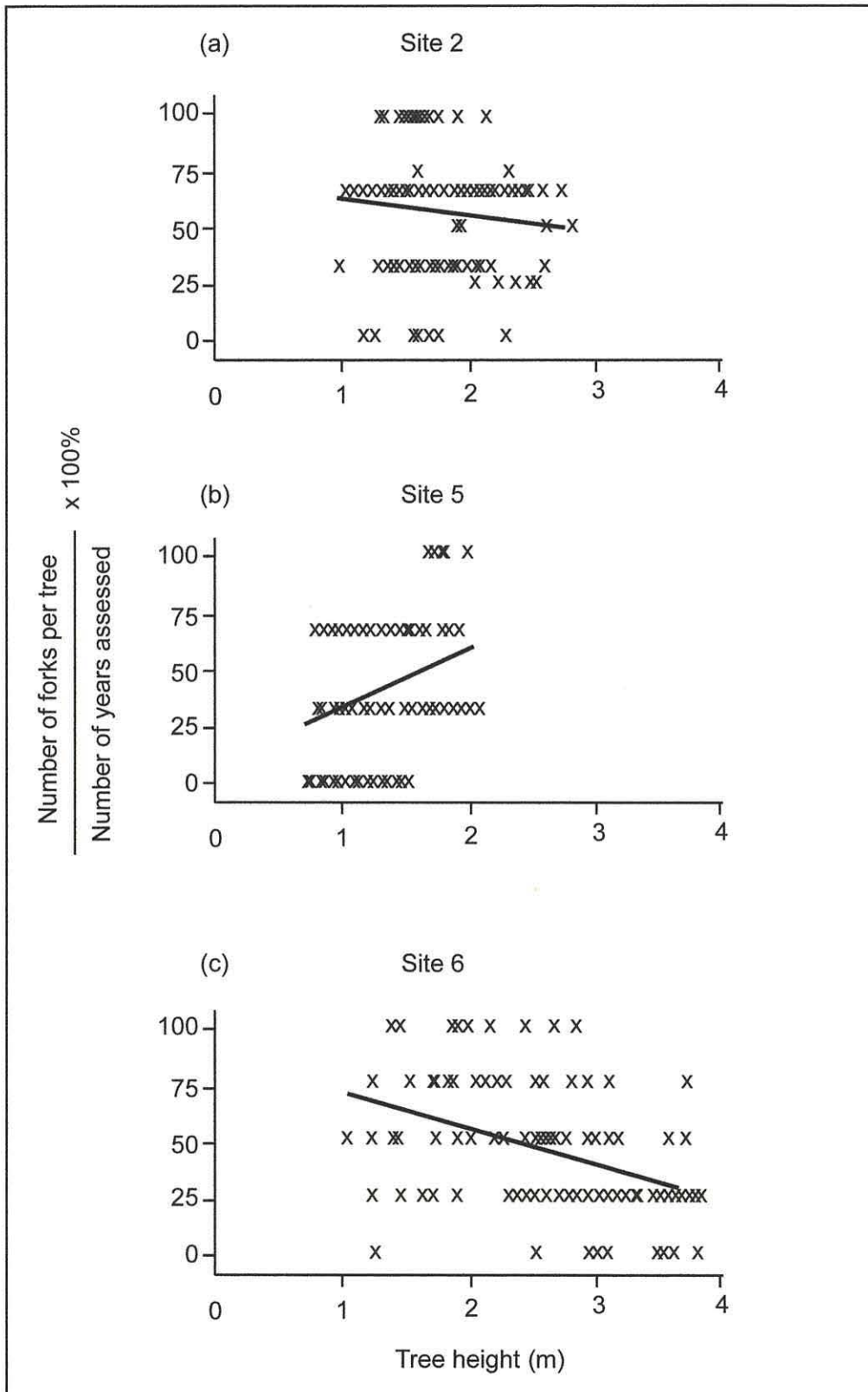
4.4 Discussion

The results of the survey confirm that forking is a major cause of stem defect in young ash trees; 69% of trees in the survey had forked and on some sites the figure was 84%. These figures are close to the 70% reported by Ningre *et al.* (1992), although their data were from a single site 13 years after planting. The results also showed that at 33% of sites trees which were forked tended to be shorter than unforked trees, although a causal relationship between forking and tree height was not demonstrated. This phenomenon has been studied by Foggo (1996a), who artificially removed terminal buds of young ash trees and found that damaged saplings produced shorter shoots and became increasingly forked. However, it is also likely that smaller trees are at greater risk because damaging frosts are more frequent near the ground.

The proportion of trees which forked in 1995 and 1996 was higher than in the preceding four years. One possible explanation is that the springs of 1995 and 1996 had many instances of freezing air temperatures whereas the same period in the years before were much milder. The frostiness factor for each year supports this contention. However, at the site level, there was little evidence of a direct link between adjusted minimum air temperature and forking. There are a number of possible explanations for this: (i) the link between frosts and forking is weaker than commonly perceived and other factors such as genotype, which were not assessed, are more important; (ii) forking is mainly caused by frosts but the air temperature data were collected too remotely and did not accurately reflect actual on-site temperatures.

If the hypothesis that frosts are not a major cause of forking is accepted then other factors must be responsible. This is a possibility; little is known about the genetic control of forking and the young shoots of ash are very tender and susceptible to damage from birds, wind and other agents which could cause leader breakage. Another factor not considered is terminal bud abortion, which has been reported for mature green ash (Remphrey and Davidson, 1992) and was implicated in the development of different shape classes of trees (Remphrey and Davidson, 1994a and b). However, there is little evidence of this occurring in ash. On the other hand, evidence from other sources indicates a strong link between air temperature and forking (Day and Peace, 1946; Wardle, 1961).

The most likely explanation is that the air temperature data were collected too remotely and did not accurately reflect on-site temperatures. Two adjustments were made to the data in an attempt to make them more site specific: interpolation between MSs and application of a correction for altitude. However, with data from 27 MSs and 42 field sites,

it was inevitable that some MSs would be shared amongst sites, particularly where sites were close. There is good evidence to support the supposition that much variation in the adiabatic lapse rate can be introduced by topography, largely as a result of the influence of aspect and slope on the local energy balance (Day and Peace, 1946). Similar problems have been reported by Wörlen *et al.* (1999), who demonstrated the difficulties of interpolating temperature data for complex terrain in Germany. The anticipated frostiness score (Table 4.4) was an attempt to describe how the local topography could influence temperature, and it is interesting that it showed a better relationship with the proportion of forked trees than the adjusted air temperature data.

In conclusion, it is highly likely that frosts were the main cause of forking but this has been impossible to demonstrate because the air temperature data used here may not have reflected on-site temperatures during the period when ash was flushing. However, the data were the best available at the time of carrying out the study. In a future study it would be advisable to monitor meteorological variables on site.

This is not the first time that a weak link between air temperature and winter injury of trees has been reported. Steiner *et al.* (1988) describe a provenance test of green ash at 10 sites in the central and eastern states of the USA and observed some interesting variations in winter injury. They found no obvious relationship between winter injury and geographic location of the trials; in fact sites with high and low levels of injury were situated close to each other in Michigan. One provenance from Arkansas (700 km to the south) sustained no injury at either of the two Michigan sites, but 98–100% injury on the other four sites in other states where it was represented. The winters involved were not mild, and the authors state that two of the latter four sites had winter minimum temperatures within $2^{\circ}C$ of those of the Michigan sites. The source of the temperature data was not clear but if collected remotely then the investigation probably suffered the same problems as the present study.

There are two main types of damage caused by cold temperatures in the winter and spring. The first is caused when the tree is dormant and air temperature is lower than the tree's cold hardiness mechanisms allow it to tolerate. This type of damage is often called winter injury, as in Steiner *et al.* (1988) and Goldsmith and Boldreau (1979), but has not been widely reported for ash. The seasonal variation in cold hardiness of manna ash (*Fraxinus ornus* L.) has been studied by Mair (1968; quoted in Etherington, 1982) who showed that the apical bud tolerated -27 °C in mid-winter rising to -3 °C as the buds began to swell in spring. During the same period the temperature tolerated by the vascular cambium in 2-year-old wood increased from -39 °C to -5 °C. The second type of damage

is caused by unseasonal frosts before the tree has become dormant or after it has flushed in the spring. This is the type of damage often reported for ash: for example, Wardle (1961) showed that newly emerging ash foliage can be killed by temperatures of -3 °C . In addition, Day and Peace (1946) observed, from the effects of the severe May frost of 1935, that the leading shoot of ash flushes at approximately the same time as the side shoots and that both are therefore vulnerable to damage. However, the actual damage caused to ash is a balance between time of flushing and the occurrence of freezing temperatures.

Kramer (1994) investigated the effects of climatic warming on the probability of spring frost damage in The Netherlands and Germany. Of interest here are his data showing that for the period 1951–1990 the average date of leaf unfolding for ash was 7 May ($\pm$8.7 days) and the probability of a sub-zero temperature around the date of leaf unfolding was 0.18. This probability is low compared with the values for other broadleaved species such as silver birch (0.43), beech (0.37) and oak (0.27). These data suggest that the probability of damage is greater in birch, beech and oak but is possibly more noticeable in ash because it often results in forking.

The results of the survey showed that for buds collected in March 1997 damage from ash bud moth was very small. Bud size was not thought to be an important factor influence on levels of damage because a very large proportion of buds were above the minimum size for exploitation. Results from the re-sampling of five sites in early 1998 and 1999 did not reveal any large fluctuations in populations of the moth. The small number of buds which contained larvae were larger than those which did not, which supports the findings of Foggo and Speight (1995) that the preference for buds selected by ash bud moth is strongly affected by size. Interestingly, buds which showed signs of attack, but did not contain a larva, were generally the same size as the rest of the sample. This may indicate that these smaller buds had been rejected due to interactions between bud size, scale thickness and food availability (Foggo and Speight, 1995).

Some care in the interpretation of the results is necessary as insect populations are notoriously variable between years and places, and it could be argued that ash bud moth numbers might have been higher before 1996. In addition, it could also be claimed that the data are not an adequate reflection of the numbers of moth larvae likely to have been in the terminal buds of the leading shoot. Some insects are known preferentially to attack certain parts of trees: for example, pine shoot moth (*Rhyacionia buoliana* Denis and Schiffermüller) preferentially attacks the leading shoot of pine trees. However, we know from the work of Foggo and Speight (1995) that the main factor involved in ash bud moth

132

attack is bud size rather than location and that larval densities in adjacent buds are a good guide to densities in the terminal bud.

Work by Foggo (1996b) showed that 25% of all buds on a sample of 100 saplings had been attacked by ash bud moth and that of these 71% were dead. Foggo's study was carried out in a mature ash woodland in Oxfordshire, very different conditions to those of the present study which considered newly planted sites. It is a strong possibility that as newly planted trees develop into a stand, there are increases in the population of ash bud moth and in damage to buds of ash trees. However, the results from this study indicate, contrary to the suggestions of Foggo (1996b), that ash bud moth is unlikely to be a serious cause of forking of newly planted ash trees in southern Britain.

Chapter 5

Concluding discussion

The common thread in this thesis is the objective study of factors affecting the early growth of ash, and the implications of findings for silvicultural practice in southern Britain. The motivations for carrying out the work were (i) the paucity of work published on the subject, and (ii) a desire for a more objective framework on which to base silvicultural guidance. Evans (1984) is an admirable compilation of knowledge on the subject of broadleaved silviculture in Britain, but one has only to scan the reference list to confirm the limited amount of scientific research carried out on broadleaves. This observation reflects the fact that, in terms of the development of forestry policy and support for forest research, broadleaved species were a minor consideration until the early 1980s. However, on a broader global scale there has also been only a small amount of work carried out on the silviculture of the genus *Fraxinus*. To demonstrate this the bibliographic search facility TREECD (1939–2001) was searched for references relating to the main themes of this thesis; the results are shown in Table 5.1.

Table 5.1 References located in TREECD searches of key words

Details of TREECD search	Numbers of references	Number directly related to silviculture of *Fraxinus*
Fraxinus in title or abstract[#1]	6167	n/a
#1 and 'spacing' in title	6	5
#1 and 'density' in title	35	12
#1 and 'mixture' in title	0	0
#1 and 'forking' in title	1	1
#1 and *Prays'* in title	5	5
#1 and 'site' in title	91	63

The results of these searches confirm the paucity of scientific literature on the subject of the silviculture of *Fraxinus*. The scarce information that exists is heavily skewed towards examination of the site requirements of the genus, mainly from an ecological point of view.

As a result of work reported in this thesis, knowledge of ash silviculture has been advanced in the following ways.

1. It has been shown that the relationship between initial spacing and growth of ash is different from that expected from consideration of the general relationships established between density and plant growth; i.e. growth at close spacing is better than at wider

spacing in the range 10 000 trees ha^{-1} to 100 trees ha^{-1} and in the absence of intraspecific competition.

2. In response to interspecific competition ash alters stem form to ensure that it maintains a position in the upper canopy of a mixture.

3. Ash in mixture with other broadleaved tree species is likely to be more productive than in equivalent areas of the pure species.

4. The nursing or 'help to grow' benefit of planting ash in mixture has been demonstrated with ash in mixture with both oak and beech.

5. The level of forking in newly planted ash is high (69% of 4147 trees < 6 years old) and important causes of this are thought to be unseasonal frosts and genotype. However, the influence of ash bud moth on forking is less important and it appears that its capacity for causing damage to planted trees has been overstated in the past.

Landsberg (1986) has proposed a detailed model of tree growth, shown schematically in Figure 5.1, and it is interesting to consider how some of the observed effects described above could be explained using this model (references to terms in the model are in *italics*).

1. The observation of better growth at closer spacing may be the result of (i) constrained growth at wide spacing (ii) improved growth at close spacing, or a combination of (i) and (ii). For example, the process of *energy interception* at wide spacing may result in a high proportion of leaves overheating and closing their stomata for long periods during the day. This affects *water uptake*, *plant water status*, *leaf photosynthetic characteristics* and finally lower *carbohydrate production*, resulting in reduced growth. At close spacing the changes in air temperature, solar radiation, relative humidity, soil moisture and soil temperature, which result from the sheltered environment (Heiligmann and Schneider, 1975), interact to prevent a reduction in *net photosynthesis* and maintain, or even enhance, growth.

2. The stem plasticity which was observed in the mixture experiments is most likely to result from changes in the process of *carbohydrate partitioning*. In the spacing experiment intraspecific competition resulted in significant changes in the shoot:root ratio. However, in the mixture experiment, no destructive sampling took place and the effects of the mixture on total biomass remain unknown, although as the experiments still exist, destructive sampling remains an option for the future. In the ash:cherry there

was no relationship between stem volume and the composition of the mixture. A different mechanism was apparent in the mixtures of ash with oak, and ash with beech, where the stem volume of ash was greater when surrounded by oak or beech. A possible explanation for this is that the level of intraspecific competition was greater than that of interspecific competition for *soil water* and *soil nutrients*, allowing ash trees surrounded by more oak or beech to *partition a greater proportion of their carbohydrate* to the stem rather than the root.

3. From Figure 5.1 it is apparent that the main resources governing the growth of a tree are water, nutrients and radiant energy, the latter mainly in the form of light. The most likely explanation for greater productivity of the mixtures compared with equivalent areas of both pure species, is that the two species exploit resources differentially and therefore more efficiently (Kerr *et al.*, 1992). Different rooting patterns between the species would allow them to exploit soil water and soil nutrients in contrasting ways. In addition, work by Van Miegroet (1970) has shown that the four species used in the mixture study will use different parts of the light spectrum for photosynthesis.

4. There are two possible mechanisms which might explain the nursing or 'help to grow' observations. Firstly, species 1 protects species 2 from negative growth influences such as unseasonal frosts. Work on the influence of shelterwoods on survival and growth of planted seedlings demonstrates the mechanisms involved (e.g. Langvall and Örlander, 2001), and these effects would be similar but on a much smaller scale for the early growth of a mixture. Secondly, the presence of a proportion of species 1 around species 2 improves *leaf photosynthetic characteristics* of species 2 to such an extent that growth is improved. The two examples of the nursing effect described in this thesis occurred in the first year after planting and therefore the second of the two above mechanisms is thought to be the more likely to explain the observed effects.

5. The ability of the model shown in Figure 5.1 to explain tree forking is less obvious. However, the main influence may be plant genotype which exerts some degree of control on many of the processes shown in the figure. An ability or propensity for a tree to fork, although this has a negative effect on the monetary value of the tree, could be a means of improving the tree's competitive position. Forked trees have greater crown volumes and foliage areas, and therefore take up a more competitive position in a canopy.

Figure. 5.1   Schematic representation of a detailed mechanistic model of tree growth (from Landsberg, 1986)
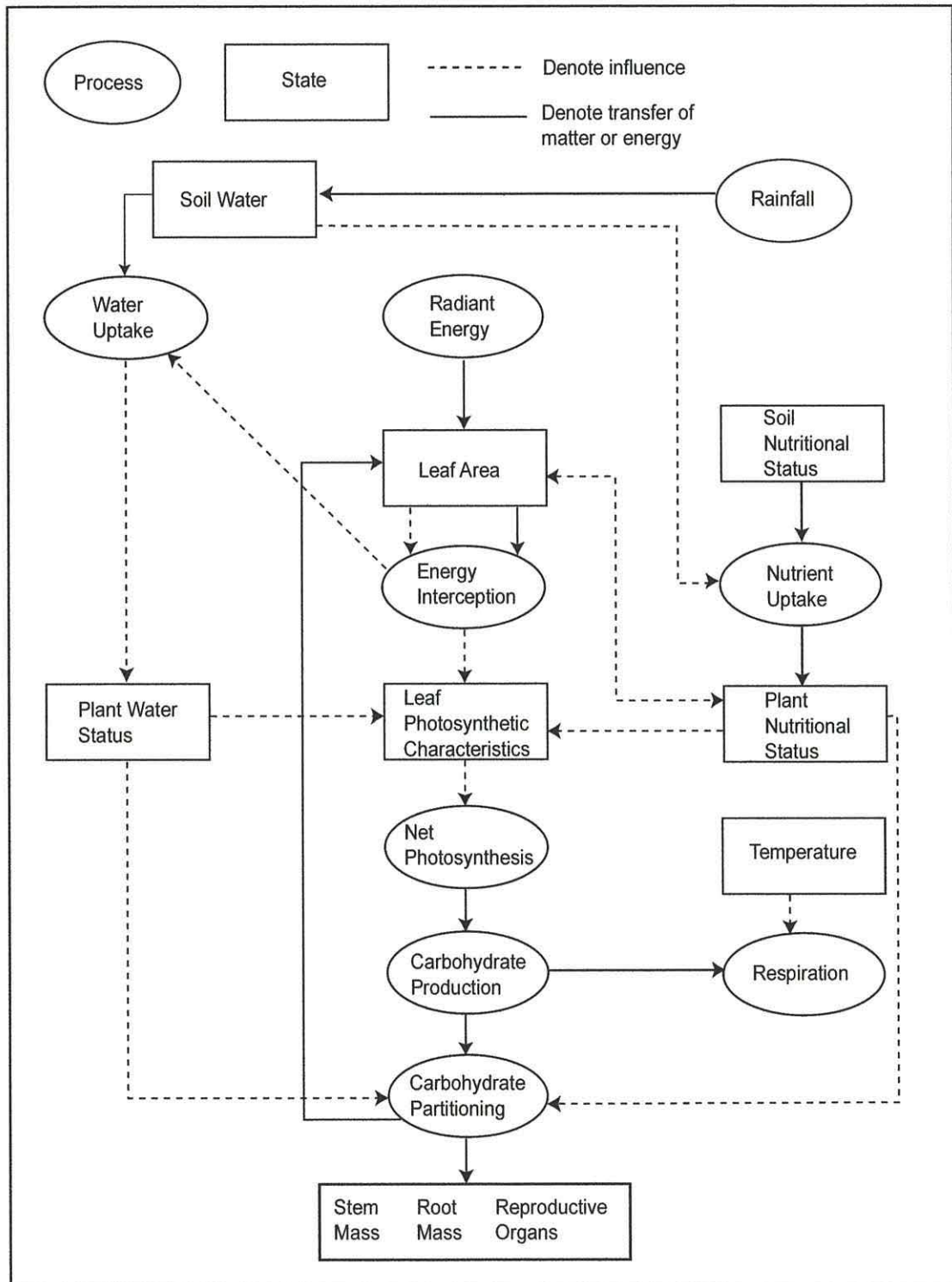
In conclusion, the thesis has increased knowledge of ash silviculture on a number of fronts. Any future work on ash silviculture should take a more fundamental approach and attempt to explain the effects of spacing and mixtures shown in this thesis, as well as other silvicultural characteristics, in terms of plant physiology. This could possibly be done in a comparative study of ash and another widely planted broadleaved tree species, such as oak. The methods of Jinks (1995) could be used to generate clonal material for these studies to minimise the effects of genetic variability.

Appendices

In each Appendix the prefix number relates to the chapter to which it is linked.

Design of the Nelder spacing experiment

It was specified that the range of spacings to investigate in the design was 1 m × 1 m to 4 m × 4 m and that eight different spacings were required. Nelder (1962) gives a number of equations for generating experimental layouts; where these are used below they are marked with an asterisk (*). Using the above information the main parameters were specified as:

$N = 8$ (number of different spacings)

$A_1 = 1$ (area available for growth at closest spacing in m^2)

$A_N = 16$ (area available for growth at widest spacing in m^2)

$\tau = 1$ (set as the objective was to investigate square spacing).

The main steps in calculating the parameters of the design were: (i) derive the multiplier (α) for generating the geometric progression with which spacings increase from the middle of the fan to the outside; (ii) calculate the angle between rays (θ); and (iii) calculate the distance between the middle of the fan and the first arc (r_2).

1.   *The geometric multiplier α*

   Solving for α in the equation below:

   $(2N - 2) \log \alpha = \log A_N - \log A_1$ *   [A1]

   This simplifies to:

   $\log \alpha = 0.0860$

   $\alpha = 1.219$

2.   *The angle between rays θ*

   Solving for θ in the equation below:

   $\theta = \tau \left(\alpha^{\frac{1}{2}} - \alpha^{-\frac{1}{2}} \right)$ *   [A2]

   gives

   $\theta = 0.1983^c = 11.36°$ (conversion of degrees to radians is $\pi/180 \times Y° = Y^c$)

   However, the layout of the Nelder fans on the ground demanded that they were half fans (i.e. 180°) and an angle between radii of 11.36° was impractical. An angle of 15° was therefore chosen and the formulae recalculated using:

   $\theta = 15° = 0.26312^c$

This also meant that α had to be recalculated using equation [A2] to obtain a value of 1.3.

3.   *Distance to the first arc (r_2) and guard row (r_1)*

Substituting $A_1 = 1$ in the following equation:

$$r_2 = \sqrt{(2A_1/\theta(\alpha^3 - \alpha))^*}$$ [A3]

and using $\theta = 0.26312$ and $\alpha = 1.3$

$r_2 = 2.91$ m

and $r_1 = r_2 \div \alpha = 2.24$ m   (inner guard row)

and $r_3 = r_2 \times \alpha = 3.78$ m   (arc outside r_2)

and $r_4 = r_3 \times \alpha = 4.92$ m   (arc outside r_3)

and so on to give the values in Table 2.2 on page 26.

Appendix 2.2

Leaf area investigation on Nelder fan at Neroche 46

Objective

To determine a method for estimating the area of an ash leaf from a feature of the leaf which was easy to measure in the field.

Method

In July 1997 one of the three Nelder fans was randomly chosen for the investigation. Of the 11 rays, eight were chosen at random and one leaf was chosen from each tree in each ray, i.e. 8 × 8 leaves. The leaves were selected systematically to cover the range of: (i) overall leaf size (small, medium and large) and (ii) number of leaflets on the leaf (5, 7, 9, 11 and 13). The spacing from which each leaf was sampled was recorded. In addition a further 16 'spare' leaves were randomly chosen and the spacings at which sample trees were growing were recorded.

Each leaf was placed in a polythene bag and transported back to Alice Holt where all leaves were placed in a fridge until they were measured. The leaves were measured for: (a) length of leaf, (b) width of leaf (measured from mid leaflet pair tip-to-tip or upper mid pair if there was an even number of leaflet pairs), (c) number of leaflets, and (d) total area of leaf (leaflets + rachis). Then each leaflet was systematically separated from the rachis and numbered from 1 (bottom left with leaf facing upwards) to between 5 and 13 (bottom right); these were measured for: (e) length of leaflet, (f) width of leaflet at widest point, (g) an estimate of % area of holes (usually caused by insect feeding), (h) area of the leaflet, and (i) area of the rachis. All areas were measured with a Delta area meter system (Delta-T Devices, Cambridge, UK). The area measured excluded holes and this was adjusted using a correction factor:

$$\text{Adjusted area} = \text{measured area} \times \left(\frac{100}{100 - \% \text{ area of holes}} \right) \qquad \text{[A4]}$$

Data analysis

Initial exploration of the data in the statistical package Statistica attempted to find a parameter that would be easy to measure in the field (e.g. a length, width or combination of the two) that could be used to accurately predict leaf area. The best relationship which could be found was quadratic using length of leaf which accounted for 93% of the variation:

$$y = 42.5x + 1.032x + 0.0145x^2 \qquad\qquad \text{[A5]}$$

where: y = estimated area and x = length of leaf.

This result was excellent as previously published work by Wiltshire *et al.* (1996) had separated ash leaves into those with 9, 11 and 13 leaflets and generated separate regressions for each sub-group using a three parameter model (leaflet length, leaflet width of the third leaflet from the axil, and number of leaflets) which had R^2 values between 0.93 and 0.96. Initially it seemed possible that a similar level of resolution could be attained from one easy-to-measure parameter.

A second model was fitted using the above procedure but restricting it to go through the origin (i.e. no length, no area). The model (R^2 = 0.931) was:

$$y = 0.37x + 0.01752x^2 \qquad\qquad \text{[A6]}$$

Although this was a generally satisfactory result it was decided to take the analysis one step further and investigate the data in more detail using stepwise regression. Because each of the leaves had different numbers of leaflets a regression of the whole data set was not possible as the number of leaflets was not equal and therefore the statistical software Genstat would have produced 'missing values' which would have biased the analysis. Analysis was therefore done on subsets of the data with 7, 9 and 11 leaflets. For each of these subsets stepwise regression was used to: (i) find the model of best fit using all parameters (a) to (i); (ii) fit a quadratic model using leaflet length (this was not model [2.1] or [A6] both of which used the full dataset); and (iii) fit a 'Wiltshire' type model. The results of this in terms of the proportion of variance accounted for are summarized in Table A1.

Table A1 Comparison of three types of model using stepwise regression

Number of leaflets	Best fit model (R^2)	Quadratic model (R^2)	Wiltshire model (R^2)
7	0.97	0.92	0.97
9	0.99	0.89	0.99
11	0.96	0.84	0.93

In each case the 'best fit' model selected contained explanatory variables (Crawley, 1993) which were different combinations of leaflet area. However, although very high R^2 values were found, the measures were not practical for field assessment. Similarly the explanatory variables in the 'Wiltshire' type model required length and width of certain

leaflets and would be difficult to measure in the field. Hence although R^2 values were lower for the quadratic model it seemed to be a good compromise between accuracy and practicality, and on this basis the quadratic model for the whole data set [A6] was used in the subsequent estimates of leaf area.

The reduction in R^2 for the quadratic model with increasing numbers of leaflets indicates that precision of estimation reduced with increasing number of leaflets (which related to leaf length). This was also apparent in the relationship between leaf length and estimated area (Figure A1), where variances increased with increasing leaf length.

Figure A1 Relationship between leaf length and estimated area in August 1997 at Neroche 46: fan 1
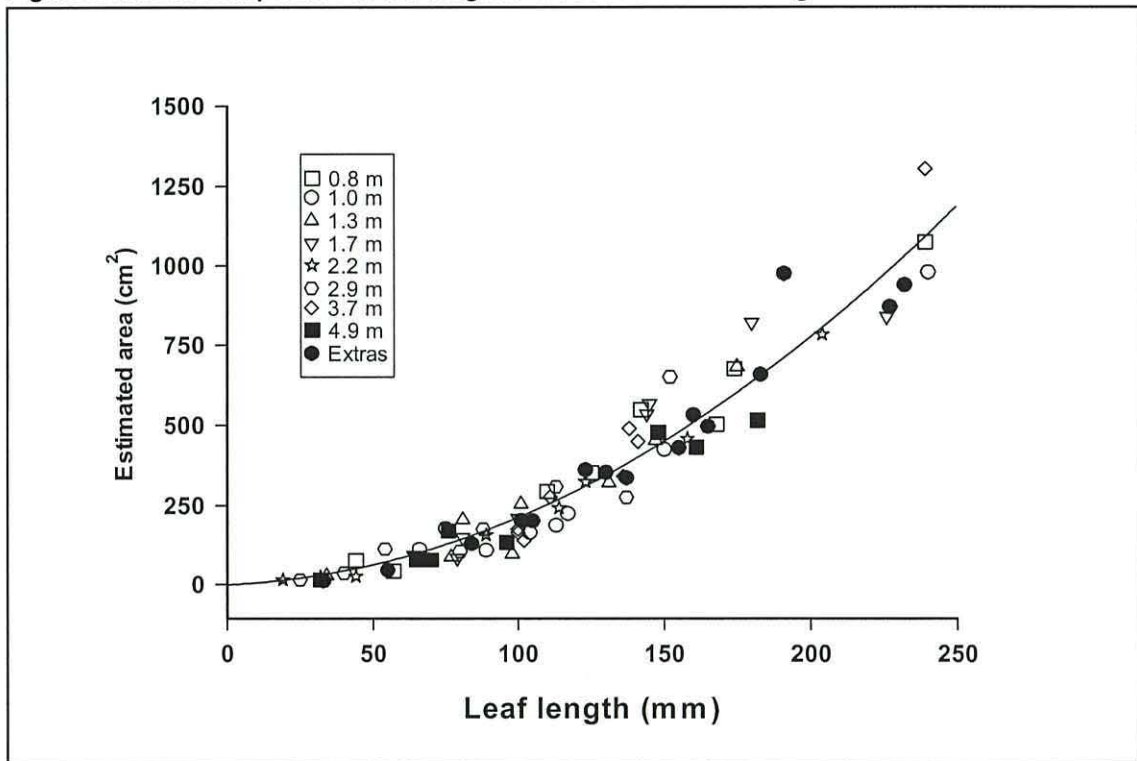
Appendix 2.3

Procedure for compensating for missing trees in Nelder experiment

1. The experiment can be viewed as a series of concentric rings which can then be sub-divided depending on the number of trees in the ring (Figures 2.1 and 2.2).

2. The area of each of the rings can then be calculated by subtracting the area of the smaller circle in the ring from that of the larger circle. For the Nelders used in this study the area for each tree is then this figure divided by 24 (the number of trees there would be if the Nelder was a full circle).

3. The location of missing trees is then plotted on a fan layout diagram and the 'missing' area is divided up into quarters and shared out amongst the four trees neighbouring the 'missing' area.

4. One missing tree affects the spacing of trees in three adjacent semi-circles. In the example of Figure A2 (Neroche experiment, fan 1) dead trees 79 and 49 effectively increase the area of trees in the outer (guard) row (80 and 50), their own row (89, 69, 59, 39) and the one inside (78, 48). On two occasions two trees died next to each other; in these cases the area available was divided into six and shared amongst adjacent trees.

5. The method of analysis of data from the Nelders required a mean parameter (e.g. height) from all trees in the same arc and for this to be related to a single figure for spacing. As can be seen from 1–4 above, when there were missing trees it is not possible to use the area available (or equivalent spacing) when all trees were alive. The convention adopted to overcome this problem was to calculate a weighted average spacing for the arc. For instance using the example in Figure A2:

    for trees 19, 29, 99, 109, 119 area available = 23.598 m^2 (spacing = 4.85 m)
    for trees 39, 59, 69, 89 area available = (23.598 + (23.598/4) = 29.475 m^2 (spacing = 5.43 m)
    weighted average = 26.22 (5.12 m)

6. This accounts for the fact that when data from the three fans are examined on the same axes one of the fans may give a slightly different spacing from the other two.

For example, the 1998 height data in Figure 2.3 illustrate the problem described above.

Figure A2 The influence of missing trees 49 and 79 in Neroche 46
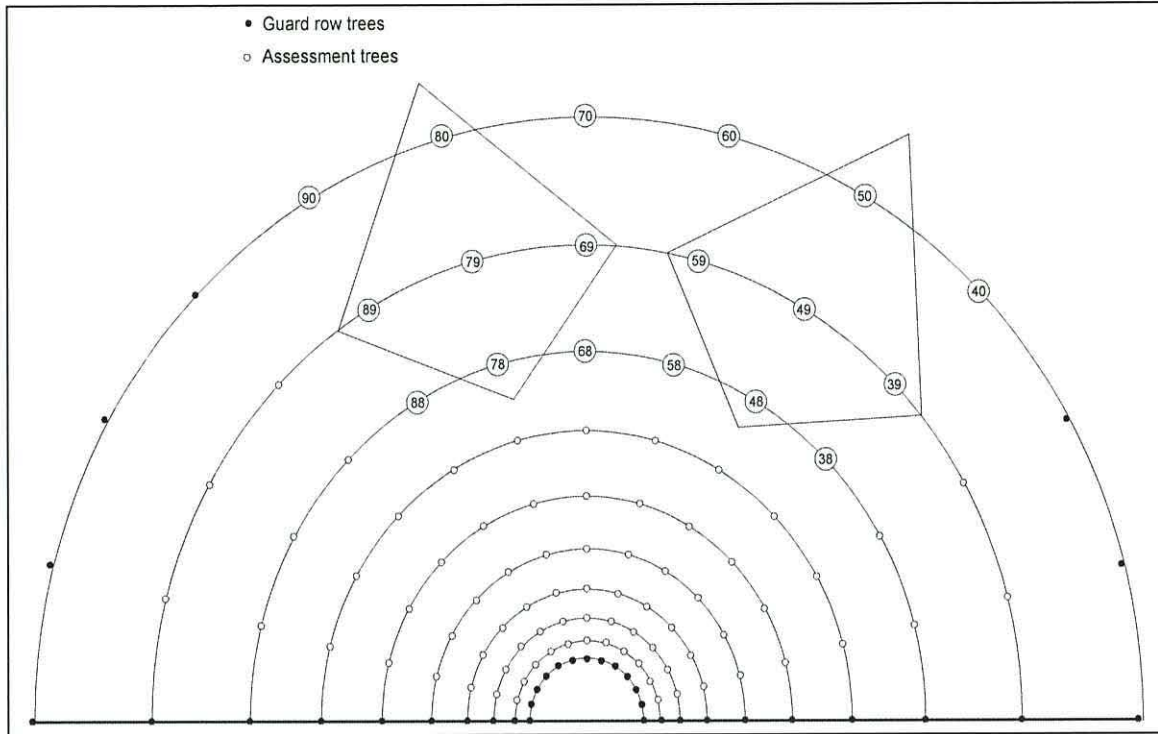
Appendix 2.4

Height, stem diameter and height:stem diameter ratio data for Neroche 46

Table A2 Mean height

Assess-ment/ Fan	Mean height (cm) at spacings (m)								Signif. of spacing
	0.8	1.0	1.3	1.7	2.2	2.9	3.7	4.9	
Oct 95/1	49.91	47.91	49.18	45.91	42.64	46.64	46.45	41.91	
Oct 95/2	43.00	43.91	42.82	42.54	42.09	46.64	41.73	40.09	ns
Oct 95/3	46.27	36.82	45.18	46.28	45.22	43.55	43.18	45.73	
Oct 96/1	52.45	48.45	51.91	49.36	49.00	51.00	56.64	53.91	
Oct 96/2	49.18	52.27	41.91	37.36	50.60	46.82	47.18	47.00	ns
Oct 96/3	69.91	55.36	64.46	60.27	66.82	74.45	63.55	64.83	
Oct 97/1	110.45	79.00	83.18	70.00	69.00	66.09	70.09	56.56	
Oct 97/2	72.09	79.73	56.60	60.40	52.78	58.82	62.45	56.82	***
Oct 97/3	147.73	145.60	131.18	129.36	97.18	126.45	124.45	99.36	
Oct 98/1	185.55	148.45	137.00	114.82	113.91	108.82	103.36	70.78	
Oct 98/2	125.18	160.27	89.00	106.78	82.11	87.18	89.16	85.55	***
Oct 98/3	224.27	238.10	223.73	224.55	161.09	182.09	205.30	142.82	

ns = not significant; *** $P \leq 0.001$.

Table A3 Stem diameter

Assess-ment/ Fan	Mean stem diameter (mm) at spacings (m)								Signif. of spacing
	0.8	1.0	1.3	1.7	2.2	2.9	3.9	4.9	
Oct 95/1	7.09	6.73	5.82	5.73	5.73	6.18	5.18	5.55	
Oct 95/2	5.55	5.82	4.55	5.18	5.36	5.55	5.27	5.55	ns
Oct 95/3	7.72	6.09	6.64	7.27	6.78	7.00	6.64	6.73	
Oct 96/1	7.72	6.73	7.91	7.45	7.45	7.36	8.09	7.27	
Oct 96/2	6.82	7.18	5.73	5.91	7.30	6.27	7.36	7.45	ns
Oct 96/3	9.64	8.27	7.91	9.45	9.73	11.09	9.55	9.82	
Oct 97/1	14.55	11.27	10.82	10.64	10.18	11.60	9.82	7.11	
Oct 97/2	10.73	10.18	7.70	8.90	8.89	8.64	8.64	9.00	***
Oct 97/3	18.55	16.60	15.18	17.27	14.00	16.09	15.91	13.45	
Oct 98/1	22.82	18.36	18.55	17.27	16.18	16.45	14.27	10.22	
Oct 98/2	16.45	19.00	12.90	14.11	12.22	13.45	12.73	13.36	***
Oct 98/3	31.73	30.50	29.09	32.00	22.64	26.55	26.90	19.91	

ns = not significant; *** $P \leq 0.001$.

Table A4 Height: stem diameter ratio

Assess-ment/ Fan	Mean height:stem diameter ratio (cm mm^{-1}) at spacings (m)								Signif. of spacing
	0.8	1.0	1.3	1.7	2.2	2.9	3.9	4.9	
Oct 95/1	7.11	7.21	8.73	8.22	7.57	7.70	9.09	7.60	
Oct 95/2	7.86	7.79	9.54	8.59	7.94	8.57	8.12	7.41	ns
Oct 95/3	6.06	6.17	7.17	6.5	11.14	6.44	6.54	6.92	
Oct 96/1	7.13	7.50	6.83	7.05	6.89	7.23	7.16	7.79	
Oct 96/2	7.36	7.36	7.39	6.55	7.04	7.57	6.67	6.49	ns
Oct 96/3	7.19	6.67	8.26	6.51	7.06	6.87	6.69	6.76	
Oct 97/1	7.50	6.93	8.00	6.71	6.76	6.11	7.30	8.52	
Oct 97/2	6.71	7.74	7.38	7.03	5.87	6.91	7.33	6.44	ns
Oct 97/3	7.95	8.79	8.69	7.47	6.97	7.88	7.51	7.36	
Oct 98/1	8.24	8.00	7.25	6.60	6.91	6.43	7.16	7.59	
Oct 98/2	7.64	8.27	6.54	7.39	6.31	6.31	6.95	6.25	ns
Oct 98/3	7.19	7.97	7.90	7.22	7.14	6.78	7.69	7.36	

ns = not significant.

Height and stem diameter data for Swadlincote 1

Table A5 Mean height and stem diameter for Swadlincote 1 in January 2000

Spacing (m) /Fan	Height (cm)	Stem diameter (mm)
0.8/1	191.5	24.4
1.0/1	193.3	23.7
1.3/1	182.0	22.5
1.7/1	163.0	21.5
2.2/1	163.0	21.5
2.9/1	175.2	22.4
3.7/1	160.6	21.1
4.8/1	178.4	22.3
0.8/2	183.5	23.2
1.0/2	181.8	24.1
1.3/2	182.4	23.9
1.7/2	163.9	22.2
2.2/2	160.2	20.7
2.9/2	166.7	20.5
3.7/2	161.4	21.6
4.8/2	169.0	21.9
0.8/3	201.6	22.3
1.0/3	190.6	21.4
1.3/3	179.0	23.9
1.7/3	189.7	23.6
2.2/3	172.9	21.3
2.9/3	164.4	19.4
3.7/3	165.5	19.7
4.8/3	153.3	19.9

Appendix 2.6

Diameter distribution data for Neroche 46

Table A6 Results of analysis of diameter distributions for October 1997 and October 1998 at Neroche 46

Assess-ment/ Fan	Number of trees in diameter classes[1]										Significance[2]
	1	2	3	4	5	6	7	8	9	10	
Oct 97/0.8	0	0	3	9	7	9	2	2	1	0	0.47
Oct 97/1.0	0	2	5	12	8	2	1	2	0	0	0.21
Oct 97/1.3	0	6	6	7	6	4	3	0	0	0	0.39
Oct 97/1.7	0	4	7	6	4	7	3	1	0	0	0.42
Oct 97/2.2	0	3	10	8	6	1	2	1	0	0	0.42
Oct 97/2.9	0	3	8	8	7	3	0	3	0	0	0.25
Oct 97/3.7	0	6	7	9	5	2	3	1	0	0	0.058
Oct 97/4.9	1	9	5	7	4	4	1	0	0	0	0.24
Oct 98/0.8	0	0	6	9	3	7	5	2	1	0	0.37
Oct 98/1.0	0	3	4	8	8	5	3	0	2	0	0.24
Oct 98/1.3	2	4	6	3	10	5	1	1	1	0	0.41
Oct 98/1.7	1	5	5	5	5	4	3	3	1	0	0.74
Oct 98/2.2	4	2	11	5	6	3	2	0	0	0	0.45
Oct 98/2.9	0	5	8	8	4	5	0	3	0	0	**0.033**
Oct 98/3.7	3	3	8	9	3	6	0	1	0	0	0.32
Oct 98/4.9	6	8	6	6	3	3	1	0	0	0	0.80

[1]Diameter classes were 3, 6, ...27 (cm) for October 1997; 5,10, ...45 (cm) for October 1998.
[2]This was the χ^2 probability that the observed distribution is different from a Normal (Gaussian) distribution.

Appendix 2.7

Properties of height distributions for Neroche 46

Table A7 October 1997

Spacing (m)	Probability of distribution being normal	Normal distribution (✔ = yes ✘ = no)	Shape parameters	
			Skewness[1]	Kurtosis[2]
0.8	0.450	✔	0.92	1.01
1.0	0.026	✘	0.69	-0.79
1.3	0.019	✘	0.31	-1.17
1.7	<0.001	✘	0.73	-0.86
2.2	0.031	✘	0.96	-0.06
2.9	0.006	✘	0.74	-0.34
3.7	0.099	✔	0.67	-0.69
4.8	0.013	✘	0.89	-0.15

Table A8 October 1998

Spacing (m)	Probability of distribution being normal	Normal distribution (✔ = yes ✘ = no)	Shape parameters	
			Skewness[1]	Kurtosis[2]
0.8	0.874	✔	0.09	-0.21
1.0	0.447	✔	0.05	-0.46
1.3	0.029	✘	-0.25	-1.48
1.7	0.326	✔	0.11	-1.16
2.2	0.733	✔	0.27	-1.21
2.9	0.137	✔	0.41	-0.94
3.7	0.507	✔	0.36	-0.95
4.8	<0.001	✘	0.52	-0.98

[1]Positive values indicate skewness to the right, negative values indicate skewness to the left.

[2]Positive values indicate 'leptokurtosis', i.e. that the distribution has longer tails and is more pointy than a bell-shaped normal distribution; negative values indicate 'platykurtosis', i.e. that a distribution is more flat-topped than a normal one.

Appendix 2.8

Dry weight data for Neroche 46

Table A9 Mean dry weight data for Neroche 46

Spacing (m) /Fan	Mean dry weight (g)					Dry weight ratio	
	Stem (1)	Branch (2)	Top (1+2)	Root (3)	Total (1+2+3)	Shoot: root	Stem: branch
0.8/1	140.3	18.5	158.8	112.7	271.5	1.003	10.32
1.0/1	333.8	12.75	346.6	363.7	710.3	0.841	51.64
1.3/1	493.8	65.8	559.6	619.8	1332.8	1.103	44.04
1.7/1	371.8	27.6	505.8	347.3	947.2	1.126	65.2
2.2/1	414.9	30.23	445.1	403.7	848.8	1.110	22.2
2.9/1	442.9	42.97	485.9	443.8	929.7	1.192	15.07
3.7/1	147	28.57	175.6	85.5	234.5	1.940	31.95
4.8/1	218.9	26.23	245.1	96.2	355.4	2.169	16.19
0.8/2	169.1	35.05	214.4	134.1	376.1	1.279	18.64
1.0/2	34.5	1.55	36.1	24.3	60.4	1.567	94.49
1.3/2	33.7	1.92	35.6	34.9	70.5	1.338	16.92
1.7/2	14.4	0.6	15	14.8	29.8	1.150	20.83
2.2/2	32.1	0.93	33.1	37.2	80.6	1.394	47.79
2.9/2	22.4	2.12	24.5	15.9	40.04	1.528	9.62
3.7/2	129.2	10.83	140	68.3	208.3	2.054	30.74
4.8/2	66.5	9	75.5	35.2	110.7	2.271	9.54
0.8/3	773	60.15	833.2	506.5	1339.7	1.597	19.54
1.0/3	649.7	76.97	726.6	618.5	1345.2	1.018	8.6
1.3/3	889.2	115.1	1004.3	856.5	1860.8	1.302	26.67
1.7/3	461.5	18.2	479.7	418.7	898.4	1.225	78.22
2.2/3	776.1	226.35	1034.7	597.1	1704.1	1.506	6.12
2.9/3	641	131.9	773	487.7	1260.7	1.642	28.62
3.7/3	364.3	35.8	400.1	187.2	587.3	2.279	32.84
4.8/3	411.1	102.7	513.7	242.9	756.6	2.778	6.72
Significance of spacing	*	ns	ns	**	*	***	ns

ns = not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Appendix 3.1

A note on the use of generalized linear models in the thesis for the three mixture experiments

This is a brief and incomplete guide to the use of generalized linear models. For a full account the reader is referred to Crawley (1993).

In linear regression the straight line is:

$$y = a + bx \qquad \text{[A7]}$$

where a *response variable y* is hypothesized as being a linear function of the *explanatory variable x* and the two parameters *a* (the intercept) and *b* (the gradient). Any errors are assumed to be confined to *y*, to be normally distributed and independent of the level of *x*. However, for some data in this thesis errors are non-normal and variances change with the mean value *y*. Generalized linear models (GLM) or generalized mixed models (GLMM) provide methods for overcoming these difficulties.

A linear model is not always a straight line; the definition of a linear model is an equation that contains mathematical variables, parameters and random variables, that is linear in the parameters and the random variables (Crawley, 1993). Hence [A8] is a linear model but so also is the exponential model

$$y = a + be^x \qquad \text{[A8]}$$

because we can create a new variable $z = \exp(x)$, so that

$$y = a + bz \qquad \text{[A9]}$$

A generalized linear model has three important properties:

1. the error structure
2. the linear predictor
3. the link function

Error structure

Many types of biological data have non-normal errors. The main examples in this thesis are count data, which usually have a Poisson error distribution where the mean is equal to the variance, and proportional data, which usually have a binominal error distribution where the variance changes with the mean. Analysis using GLM allows this to be taken into account.

Linear predictor

In linear regression, the linear model predicts values of the response variable *y* for different values of the explanatory variable *x*. In the GLM, the linear model describes η, the linear predictor, and is related to the response variable via the link function.

To determine the fit of a given model GLM (or the statistical package doing the analysis) evaluates the linear predictor for each value of the response variable, then compares the predicted value with the *transformed* value of *y*. The transformation is specified in the link function.

Link function

The two link functions used in the thesis are the log and logit. The log function is

$$\eta = \log\mu \qquad\qquad [A10]$$

and is useful with count data to prevent negative values. The logit link function is used for proportion data, where a fraction of *p* individuals from a population of *t* is affected.

$$\eta = \log\left(\frac{p}{t - p}\right) \qquad\qquad [A11]$$

This is a simple way of ensuring that fitted values are bounded from both above and below as predictor proportions may not be greater than 1 or less than 0.

Two examples are described of how GLM was used on sets of data in the thesis.

Example 1   Use of log link function in GLM analysis of the number of buds (bu98a2) described in section 3.3.2.2.

The following shows the information input into a GLM in Genstat and then three tables of output. The first table (***summary of analysis***) describes how well the model describes the data; if $P \leq 0.05$ the model is a reasonable representation of the data. The second table (***estimates of parameters***) shows the values for the terms in the model. The third table (***accumulated analysis of deviance***) shows whether each of the terms in the model make a significant contribution to description of the data, i.e. if $P > 0.05$ the term need not be included in the best model (i.e. Crawley's minimal adequate model).

The following were specified as a possible 'best' model:

Response variable: bu98a2
Distribution: Poisson
Link function: Log
Fitted terms: Constant + mixture

*** Summary of analysis ***

	d.f.	deviance	mean deviance	deviance ratio	approx. F pr.
Regression	1	10.52	10.521	7.18	0.010
Residual	46	67.38	1.465		
Total	47	77.90	1.658		

Dispersion parameter is estimated to be 1.46 from the residual deviance.

*** Estimates of parameters ***

	estimate	s.e.
Constant	-0.152*	0.323
Mixture	0.1618*	0.0617

* Used in equation A12.

*** Accumulated analysis of deviance ***

Change	d.f.	deviance	mean deviance	deviance ratio	approx. F pr.
+ Mixture	1	10.521	10.521	7.18	0.010
Residual	46	67.382	1.465		
Total	47	77.903	1.658		

A third explanatory term 'block' was then fitted.

Response variate: bu98a2
Distribution: Poisson
Link function: Log
Fitted terms: Constant + mixture + block

*** Summary of analysis ***

	d.f.	deviance	mean deviance	deviance ratio	approx.. F pr.
Regression	12	35.47	2.956	2.44	0.020
Residual	35	42.44	1.212		
Total	47	77.90	1.658		
Change	-11	-24.95	2.268	1.87	0.079

Dispersion parameter is estimated to be 1.21 from the residual deviance

*** Estimates of parameters ***

These are not shown as Genstat produces different intercept values for each of the 12 blocks.

*** Accumulated analysis of deviance ***

Change	d.f.	deviance	mean deviance	deviance ratio	approx. F pr.
+ Mixture	1	10.521	10.521	8.68	0.006
+ block	11	24.946	2.268	1.87	0.079
Residual	35	42.436	1.212		
Total	47	77.903	1.658		

However, the last table shows that addition of 'block' term was not significant (P=0.079) and therefore is not required in the best model. The model (with constant + mixture) was then used to predict the response variable for different levels of the explanatory variables 0, 2, 4, 6. The model was:

$$\eta = 0.1618x - 0.152 \qquad \text{[A12]}$$

where y = bu98a2, x = mixture, η = linear predictor; and the predictions are:

Mixture	Model prediction	s.e.	Observed value
0.00	0.859	0.278	1.00
2.00	**1.187**	0.257	**1.25**
4.00	1.641	0.231	2.25
6.00	2.267	0.344	2.50

Values of 0, 2, 4, 6 do not give the correct values when used in equation A12 because of the log link function. For example for x = 2

$$\eta = 0.1618x - 0.152 \; [x = 2]$$

$$\eta = 0.1716 \quad \text{(transform to antilog)}$$

$$y = 1.187 \quad \text{(as predicted by the model - see above)}$$

157

Example 2   Use of the logit link function in GLM analysis of the proportion of forks in 1999 in the ash : cherry experiment described in section 3.2.5.1.

The following were specified as a possible 'best' model:

Response variable: nfork99 (number of forks in 1999)
Distribution: Binomial
Link function: Logit
Fitted terms: Constant + mixture

*** Summary of analysis ***

	d.f	deviance	mean deviance	deviance ratio	approx. chi pr
Regression	1	4.22	4.216	4.22	0.040
Residual	46	58.18	1.265		
Total	47	62.40	1.328		

Deviance ratios are based on dispersion parameter with value 1.

*** Estimates of parameters ***

	estimate	s.e.
Constant	-1.819*	0.719
Mixture	0.289*	0.147

* Used in equation A13.

*** Accumulated analysis of deviance ***

Change	d.f.	deviance	mean deviance	deviance ratio	approx. chi pr
Mixture	1	4.216	4.216	4.22	0.040
Residual	46	58.183	1.265		
Total	47	62.399	1.328		

Ratios are based on dispersion parameter with value 1.

Hence, the best model is

$$\eta = 0.289x - 1.819 \qquad\qquad\qquad [A13]$$

where y = proportion of forks, x = mixture level , η = linear predictor

This produces the following prediction:

Mixture	Model prediction	s.e.	Actual value	Actual value as a proportion
0.00	0.1396	0.0864	3	0.176
2.00	**0.2242**	0.0824	**2**	**0.118**
4.00	0.3405	0.0720	5	0.294
6.00	0.4795	0.0980	7	0.412
Total			**17**	

s.e.s are approximate, since model is not linear and are based on dispersion parameter with value 1.

The model predicts the actual value as a proportion of the total, e.g. for $x = 2$, the proportion is $^2/_{17} = 0.118$.

Substituting $x = 2$ in [A13]

$$\eta = 0.289\,x - 1.819$$

$$\eta = -1.241$$

However, because of the log link function the predicted model value can only be calculated by using the following back transformation procedure:

(i)   log η, log (-1.241) = 0.289

(ii)   solve for y as a proportion p; $p = \dfrac{1}{1 + 1/\log \eta}$

(iii) $p = 0.2242$ for $x = 2$ (as in model prediction table above).

Appendix 3.2

Detailed results for analysis of height and stem diameter for the three mixture experiments

Tables A10, A11, A12 and A13 give the detailed results for the analysis of variance of height and stem diameter for ash, and of height and stem diameter for cherry, oak and beech.

Table A10 Results of the analysis of variance of height for ash

Experiment	Assessment date	Mixture treatment[1] (Height (cm))							Standard error of difference	Signif.	Relationship
		$A_6:B_0$	$A_5:B_1$	$A_4:B_2$	$A_3:B_3$	$A_2:B_4$	$A_1:B_5$	$A_0:B_6$			
Ash:cherry	Jan 96	34.0	35.8	33.8	35.5	34.7	36.0	34.8	1.62	ns	
	Sep 96	42.3	43.2	42.0	46.0	44.2	48.0	44.6	2.55	ns	
	Jan 98	115.5	115.7	112.5	107.2	106.7	117.3	113.8	9.88	ns	
	Mar 99	195.2	198.2	184.7	178.3	173.7	192.2	190.0	13.29	ns	
	Feb 00	267.8	264.3	258.6	233.8	230.8	265.7	254.8	18.67	ns	
Ash:oak	Jan 96	31.3	34.2	34.5	33.7	35.3	32.2	32.7	2.21	ns	
	Sep 96	37.8	43.0	41.5	42.1	43.5	38.4	39.2	3.32	* quadratic	$y=38+2.6x-0.46x^2$
	Jan 98	82.6	87.4	91.7	91.1	86.8	78.9	103.0	13.45	ns	
	Mar 99	154.2	159.0	167.8	160.7	162.3	155.0	161.8	20.23	ns	
	Feb 00	224.7	227.8	254.5	232.3	258.0	231.9	242.9	22.26	ns	
Ash:beech	Jan 96	32.5	29.5	32.2	32.5	34.2	36.3	31.8	1.97	ns	
	Sep 96	39.0	35.7	40.5	42.5	46.3	41.5	38.3	2.65	* quadratic	$y=36+3.7x-0.52x^2$
	Jan 98	85.2	71.2	94.2	98.3	100.1	83.2	88.2	10.83	ns	
	Mar 99	151.2	133.0	161.0	172.0	180.1	149.5	169.2	16.98	ns	
	Feb 00	224.0	197.7	234.4	256.3	255.5	212.0	233.1	19.47	* higher order	

Degrees of freedom = 66; Student's t for $P \leq 0.05$ = 2.00; ns - not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$; subscripts are the relationship in last column.

[1] Ratios given as numbers of trees (N) of ash A_N: other species B_N.

Table A11 Results of the analysis of variance of stem diameter for ash

Experiment	Assessment date	Mixture treatment[1] (Stem diameter (cm))							Standard error of difference	Signif.	Relationship
		$A_6{:}B_0$	$A_5{:}B_1$	$A_4{:}B_2$	$A_3{:}B_3$	$A_2{:}B_4$	$A_1{:}B_5$	$A_0{:}B_6$			
Ash:cherry	Jan 96	5.25	5.67	5.42	5.83	5.67	6.17	5.92	0.40	*linear	$y=5.35+0.12x$
	Sep 96	8.25	8.58	8.00	9.17	8.50	9.33	8.42	0.66	ns	
	Jan 98	14.83	14.42	13.92	14.67	13.58	14.58	13.92	0.99	ns	
	Mar 99	21.42	20.83	18.58	19.08	17.50	18.25	18.08	1.69	*linear	$y=20.85-0.58x$
	Feb 00	25.58	24.42	21.42	21.58	19.83	21.33	21.92	2.25	*linear	$y=24.31-0.67x$
Ash:oak	Jan 96	4.50	4.75	4.92	4.92	5.08	4.58	4.83	0.43	ns	
	Sep 96	6.33	7.17	7.83	7.25	8.00	6.75	8.08	0.67	ns	
	Jan 98	10.92	13.75	14.08	12.92	12.92	11.83	14.33	1.24	ns	
	Mar 99	18.42	21.67	22.00	21.25	22.50	21.00	24.75	2.42	*linear	$y=19.71+0.65x$
	Feb 00	23.58	28.75	28.92	28.25	31.50	30.58	36.33	3.19	*linear	$y=24.93+1.59x$
Ash:beech	Jan 96	5.83	4.58	5.17	6.25	6.58	5.58	6.00	0.48	*linear	$y=5.29+0.14x$
	Sep 96	7.08	5.58	6.08	8.17	8.17	6.50	6.58	0.625	*** h order	
	Jan 98	12.92	11.08	12.42	14.58	14.59	11.75	13.25	1.073	** h order	
	Mar 99	20.33	18.08	21.67	24.83	25.58	23.50	25.33	2.208	***linear	$y=19.57+1.06x$
	Feb 00	26.75	23.00	29.42	33.58	35.55	33.08	36.08	2.94	*** linear	$y=25.25+1.94x$

Degrees of freedom = 66; Student's t for $P \le 0.05$ = 2.00; ns - not significant, * $P \le 0.05$, ** $P \le 0.01$, *** $P \le 0.001$; subscripts are the relationship in last column.
[1] Ratios given as numbers of trees (N) of ash A_N: other species B_N.

Table A12 Results of the analysis of variance of height for cherry, oak and beech

Experiment	Assessment date	Mixture treatment[1] (Height (cm))							Standard error of difference	Signif.	Relationship
		$A_6:B_0$	$A_5:B_1$	$A_4:B_2$	$A_3:B_3$	$A_2:B_4$	$A_1:B_5$	$A_0:B_6$			
Cherry:ash	Jan 96	34.67	36.33	36.17	37.83	34.83	36.67	36.33	2.48	ns	
	Sep 96	92.2	76.2	70.2	82.2	72.2	87.0	75.7	6.35	*quadratic	$y=81-5x+0.99x^2$
	Jan 98	180.2	166.2	145.8	164.7	140.8	160.8	146.8	10.61	**linear	$y=145.5+4.13x$
	Mar 99	225.0	219.2	200.0	228.0	196.7	222.0	213.0	13.16	ns	
	Feb 00	306.7	284.4	260.7	300.4	254.8	285.9	279.4	17.87	ns	
Oak:ash	Jan 96	37.33	35.83	37.00	37.17	36.17	39.67	38.00	1.98	ns	
	Sep 96	39.67	40.00	43.83	45.00	40.00	42.33	41.83	2.83	ns	
	Jan 98	59.2	64.8	66.2	70.5	58.0	61.8	58.2	6.21	ns	
	Mar 99	98.3	90.2	87.7	91.5	85.6	85.4	87.7	11.65	ns	
	Feb 00	119.2	134.5	116.1	120.3	114.4	107.7	112.3	14.76	ns	
Beech:ash	Jan 96	25.3	25.5	22.6	24.8	23.0	27.3	23.3	1.98	ns	
	Sep 96	30.3	30.0	29.5	30.1	26.0	32.5	28.5	2.46	ns	
	Jan 98	42.3	35.0	39.2	40.9	36.0	47.1	38.6	5.97	ns	
	Mar 99	60.3	52.7	54.1	51.0	57.5	77.5	57.7	12.72	ns	
	Feb 00	83.2	88.0	87.7	91.9	107.8	135.3	90.7	15.22	*linear	$y=112.5-4.9x$

Degrees of freedom = 66; Student's t for $P \leq 0.05 = 2.00$; ns - not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$; subscripts are the relationship in last column.
[1] Ratios given as numbers of trees (N) of ash A_N: other species B_N.

163

Table A13 Results of the analysis of variance of stem diameter for cherry, oak and beech

Experiment	Assessment date	Mixture treatment[1] (Stem diameter (cm))							Standard error of difference	Signif.	Relationship
		$A_6:B_0$	$A_5:B_1$	$A_4:B_2$	$A_3:B_3$	$A_2:B_4$	$A_1:B_5$	$A_0:B_6$			
Cherry:ash	Jan 96	5.08	5.92	5.00	6.17	5.75	5.75	5.67	0.387	*h order	
	Sep 96	11.67	12.92	11.00	12.25	11.00	12.58	13.92	0.970	*quadratic	$y=12-0.7x+0.15x^2$
	Jan 98	23.17	25.17	20.42	25.67	23.92	27.42	31.17	2.532	**linear	$y=21.85+1.14x$
	Mar 99	29.50	32.58	26.25	34.58	31.92	37.08	44.58	3.601	***linear	$y=27.37+2.14x$
	Feb 00	33.1	36.5	29.7	39.6	36.3	43.8	53.5	4.600	***linear	$y=30.1+2.95x$
Oak:ash	Jan 96	5.58	5.58	5.83	6.42	5.17	5.42	5.58	0.618	ns	
	Sep 96	6.75	7.33	7.67	7.67	7.25	6.83	7.08	0.729	ns	
	Jan 98	10.00	10.83	11.08	12.17	10.25	10.50	10.67	1.054	ns	
	Mar 99	14.59	15.81	15.42	16.83	13.76	16.83	14.25	1.821	ns	
	Feb 00	17.68	17.85	18.68	19.08	16.30	17.96	17.04	2.118	ns	
Beech:ash	Jan 96	2.75	3.08	2.83	3.00	2.75	2.67	2.83	0.283	ns	
	Sep 96	3.17	4.25	3.75	3.42	3.42	3.75	3.67	0.373	*h order	
	Jan 98	5.81	7.53	6.55	6.13	6.48	6.02	6.13	0.773	ns	
	Mar 99	9.17	12.47	9.10	8.92	10.17	8.50	9.65	1.66	ns	
	Feb 00	15.00	20.51	19.32	16.57	14.62	12.6	13.03	2.010	***linear	$y=18.72-0.94x$

Degrees of freedom = 66; Student's t for $P \le 0.05$ = 2.00; ns - not significant, * $P \le 0.05$, ** $P \le 0.01$, *** $P \le 0.001$; subscripts are the relationship in last column.
[1] Ratios given as numbers of trees (N) of ash A_N: other species B_N.

Appendix 3.3

Accumulated analysis of deviance tables for the forking data

Table A14 Ash : cherry 1998

	d.f.	dev.	mean dev.	dev. ratio	Approx. χ^2 prob.
Mixture	1	6.69	6.69	6.69	0.010
Blocks	11	10.62	0.97	0.97	0.476
Residual	35	29.02	0.83		
Total	47	46.33	0.99		

Deviance ratios were based on dispersion parameter = 1.

Table A15 Ash : cherry 1999

	d.f.	dev.	mean dev.	dev. ratio	Approx. χ^2 prob.
Mixture	1	4.22	4.22	4.22	0.040
Blocks	11	9.58	0.87	0.87	0.568
Residual	35	48.60	1.39		
Total	47	62.40	1.33		

Deviance ratios were based on dispersion parameter = 1.

Table A16 Ash : oak 1999

	d.f.	dev.	mean dev.	dev. ratio	Approx. χ^2 prob.
Mixture	1	4.76	4.76	4.76	0.049
Blocks	11	9.35	0.85	0.85	0.589
Residual	33	8.07	0.24[a]		
Total	47	22.18	0.49		

Deviance ratios were based on dispersion parameter = 1.
[a] This value is low (it should be ≈1) and makes the analysis very sensitive.

Appendix 3.4

Results from stage 1 analysis of buds and branches mean number for each section at each assessment

Ash : cherry experiment

Table A17 Section 1 (lowest)

	1996	1997	1998	1999
Buds:				
terminal	0	0	0	0
axillary	12.7	2.3	0.4	0
scale	0.3	0	0	0
Total	13.0	2.3	0.4	0
Branches:				
terminal	0.0	0	0	0
axillary	3.9	6.0	4.8	2.9
scale	0.0	0	0	0
Total	3.9	6.0	4.8	2.9
TOTAL	16.9	8.3	5.2	2.9

Table A18 Section 2

	1996	1997	1998	1999
Buds:				
terminal	1.0	0	0	0
axillary	8.1	4.4	1.8	0.06
scale	2.2	0.6	0.2	0
Total	11.3	5.0	2.0	0.06
Branches:				
terminal	0	0.2	0.2	0
axillary	0	3.2	2.9	2.6
scale	0	0	0	0
Total	0	3.4	3.0	2.6
TOTAL	11.3	8.4	5.0	2.7

Table A19 Section 3

	1997	1998	1999	
Buds:				
terminal	0.9	0	0	
axillary	22.9	8.2	0.17	
scale	1.4	0.8	0	
Total	25.1	8.9	0.17	
Branches:				
terminal	0.1	0.1	0	
axillary	0.5	8.8	0.58	
scale	0	0	0	
Total	0.6	9.0	0.58	
TOTAL	25.7	17.9	0.75	

Table A20 Section 4

	1998	1999
Buds:		
terminal	0.9	0.02
axillary	26.3	4.4
scale	2.1	0.54
Total	29.4	5.0
Branches:		
terminal	0	0
axillary	0.9	9.0
scale	0	0.02
Total	0.9	7.7
TOTAL	30.1	12.7

Section 5

	1999
	0.96
	18.31
	1.98
	21.25
	0
	0.54
	0.02
	0.56
	21.81

Ash : beech experiment

Table A21 Section 1 (lowest)

	1996	1997	1998	1999
Buds:				
terminal	0	0	0	0
axillary	14.65	5.43	2.06	0.26
scale	0.42	0	0	0
Total	15.07	5.43	2.06	0.26
Branches:				
terminal	0	0.04	0.04	0.02
axillary	3.6	7.06	7.17	7.57
scale	0.08	0	0	0
Total	3.68	7.1	7.21	7.59
TOTAL	18.75	12.53	9.27	7.85

Table A22 Section 2

	1996	1997	1998	1999
Buds:				
terminal	1.0	0	0	0
axillary	7.81	5.94	3.51	0.21
scale	2.15	0.96	0.21	0
Total	10.96	6.9	3.72	0.21
Branches:				
terminal	0	0.21	0.19	0
axillary	0	2.11	2.96	2.54
scale	0	0	0.04	0
Total	0	2.32	3.19	2.54
TOTAL	10.96	9.22	6.91	2.75

Table A23 Section 3

	1997	1998	1999	
Buds:				
terminal	0.98	0	0	
axillary	23.8	11.49	1.28	
scale	1.34	1.04	0	
Total	26.12	12.53	1.28	
Branches:				
terminal	0	0	0	
axillary	0	8.34	1.51	
scale	0	0	0	
Total	0	8.34	1.51	
TOTAL	26.12	20.87	2.79	

Table A24 Section 4

	1998	1999
Buds:		
terminal	0.94	0.02
axillary	21.81	5.74
scale	2.17	0.51
Total	24.92	6.27
Branches:		
terminal	0	0
axillary	0.21	12.77
scale	0	0
Total	0.21	12.77
TOTAL	25.13	19.04

Section 5

	1999
	0.96
	20.40
	1.94
	23.3
	0
	0.11
	0
	0.11
	23.41

Ash : oak experiment

Table A25 Section 1 (lowest)

	1996	1997	1998	1999
Buds:				
terminal	0	0	0	0
axillary	15.5	5.74	2.02	0.02
scale	0.17	0	0	0
Total	15.67	5.74	2.02	0.02
Branches:				
terminal	0.04	0.04	0	0
axillary	3.49	6.63	6.57	4.93
scale	0.04	0	0	0
Total	3.57	6.67	6.57	4.93
TOTAL	19.24	12.41	8.59	4.95

Table A26 Section 2

	1996	1997	1998	1999
Buds:				
terminal	1.0	0	0	0
axillary	7.72	5.17	3.07	0.04
scale	2.13	0.57	0.24	0
Total	10.85	5.74	3.31	0.04
Branches:				
terminal	0	0.07	0.02	0
axillary	0	3.04	3.54	2.82
scale	0	0	0	0
Total	0	3.11	3.56	2.82
TOTAL	10.85	8.85	6.87	2.86

Table A27 Section 3

	1997	1998	1999	
Buds:				
terminal	0.96	0	0	
axillary	23.26	9.39	0.15	
scale	1.24	0.93	0	
Total	25.46	10.32	0.15	
Branches:				
terminal	0.02	0.13	0	
axillary	0.33	10.04	1.91	
scale	0	0.04	0	
Total	0.35	10.21	1.91	
TOTAL	25.81	20.53	2.06	

Table A28 Section 4

	1998	1999
Buds:		
terminal	0.96	0
axillary	20.54	4.35
scale	1.87	0.15
Total	23.37	4.5
Branches:		
terminal	0	0
axillary	0.37	11.87
scale	0	0
Total	0.37	11.87
TOTAL	23.74	16.37

Section 5

	1999
	0.98
	21.46
	2.61
	25.05
	0
	0.28
	0
	0.28
	25.33

Results from stage 2 analysis of buds and branches: assessments with significant differences between mixture treatments

Table A29 Ash : cherry - br99a5

Mixture	Mean	Min.	Max.	Total
A_0B_6	0.17	0	2	2
A_2B_4	0.58	0	4	7
A_4B_2	0.33	0	2	4
A_6B_2	1.08	0	5	13

Accumulated analysis of deviance table

	d.f.	dev.	mean dev.	dev. ratio	F prob.
Blocks	11	33.79	3.07	2.38	0.025
Mixture	1	7.14	7.14	5.54	0.024
Residual	35	45.16	1.29		
Total	47	86.11	1.83		

Table A30 Ash : cherry - bu98a2

Mixture	Mean	Min.	Max.	Total
A_0B_6	1.00	0	4	12
A_2B_4	1.25	0	4	15
A_4B_2	2.25	0	6	27
A_6B_2	2.50	0	5	30

Accumulated analysis of deviance table

	d.f.	dev.	mean dev.	dev. ratio	F prob.
Blocks	11	24.946	2.268	1.87	0.079
Mixture	1	10.521	10.521	8.68	0.006
Residual	35	42.436	1.212		
Total	47	77.903	1.658		

Table A31 Ash : cherry - br98a4

Mixture	Mean	Min.	Max.	Total
A_0B_6	0.42	0	3	5
A_2B_4	0.75	0	4	9
A_4B_2	0.92	0	6	11
A_6B_2	1.50	0	6	18

Accumulated analysis of deviance table

	d.f.	dev.	mean dev.	dev. ratio	F prob.
Blocks	11	41.73	3.79	2.02	0.057
Mixture	1	7.98	7.98	4.25	0.047
Residual	35	65.83	1.88		
Total	47	115.55	2.46		

Table A32 Ash : beech - br97a2

Mixture	Mean	Min.	Max.	Total
A_0B_6	4.75	0	10	57
A_2B_4	5.52	0	10	65
A_4B_2	6.27	2	9	69
A_6B_2	7.33	4	12	88

Accumulated analysis of deviance table

	d.f.	dev.	mean dev.	dev. ratio	F prob.
Blocks	11	12.69	1.15	0.77	0.668
Mixture	1	7.49	7.49	4.99	0.032
Residual	35	51.09	1.503		
Total	47				

Table A33 Ash : beech - br97a2

Mixture	Mean	Min.	Max.	Total
A_0B_6	18.67	8	26	224
A_2B_4	21.00	14	30	252
A_4B_2	22.64	12	30	249
A_6B_2	25.00	14	30	300

Accumulated analysis of deviance table

	d.f.	dev.	mean dev.	dev. ratio	F prob.
Blocks	11	12.99	1.18	0.66	0.761
Mixture	1	11.66	11.6	6.56	0.015
Residual	35	60.48	1.77		
Total	47	85.13	1.85		

Table A34 Ash : beech - br97a1

Mixture	Mean	Min.	Max.	Total
A_0B_6	6.00	1	11	72
A_2B_4	6.17	3	10	74
A_4B_2	8.82	4	17	97
A_6B_2	7.83	4	14	94

Accumulated analysis of deviance table

	d.f.	dev.	mean dev.	dev. ratio	F prob.
Blocks	11	26.36	2.39	2.14	0.044
Mixture	1	5.19	5.19	4.64	0.038
Residual	35	38.04	1.11		
Total	47	69.59	1.513		

Table A35 Ash : beech - br97a2

Mixture	Mean	Min.	Max.	Total
A_0B_6	10.25	4	19	123
A_2B_4	12.08	5	18	145
A_4B_2	12.73	6	19	140
A_6B_2	16.00	9	24	192

Accumulated analysis of deviance table

	d.f.	dev.	mean dev.	dev. ratio	F prob.
Blocks	11	27.93	2.54	1.37	0.232
Mixture	1	14.86	14.86	8.01	0.008
Residual	35	63.06	1.85		
Total	47	105.86	2.301		

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