Environmental influences on the growth and survival of seedlings of Acer pseudoplatanus

Heath, David B.

How to cite:

Heath, David B. (1992) *Environmental influences on the growth and survival of seedlings of Acer pseudoplatanus*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/6127/

Environmental influences on the growth and survival of seedlings of *Acer pseudoplatanus*

by

David B. Heath

A dissertation submitted in partial fulfilment of the requirements for the degree of Master of Science, Advanced Course in Ecology

Department of Biological Sciences
University of Durham
1992

ACKNOWLEDGEMENTS

I would like to thank Dr. J.A. Pearson and Dr. P. Hulme for their supervision of this study and for providing materials. Thanks to Val Standen for locating sycamore regeneration in Moorhouse Wood, and for keeping the site free from conservation volunteers. Thanks to Tim Waters for the leaf-area equation. Many thanks to all the members of the MSc. Ecology class for their invaluable support.

CONTENTS

PAGE

Appendices

List of Figures

List of Tables

SUMMARY

Stomatal index was measured in leaves of first-year seedlings of sycamore (*Acer pseudoplatanus* L.) transplanted into woodland. Leaves of seedlings growing at high density exhibited a lower stomatal index than those of seedlings growing at low density ($P<0.002$). Stomatal index was shown to be responsive to light climate and soil moisture. Seedlings at high density had higher leaf-weight ratios ($P<0.05$) and lower root:shoot ratios ($P<0.05$). The adaptive significance of these differences is discussed in relation to sycamore's shade-tolerance.

A survivorship study of first-year sycamore seedlings showed that seedling mortality was density-dependent but not distance-dependent. Mortalities due to fungal infection and wilt were particularly high and showed strong density-dependence. The relative importance of density- and distance-dependent mortality in recruitment processes in temperate and tropical forests is discussed.

INTRODUCTION

The sycamore (*Acer pseudoplatanus* L.) is a naturalized deciduous tree with remarkably successful natural regeneration. It is often considered to be an alien weed but its natural regeneration has been exploited by forestry. Its ecology is reviewed by Jones (1945) and this has been updated by Grime *et al.* (1988). The sycamore has been the subject of numerous studies for many decades, and is still being investigated. Recently, physiological mechanisms that contribute to the shade tolerance of sycamore seedlings have been proposed (Taylor and Davies 1985, 1986a, 1986b, 1988). The occurrence of abundant sycamore seedlings beneath a woodland canopy may be explained by sycamore's ability to maintain loosened cell walls and growth for limited periods in the dark. The common occurrence of sycamore in wetter areas (Pigott 1984) correlates with sycamore leaves exhibiting high cell wall extensibility and high turgor at the same time, allowing rapid growth. Other recent studies in plant physiology have investigated the influence of environmental parameters on stomatal differentiation in leaves (Schoch *et al.* 1980). A study by Ferris (1991) demonstrated that the stomatal index of leaves of sycamore seedlings responded to the environmental parameters of light intensity and soil moisture, these conditions being simulated in greenhouse experiments. It is important to determine whether this response occurs in the field where other environmental parameters are more variable compared to a greenhouse environment. Therefore the stomatal index response has been monitored for seedlings of *Acer pseudoplatanus* transplanted into the field.

Stomatal index is essential in confirming the validity of stomatal frequency as an indicator that stomatal differentiation rates have been modified in response to a change in one or more environmental parameters. Stomatal density (SD) is influenced directly by leaf expansion, in particular that resulting from the expansion of epidermal cells. A leaf that has its expansion restricted by factors such as light and water stress but has not otherwise altered its rate of stomatal differentiation will have an increased stomatal frequency simply as a result of the decreased space between stomata. To conclude that the variation in SD compared to another environment is due to a change in stomatal differentiation might be wrong. If the stomatal index is determined for such a leaf the differences in SD will be seen to have been caused by a reduction in the size of epidermal cells alone, and it can be concluded that the leaf is indeed showing no change in rates of stomatal differentiation. When a leaf has a stomatal frequency that is the result of a genuine change in stomatal differentiation rates then the stomatal index will show a similar change to stomatal frequency. This is illustrated by a study of the response of stomatal frequency to raised CO_2 pressure (Woodward & Bazzaz 1988), where the observation of raised stomatal frequency with decreased CO_2 pressure was confirmed by a similar raise in stomatal index, allowing the conclusion to be drawn that the raise in SD had indeed been caused by a change in rates of stomatal differentiation.

Any study of the influence of environment on stomatal differentiation should involve either the determination of SI or the determination of both SD and SI. However, when immature leaves are being assessed the SD may be inaccurate (Larsen 1968). Stomatal index remains constant as a leaf expands, but the stomatal density varies with the relative expansion of the epidermal cells. In addition the size of stomata increases as the leaf expands, so the immature leaf cannot be used to assess guard cell length, which is an indicator of leaf adaptation to environmental parameters. Therefore only SI was determined for the leaves studied.

Stomatal index is determined very early on in the lifetime of any given leaf. Studies by Schoch *et al.* (1980) on *Vigna sinensis* indicate that the SI of new leaves is determined by the light levels incident on the other mature leaves during the six days prior to the expansion of the new leaf. Therefore in the present study only the third and fourth leaves leaves were studied to ensure that the their stomatal indices were influenced by the woodland environment as recorded, and not influenced by previous conditions in the greenhouse.

The production of a large number of seeds most years by adult sycamores results in profuse natural regeneration in sycamore woods. This makes sycamore woodlands suitable sites for studying recruitment processes. There has been much study of the influence of the parent tree on its progeny (Janzen 1970; Clark & Clark 1984), involving investigations of the impact of a variety of distance-responsive and density responsive agents on the progeny. The studies attempt to determine whether survival of progeny is related to distance from the parent tree, and if so why. Many of these studies are on isolated seed-trees in tropical forests, where the distance mechanism is simple. The study in Moorhouse Wood is an investigation of the survivorship of sycamore seedlings, and in particular relative to distance from the parent tree. Due to the woodland being representative of a temperate forest the trees are closely spaced.

In Moorhouse Wood the adult sycamores are particularly closely spaced, and as a result their seed-shadows overlap. Since no isolated adult sycamores could be found with a reasonable level of seedlings beneath, the methods used in tropical forests could not be used. Instead a number of distance-scores have been devised which take into account a seedling's proximity to not one but many parent trees. Three scores are used; one to assess the proximity to a parent seed-tree, and two to assess the proximity to parent canopies. The first score, the seed-tree distance-score, is the cumulative sum of the reciprocals of the distances between a seedling and all parent trees within 25-m. The point of reference for seedlings is the centre of their quadrat. The other scores, canopy distance-scores, are based on the seed-tree score weighted by the girth of the parent trees. This is based on the assumption that tree girth and canopy size are positively correlated. Two canopy scores are calculated, one ignoring all trees over 15-m from the quadrat in question, referred to as the canopy (15m) distance-score, the other having a cutoff at 25m, referred to as the canopy (25m) distance-score. The 15m score is used to assess the influence of agents that range from the canopy for a distance up to 15m such as larvae. The 25m score is used to assess the general effect the canopy has over a wider area on factors such as light climate and soil moisture, and as a measure of the proximity to a seed source, trees of larger girth and canopy being assumed to produce more seeds than trees of smaller girth and canopy.

A survivorship study was carried out to determine the causes of seedling mortality in the wood. Mortality in seedlings is usually attributed to wilt, fungal infection or predation by animals. Predation in the form of defoliation by invertebrates ranging from the parent tree was assessed separately, to determine the relative importance of predators from and outside the canopy. Predators outside the canopy were assumed to be voles and slugs but only the latter were observed. There are numerous banks in the wood, especially along the northern edge of the study area, and much evidence of tunnels in and around these banks and throughout the wood in general. The large number of rodents in Durham woodlands has been demonstrated by trap studies (Ashby 1959), and this is assumed to be indicative of the potential impact of these predators today.

MATERIALS AND METHODS

Study sites

Hollingside Wood (NZ275405) is a deciduous woodland in Durham. The major tree species include sycamore (*Acer pseudoplatanus*), beech (*Fagus sylvatica*) and Scots pine (*Pinus sylvestris*). The transplantation study was conducted on a south-east facing slope in a stand of almost pure mature sycamore, with scattered individuals of mature beech and immature horse-chestnut (*Aesculeus hippocastanum*). The stand contains very little natural regeneration of tree species. The ground flora at the time of the study consisted of mature bluebells (*Endymion non-scriptus*) throughout the site, and scattered patches of *Rubus*.

Moorhouse Wood (NZ310460) is a deciduous woodland 5 miles north of Durham. The most abundant tree species are oak (*Quercus*), birch (*Betula*), hawthorn (*Crataegus*) and beech (*Fagus*). The natural regeneration study was conducted in an area of the wood containing mature sycamore trees. One side of the study area was bounded by the fence on the north side of the wood. The woodland in the study area is very uneven-aged with much natural regeneration of all tree species, especially sycamore. The ground flora is well-developed over most of the site but some areas lack both a ground flora and a litter layer. The ground flora consists variably of ivy (*Hedera helix*), *Brachypodium sylvaticum* , *Rubus*, *Oxalis*, and stitchwort (*Stellaria holostea*). There is much evidence of rodent activity in the study area, there being numerous burrows in the woodland floor and banks, probably of voles and rabbits.

1. Transplanted population

The source of plant material for the transplanted population was natural regeneration of sycamore from one mature garden tree in Gilesgate Moor. Emerging seedlings with only the cotyledons and in some cases the first true leaf-pair were uprooted with an intact rootball and potted into 7.5 cm pots containing ICI potting and bedding compost (medium grade sphagnum peat). The plants were established and grown in an unheated greenhouse for four weeks. Compost was kept moist and plants shaded from intense sunlight. The fluence rate of photosynthetically active-radiation (PAR) in the greenhouse was approximately 100 μmol m^{-2} s^{-1}. Two weeks prior to transplantation into the field, twelve groups of five seedlings were repotted into 18.5 cm pots with the same compost.

The plants were installed in Hollingside Wood on June 1 in a pure stand of mature sycamore (Figure 1a). At each point two metres from the east and west side of six mature sycamores one pot of five seedlings and three single potted seedlings were buried flush with the soil. The latter were the isolated treatment plants. On June 10 the lengths of all seedlings' leaves were recorded, and light levels (PAR and R/FR) 5cm above the top of the seedlings was measured with SKYE lightmeters from 3 to 4pm under a clear sky.

Measurement of leaf characteristics

Plants were removed from the wood on July 5. Lengths of all seedlings' leaves, original and new were measured, and growth rates calculated. Stomatal peels were taken from the third and fourth leaf-pairs for all the single plants and from three of the grouped-plants. One thin 0.5 cm diameter circle of clear nail varnish was applied to the abaxial side of each leaf, between the major and secondary veins, left to dry for 15 minutes and removed with Sellotape. Five fields of view of 0.048875 mm^2 (x400 magnification) were randomly selected from each peel, centred on intervenal tissue and avoiding vascular tissue. Stomatal number and epidermal number was counted. Stomatal density mm^{-2} and stomatal index were calculated for each leaf:

$$\text{Stomatal density } mm^{-2} = \text{mean of stomatal counts of five fields of view} \times (1/0.048875)$$

$$\text{Stomatal index per field of view} = \frac{\text{number of stomata per field of view}}{\text{number of stomata + number of epidermal cells per field of view}}$$

Stomatal index per leaf = mean of stomatal indices of five fields of view

Fresh and dry weights of leaves, stems and roots were determined for all surviving seedlings. Each leaf was cut from the stem at the base of the petiole, and stems cut from the roots at the soil surface. Compost was washed from the roots. All plant parts were immediately weighed fresh. Leaves were photocopied and leaf area estimated:

Leaf area = maximum width x length (from petiole insertion to tip) x 0.73

All plant parts were dried to constant weight at 80 °C for at least 24 hours and weighed again. Dry weight ratios, root:shoot ratios and dry:fresh weight ratios were calculated for each seedling:

Leaf-weight ratio = W_L / W_T
Stem-weight ratio = W_B / W_T
Root-weight ratio = W_R / W_T
Root:shoot ratio = $W_R / (W_L + W_B)$

W_L, W_B, W_R and W_T are the leaf, stem, root and total plant dry weights, respectively.

Measurement of soil moisture

Soil samples of approximately 15 g were taken from each pot and from the woodland soil adjacent to each pot. Soil was dried at 105 °C for 12 hours, and soil moisture on a wet basis calculated from the equation:

$$\text{Soil moisture} = \frac{\text{mass of fresh soil sample} - \text{mass of oven dry soil sample}}{\text{mass of fresh soil sample}}$$

2. *Field population*

In May 1992, the density of sycamore seedlings and percentage cover of ground layer species was measured in 64 systematically spaced 1 m^2 quadrats marked out every 5-m in a rectangular grid 50-m by 35-m in Moorhouse Wood (Figure 1b). In addition canopy composition above each quadrat and the percentage of ground covered by leaf litter were also recorded in each quadrat. Light levels (PAR and R/FR) were measured at seedling height in each quadrat on June 16 from 3 to 4pm under a clear sky.

Seedling survivorship was determined from May 9 to July 18 at ten day intervals. At the first census the location of all sycamore seedlings in each quadrat was recorded on graph paper, and each seedling marked with a numbered toothpick. The height (from base of stem to growing tip of shoot) and leaf-lengths (true-leaves only) of all seedlings was measured. At subsequent censuses, dead seedlings were recorded as having either wilted, rotted, disappeared or been bitten by an animal (incisor marks were often evident). The height and leaf-lengths of survivors was remeasured. Newly germinated seedlings were marked and measured, and their location recorded.

The location of all adult sycamores (n=12) in and around the grid was recorded, and the total girth (in metres) at breast-height (1.3-m) measured for each tree. The distance (in metres) from each quadrat to each adult tree was calculated. Three adult-proximity scores were calculated for each quadrat:

$$\text{Seed-tree distance-score} = [\, \Sigma\ 1/(\text{ distance to tree}_n\ )\,]^{-1} \quad \text{for } n=1..12$$

If the distance to tree$_n$ is greater than 25-m it is not included in the calculation. This score is a measure of the absolute proximity of the quadrat to adult trees.

$$\text{Canopy (15m) distance-score} = [\, \Sigma\ 1/(\ (\text{distance to tree}_n\ ) \times (\ 1/\text{ tree}_n \text{ girth}\ )\ )\,]^{-1} \quad \text{for } n=1..12$$

If the distance to tree$_n$ is greater than 15-m it is not included in the calculation.

$$\text{Canopy (25m) distance-score} = [\, \Sigma\ 1/(\ (\text{distance to tree}_n\ ) \times (\ 1/\text{ tree}_n \text{ girth}\ )\ )\,]^{-1} \quad \text{for } n=1..12$$

If the distance to tree$_n$ is greater than 25-m it is not included in the calculation.

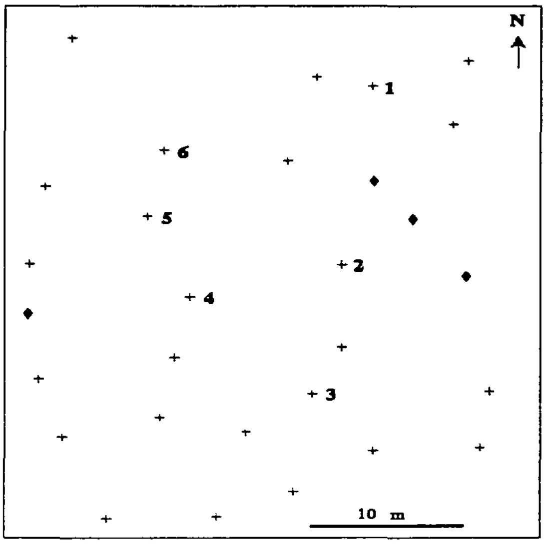


Figure 1a; Plan of site in Hollingside Wood.
Symbols: + = Sycamore; ◆ = Beech; Numbers refer to replicate sites.

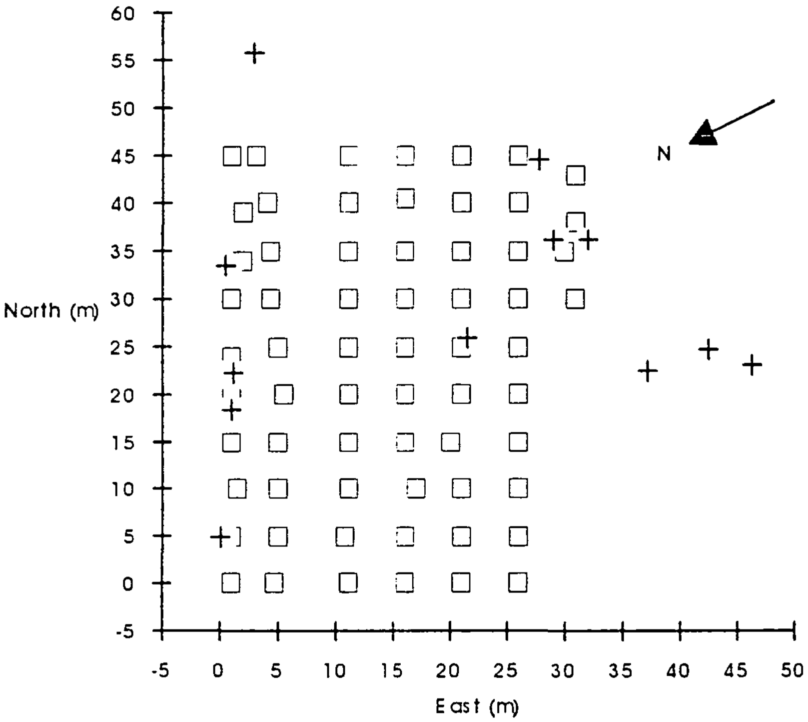


Figure 1b: Plan of site in Moorhouse Wood. Symbols: ☐ = quadrat; + = adult Sycamore.

RESULTS

Stomatal Index

Table 1 summarises the effect of competition on stomatal index (SI) for leaves 3 and 4, and the influence of pot soil moisture. Paired *t*-tests indicate significant differences in SI between the two levels of competition for both leaves, SI being lower in the competing plants than the isolated plants. Further paired *t*-tests indicate no significant difference between leaves 3 and 4, ie no pattern going up the stem in either of the treatments. A paired t-test indicates a significant difference between the moisture levels in the two treatments, but of only approximately 2.5%.

Figure 2 illustrates the correlation between SI and soil moisture summarised in Table 1. SI is significantly reduced ($P<0.1$ for isolated plants; $P<0.05$ for competing plants) by a rise in soil moisture within the treatments group.

Table 1: Summary of mean stomatal index and mean pot soil moisture at each treatment.

Treatment	SI 3rd leaf	SI 4th leaf	Soil moisture (%)
Isolated	0.081306	0.0894	81.29
2x s.e.	0.003512	0.0042	0.6537
Competing	0.062507	0.0682	78.78
2x s.e.	0.002574	0.0048	0.2040
P<	0.002	0.001	0.01

Means of SI and 2x s.e.:3rd leaf, n=10 replicates per treatment. 4th leaf n=4 plants per treatment. Mean pot soil moisture: n=10 replicates.
Data for individual replicates and treatments are listed in Appendix 1.

Plant morphology

There are significant differences in the allocation of dry matter to plant organs between the two treatments. Allocation may be expressed in three ways, weight ratios, proportions, and individual ratios (Table 2).

Table 2: Summary of allocation ratios at the two treatments, and results of paired t-tests.

Ratio	LWR	SWR	RWR	Lprop	Sprop	RSR	L:R	L:S	R:S
Treatment									
Isolated	0.5110	0.1787	0.3103	1.1306	0.2232	0.4908	1.8609	3.1024	1.8290
s.e.	0.0237	0.0122	0.0166	0.0730	0.0212	0.0590	0.1260	0.2562	0.1085
Competing	0.5741	0.1814	0.2445	1.4117	0.2268	0.3340	2.5623	3.4109	1.4743
s.e.	0.0085	0.0099	0.0096	0.0387	0.0166	0.0188	0.1068	0.1649	0.1252
P <	0.05	NS	0.01	0.01	NS	0.05	0.002	NS	0.05

LWR=leaf weight ratio; SWR=stem weight ratio; RWR=root weight ratio; Lprop=leaf / (stem+root); Sprop=stem / (leaf+root); RSR=root:shoot ratio; L:R=leaf:root ratio; L:S=leaf:stem ratio; R:S=root:stem ratio. Means of ratios and s.e.: n=10 replicates per treatment.
Data for individual replicates and treatments is shown in Appendix 2.

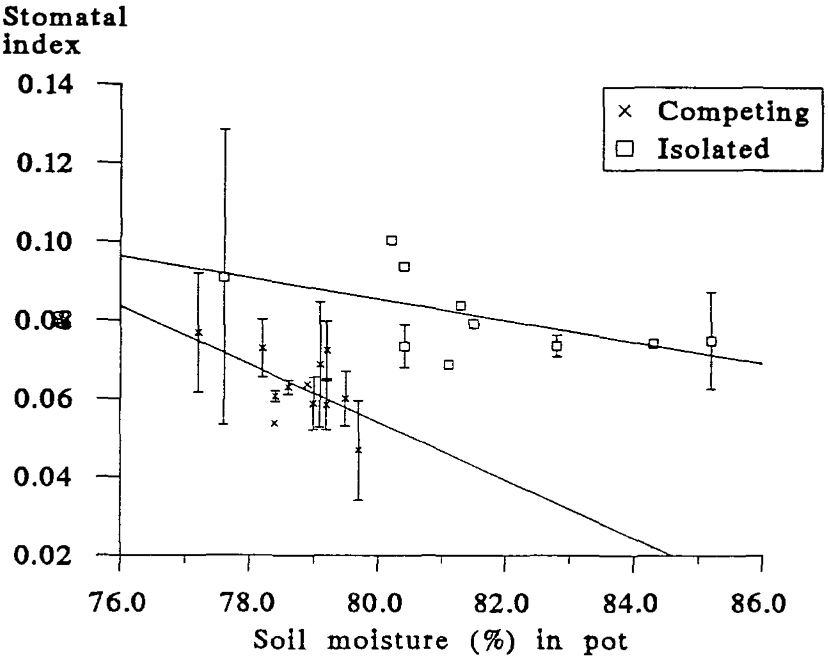


Figure 2: Response of stomatal index to pot soil moisture, for the two competition treatments. Graph shows means and 2x s.e. of SI for each replicate. Data for the competing treatment are of 12 replicates; data for the isolated treatment are of 10 replicates.

A higher level of competition results in a significantly higher allocation of dry matter to leaves (higher LWR, Lprop) and lower allocation to roots (lower RWR, RSR). This is confirmed by the ratio L:R, higher for the competing plants. When stem is considered, there is no significant difference in the L:S ratio, but there is a lower R:S ratio in the competing plants, indicating that with respect to stem, the leaf is given priority to resources over the root in the competing plants.

Table 3 shows the correlations between the total dry weights of plants and the various allocation ratios.

Table 3: Summary of the regression of the allocation ratios against total plant dry weight.

	LWR	SWR	RWR	Lprop	Sprop	RSR	L:R	L:S	R:S
r	0.3303	0.0000	0.3685	0.3041	0.0006	0.3347	0.3251	0.0067	0.2941
P<	0.002	NS	0.002	0.01	NS	0.002	0.01	NS	0.02

Regression: n=73 plants.

Total plant dry weight is correlated positively with LWR, Lprop and L:R ratio and negatively with RWR, RSR and R:S ratio. The L:S ratio does not show any significant pattern with plant dry weight, nor do the ratios Sprop or SWR.

The ratios that are significantly different between treatments also show a significant correlation with total dry weight, and the converse holds for the ratios showing no significant differences. This suggests that total dry weight is the causal agent behind the differences in ratios. Total plant dry weights are shown inTable 4.

Table 4: Means of total plant dry weights in each treatment.

Treatment	Mean total plant dry weight (g)
Isolated	0.2965
2x s.e.	0.0441
Competing	0.2961
2x s.e.	0.1112

Means and s.e.: Isolated treatment, n=23 plants; Competing treatment, n=50 plants.
Data for each treatment is given in Appendix 2.

A paired t-test finds no significant differences in total plant dry weight between the treatments. However, grouping of the mean total dry weights may obscure the individual differences between pairs of results. Appendix 2 lists the total dry weights for each site and treatment. In seven of the 11 pairs the total dry weights of the competing plants exceeds that of the isolated plants, suggesting that plant weight rather than any difference between the treatments is the cause for the difference in ratios.

There is no evidence of a correlation between pot soil moisture and any of the ratios, indicating that the higher soil moisture of the isolated treatment pots is not a cause of differences in ratios.

There is no evidence of secondary thickening as determined from dry:fresh weight ratios, of roots, stems or the total plant as plants mature. (Table 5).

Table 5: Summary of regression of dry:fresh weight ratios for roots, stems and total plant against total plant dry weight.

	roots	stem	total plant
r	0.1453	0.0134	0.1807
P<	NS	NS	NS

Regression: n=73 plants.

The difference in light intensity and spectral quality between replicates (Appendix 3) was too small for the influence of light levels to be determined.

Survivorship study

Density

623 seedlings were counted at the first census and 17 had germinated by subsequent censuses. Of these 513 had died by the final census, leaving 127 survivors. Initial seedling density ranged from 0 to 70 m^{-2}, final density from 0 to 16 m^{-2} (Figure 3). Both frequency distributions are significantly different (P<0.001) from a Poisson distribution indicating the non-randomness of seedling density.

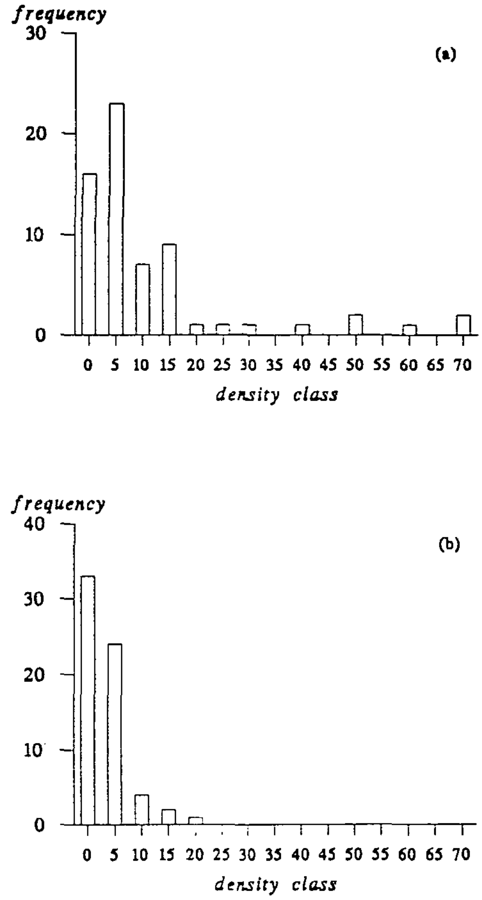


Figure 3: Frequency distributions of seedling density in Moorhouse Wood. (a) Census 1; (b) Census 7. Density classes: 0=none; 5=1-5; 10=6-10; 15=11-15 etc.

The initial pattern of seedling distribution with respect to parent trees is leptokurtic, most seedlings falling in a circle around the parent trees (Figure 4a). The final census shows a more even distribution of seedlings (Figure 4b). Distance in Figure 4 is seed-tree distance.

Seedling densities in each quadrat are given in Table 6. The survival of the population as a whole is shown in Figure 5. Two typical survivorship curves are shown in Figure 6 on a log scale. Survivorship curves of populations that have not reached zero density can be compared to determine whether there is a difference in death rates between the populations, using a statistic such as Peto & Peto's logrank test (Pyke 1988). (Populations that have reached zero are compared by the Mann-Whitney *U* test). The logrank test finds no significant difference in death rates between the numerically similar populations in quadrats (25,1) and (20,5). This statistic has not been used to compare each survivorship curve with all others, since this is tedious and probably statistically unwise. Instead the death rate in each quadrat has

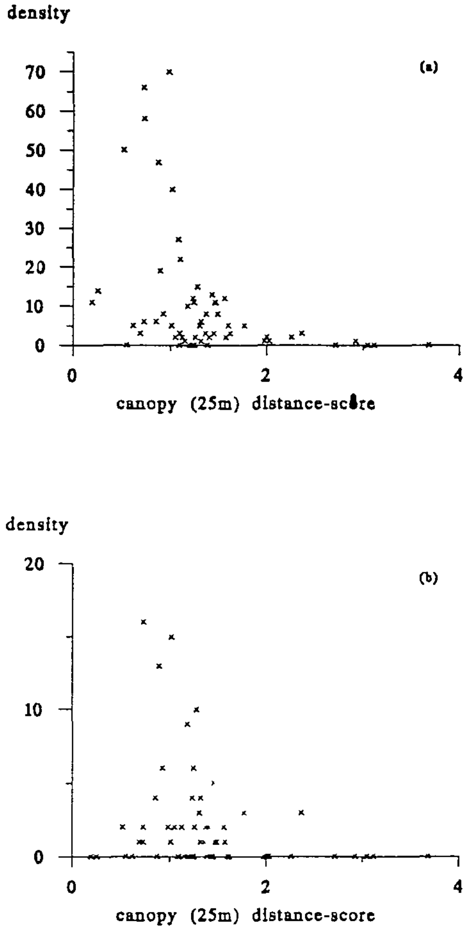


Figure 4: The change in seedling density with distance from parent trees, for quadrats in Moorhouse Wood. (a) initial density; (b) final density. Density in seedlings m $^{-2}$.

been estimated from the initial slope of decline of each curve. This was determined by fitting a regression equation to the slope between the first and fourth census datapoints of log survivorship curves such as those shown in Figure 6.

Initial density is highly correlated ($P<0.001$) with slope of decline (Figure 7), suggesting density-dependent mortality. The risk of mortality of a seedling is directly influenced by their proximity to a neighbouring seedling. A linear regression equation fitted to the data indicates a zero slope at an initial density of 1.9 seedlings m^{-2}.

Slope plotted against seed-tree distance (Figure 8) shows a distribution similar to that of Figure 4, of initial density versus seed-tree distance. The higher risk of mortality nearer the parent tree is due to density and slope being superimposed on the distance axis.

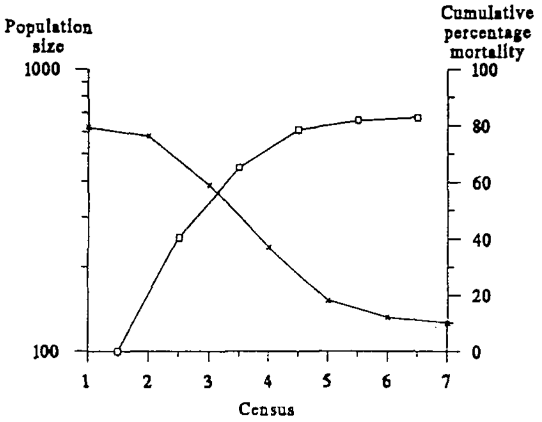


Figure 5: Survivorship curve for the total sample population of sycamore seedlings in Moorhouse Wood. Population size plotted on a log scale. Symbols:x = population size; □ = cumulative percentage mortality.

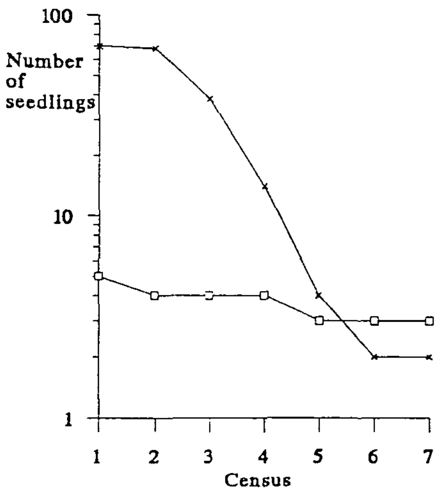


Figure 6: Survivorship curves of high and low density quadrat populations in Moorhouse Wood. Symbols: x = quadrat (20,5); □ = quadrat (15,16).

The mortality of seedlings can also be expressed by the percentage survival of seedlings in each quadrat but this is not as satisfactory as slope of decline, since only initial and final density are considered, and seedling deaths at low density are exaggerated when expressed on a percentage basis. However ultimately it is not the rate of death but the magnitude of death that determines the future distribution of seedlings, and percentage survival is a suitable measure of this. Figure 9 shows the percentage survival at different densities. There is a trend of increasing survival at lower density, which would be expected further from a parent tree. This is confirmed in Figure 10, survival being lower closer to a tree, but the pattern is obscured by the quadrats in which there was low initial density close to a parent tree. This is probably because of overlapping seed-shadows.

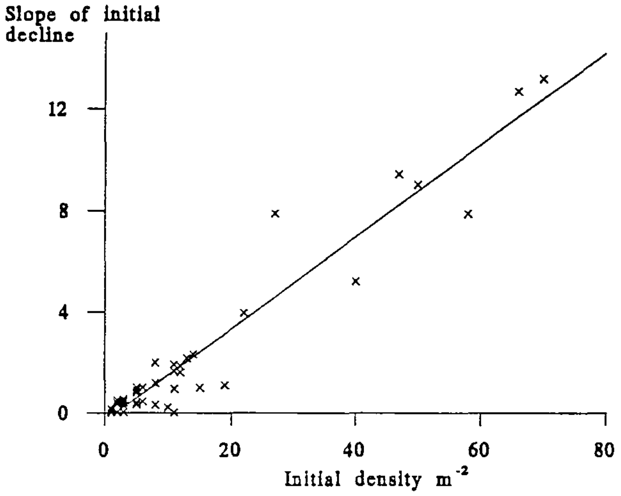


Figure 7: The relationship between seedling mortality rate and initial seedling density. (Rate of mortality or slope of decline of population estimated from the gradient of survivorship curves). Regression line equation: $y = -0.34 + 0.18x$; $r^2 = 0.93$

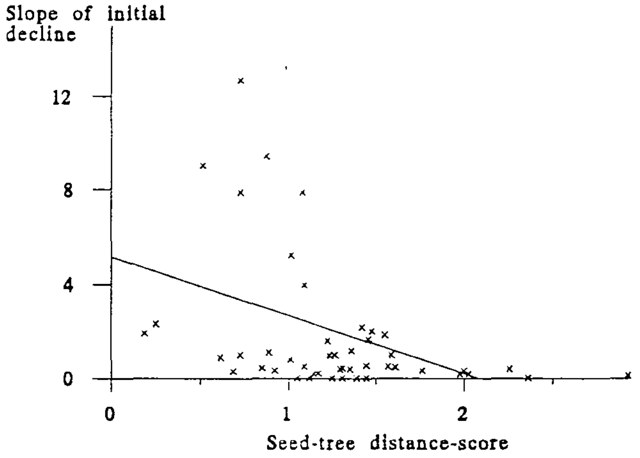


Figure 8: The change in mortality rate with distance from the parent trees. Rate of mortality as for Figure 7. Regression line equation: $y = 5.1 - 2.5x$; $r^2 = 0.15$

The totals that make up percentage survival, initial and final density are shown regressed in Figure

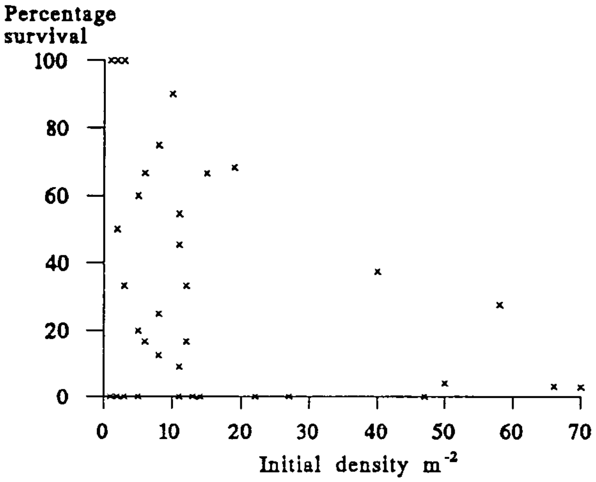


Figure 9: The relationship between seedling survival and initial density.

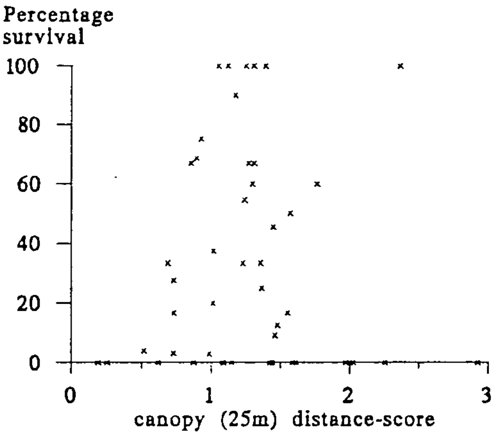


Figure 10: The relationship between seedling survival and distance from the parent trees.

11. It indicates that there is a maximum density which can be maintained (approximately 10 seedlings m^{-2}). Figure 12 shows the total number of deaths regressed against initial density. If seedling mortality fitted a model whereby densities were reduced or maintained at a "target" density such as 10 m^{-2} purely on the basis of the difference between the initial and target density, then these data would fit a straight line with the equation $y = x - 10$, (the dotted line in Figure 12). The linear regression of Figure 12

suggests that the "target" density is 1.8 seedlings m^{-2}. This confirms the estimate of a stable density of 1.9 determined from Figure 7, and the final density centred around approximately 2 seedlings m^{-2} in Figure 4b.

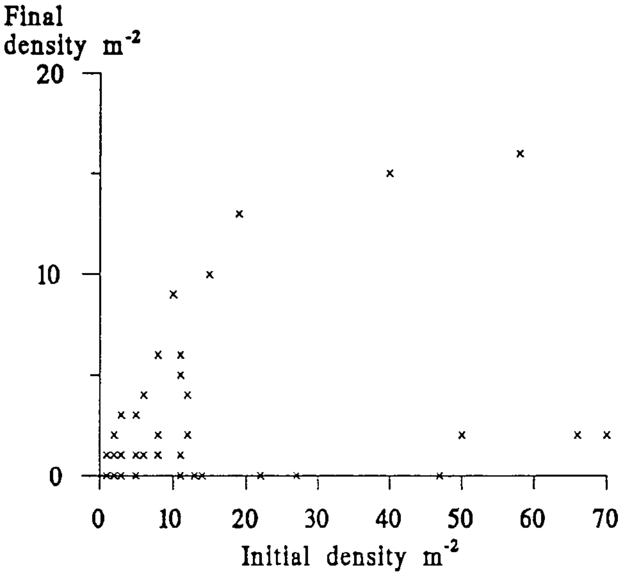


Figure 11: The relationship between final seedling density and initial density.

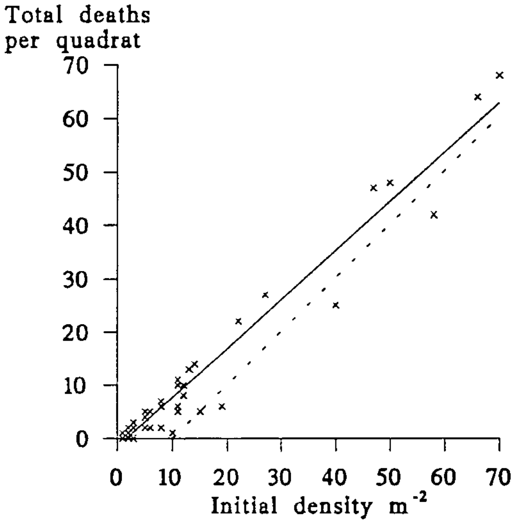


Figure 12: The relationship between initial seedling density and totals deaths. Regression line equation: $y = -1.62 = 0.92x$: $r^2=0.95$;dotted line has equation $y = x - 10$

There is no significant correlation between the percentage vegetation cover in the quadrat and percentage survival of seedlings, suggesting the seedlings can tolerate high levels of competition (Figure 13).

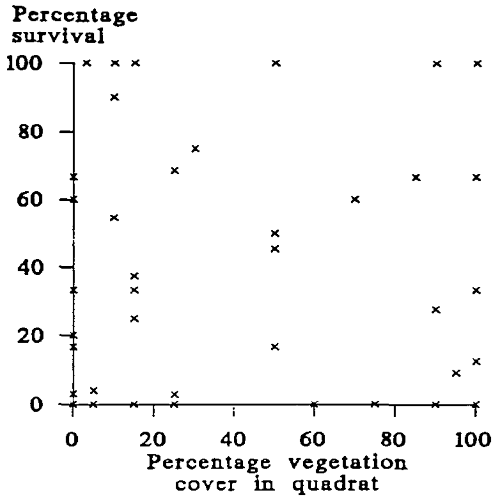


Figure 13: The relationship between seedling survival and percentage vegetation cover of the quadrat.

Table 6: Number of seedlings in each quadrat at each census. Quadrat coordinates referred to in the text are in the form (north side, east side). Dates of each census:(1) 16 May; (2) 26 May; (3) 6 June; (4) 16 June; (5) 26 June; (6) 8 July; (7) 18 July.

East coordinate	Census	North coordinate of quadrat									
		0	5	10	15	20	25	30	35	40	45
1	1	3	14	27	47	50	66	58	11	6	10
	2	2	11	27	47	46	62	54	10	6	10
	3	0	1	17	32	23	31	40	1	6	10
	4	0	0	7	11	6	12	31	0	4	10
	5	0	0	0	1	2	4	21	0	4	9
	6	0	0	0	1	2	2	16	0	4	9
	7	0	0	0	0	2	2	16	0	4	9
5	1	1	13	12	22	70	40	19	5	8	2
	2	1	11	12	18	68	41	18	5	7	2
	3	0	0	9	13	38	39	16	4	7	2
	4	0	0	7	4	14	30	14	3	7	2
	5	0	0	4	2	4	20	13	2	6	2
	6	0	0	4	1	2	15	13	1	6	2
	7	0	0	4	0	2	15	13	0	6	2
11	1	0	3	2	12	11	11	5	5	2	1
	2	0	3	2	10	12	11	5	5	2	1
	3	0	3	1	9	12	9	4	3	2	0
	4	0	3	0	5	9	8	4	2	2	0
	5	0	3	0	3	6	7	3	1	2	0
	6	0	3	0	2	6	6	3	1	2	0
	7	0	3	0	2	5	6	3	1	2	0
16	1	0	0	0	5	2	8	3	3	2	1
	2	0	0	0	4	2	8	3	2	2	1
	3	0	0	0	4	2	5	2	1	2	1
	4	0	0	0	4	2	2	1	0	2	1
	5	0	0	0	3	2	2	1	0	2	1
	6	0	0	0	3	2	2	1	0	2	1
	7	0	0	0	3	2	2	1	0	2	1
21	1	0	0	0	1	2	6	0	3	0	6
	2	0	0	0	1	1	6	0	2	0	6
	3	0	0	0	0	1	4	0	2	0	6
	4	0	0	0	0	1	1	0	0	0	5
	5	0	0	0	0	1	1	0	0	0	4
	6	0	0	0	0	1	1	0	0	0	4
	7	0	0	0	0	1	1	0	0	0	4
26	1	0	0	0	1	2	5	0	0	8	15
	2	0	0	0	0	1	5	0	0	3	15
	3	0	0	0	0	1	3	0	0	3	13
	4	0	0	0	0	1	1	0	0	2	13
	5	0	0	0	0	0	0	0	0	2	10
	6	0	0	0	0	0	0	0	0	2	10
	7	0	0	0	0	0	0	0	0	1	10
31	1							0	0	3	11
	2							0	0	2	7
	3							0	0	2	4
	4							0	0	2	2
	5							0	0	2	2
	6							0	0	1	1
	7							0	0	1	0

Causes of mortality

The causes of mortality between the censuses are summarised in Table 7.

Table 7: Summary of the number of seedlings dying from each cause between each census.

Census interval	Cause of mortality				
	wilted	gone	rotten	animal	Total
1-2	22	23	5	9	59
2-3	28	45	105	15	193
3-4	89	33	8	23	153
4-5	68	5	0	10	83
5-6	13	5	0	2	20
6-7	4	0	0	1	5
Total	224	111	118	60	513

Figure 14 illustrates the density dependent nature of each mortality, fungal infection and wilt showing this to a greater extent than the other causes.

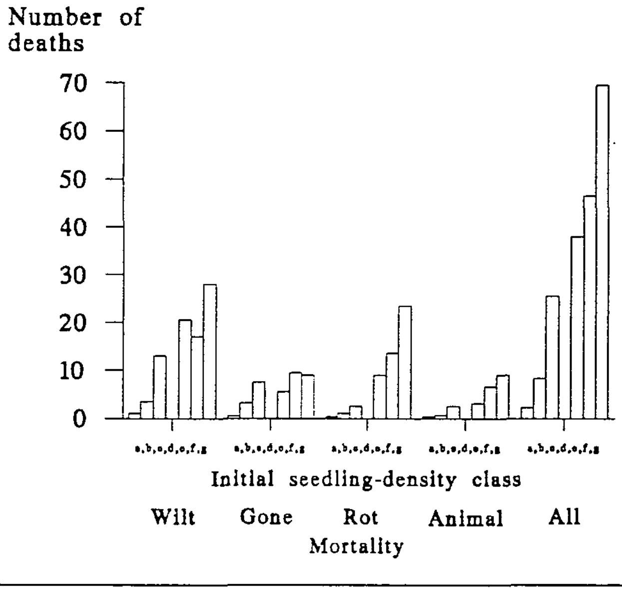


Figure 14: The relationship between seedling density and level of mortality from each cause. Seedling density classes: a, 1-9; b, 10-19; c, 20-29; d, 30-39; e, 40-49; f, 50-59; g, 60+.

Figure 15 shows the number of deaths plotted on a distance axis, using seed-tree distance. It shows a similar distribution to those of initial density (Figure 4a) and slope of decline (Figure 7).

The percentage of seedlings per quadrat dying from fungal infection or wilt are shown regressed against seed-tree distance in Figure 16. There is only a weakly significant correlation (P<0.1) for rotting and no significant correlation for wilt. There are no significant correlations between the percentage of seedlings dying from animal or unknown ("gone") causes and seed-tree distance. There is no correlation between light levels and the percentage of seedlings dying from any cause. (Light levels at each quadrat are listed in Appendix 5).

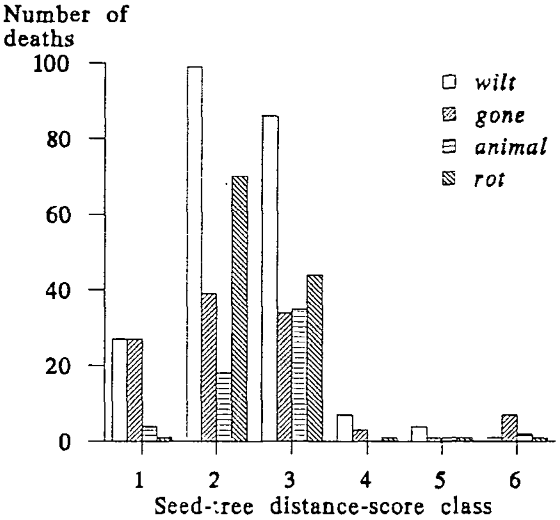


Figure 15: The relationship between mortality and distance from parent trees. Number of deaths from each cause at each distance-score class. Distance-score classes are: 1, 0-1; 2, 1.1 -2; 3, 2.1 -3; 4, 3.1-4; 5, 4.1-5; 6, 5.1-6.

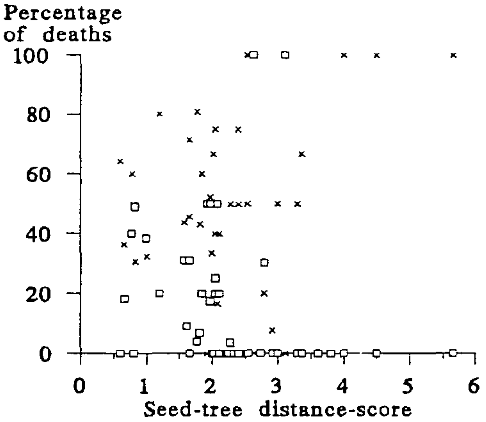


Figure 16: The relationship between deaths from fungal infection and wilting, and distance from parent trees. Symbols: ☐ = rotten; x = wilted.

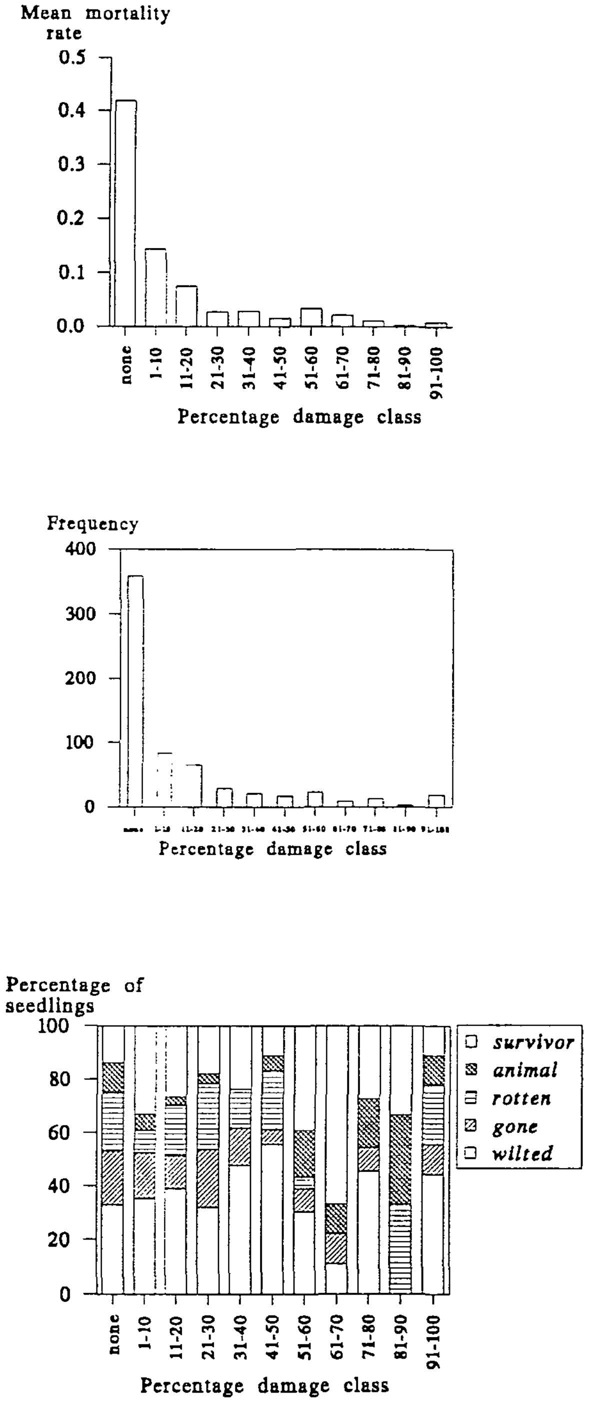


Figure 17: Influence of invertebrate leaf damage on seedling mortality. *Top (a)*: relationship between mean mortality rate of seedlings and percentage leaf damage; *Centre (b)*: frequency distribution of levels of leaf damage in all seedlings; *Bottom (c)* : relationship between leaf damage and cause of seedling death.

The influence of leaf damage apparently caused by invertebrates is shown in Figure 17. Mortality-rate (Figure 17a) suggest that plants receiving least damage are most likely to die, but this is simply because there are more undamaged leaves than damaged, as shown in Figure 17b. There is no indication

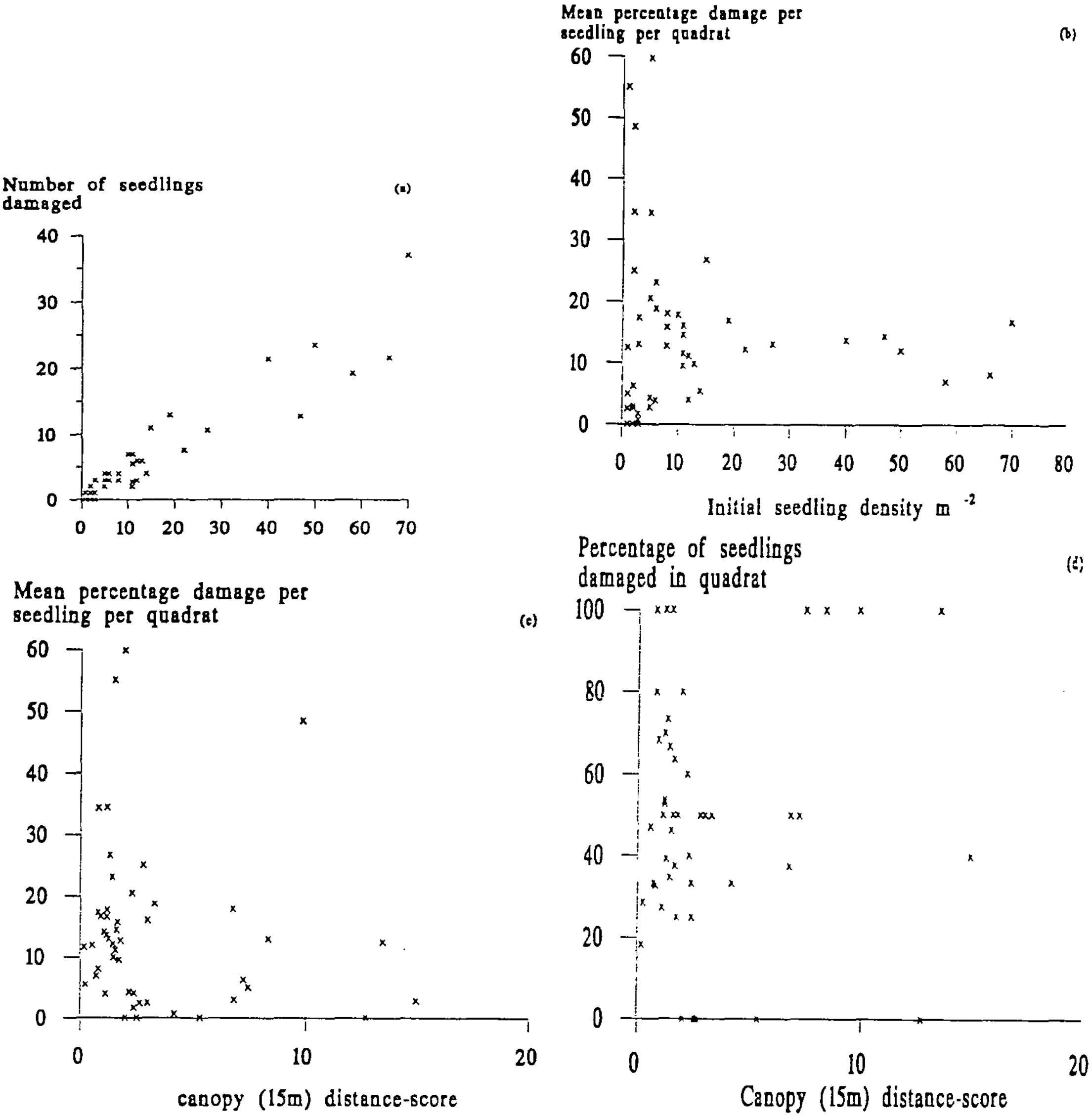


Figure 18: The influence of invertebrate leaf damage. (a) The relationship between the number of seedlings defoliated per quadrat and initial seedling density; (b) The relationship between mean leaf damage per seedling and seedling density; (c) The change in mean damage per seedling with distance from parent trees; (d) The change in the percentage of seedlings defoliated per quadrat with distance from parent trees.

that an increase in leaf damage increases the probability of dying from rot or wilt (Figure 17c). The only indication of multiple causes of mortality in the whole study is of seedlings weakened by fungal infection subsequently dying of wilt. This suggests that the various causes of mortality are compensatory and unrelated to leaf damage. If the probability of death for a particular seedling is high then the seedling will die of the first mortality cause that arises, which will be random due to the unpredictability of weather and predators.

Since invertebrate damage has been demonstrated to be of little significance, (Figure 17c), the distribution of invertebrate damage is not of particular interest, but since it may assume relevance in other situations it is therefore now considered. The distribution of invertebrate leaf-damage is shown in Figure 18. There is evidence of density-dependence in terms of the number of seedlings attacked or left unharmed per quadrat (Figure 18a). When the mean damage per seedling per quadrat is determined the pattern is less clear. Figure 18b shows the mean damage per seedling per quadrat regressed against initial density, and Figure 18c against canopy (15m) distance-score. Neither of the regressions are significant, but the general indication is that mean seedling damage is greater closer to the tree. The lack of a clear pattern in Figures 18b and 18c is due to mean seedling damage per quadrat being an unsatisfactory summary of invertebrate damage in the quadrat. An additional reason is suggested by a plot of percentage of seedlings damaged per quadrat against canopy (15m) distance-score (Figure 18d). This shows that a high percentage of seedlings are damaged at all distances from the canopy. This confirms a suspicion that seedlings are predated by invertebrates falling from canopies other than sycamore, e.g. oak and hawthorn. This could result in there being no particular pattern of the percentage damage versus distance from the parent tree, but the obvious increase in percentage damage close to the adult indicates that there is some distance-dependence. It is interesting that this is the only potential mortality factor to show distance dependence, but has no realised impact on mortality.

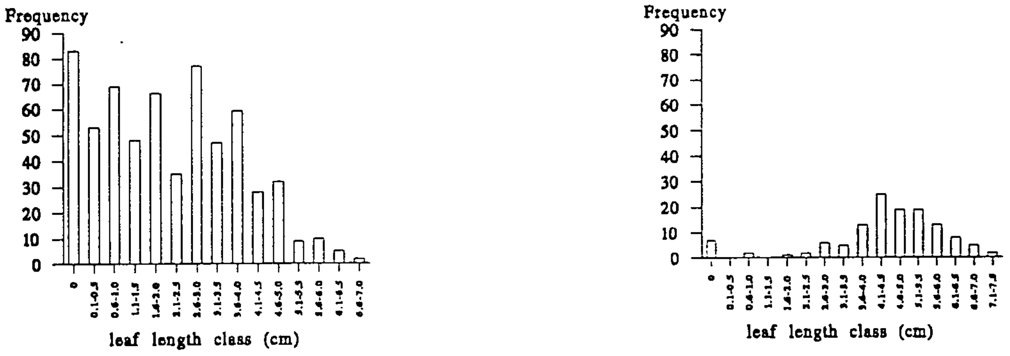


Figure 19: The influence of primary leaf length on seedling survival: (a) Frequency distribution of leaf lengths at census 1; (b) Frequency distribution of leaf lengths of survivors at census 7.

The influence of primary leaf length on seedling survival is shown in Figure 19. The initial leaf lengths of the 623 seedlings in census 1 are shown in Figure 19a, and those of the 127 survivors in Figure 19b. It should be noted that the 0-cm category in Figure 19b includes both those seedlings that had no primary leaves and those whose primary leaves were bitten off. Also the length of longer leaves has been reduced by herbivory. Increases due to growth should also be taken into account, but even when this is considered there is a clear indication that the seedlings with bigger leaves survive better. No attempt has been made to compare these distributions because the seedlings most probably had different germination dates and therefore different opportunities for leaf growth, and because of the complications described above.

The influence of leaf length on susceptibility to the various causes of mortality is shown in Figure 20. Again no attempt has been made to determine the significance of the shapes of these distributions since they are the cumulative result of deaths over the whole season, but it can be concluded that all the mortalities have their greatest effect on the 0-cm class (seedlings with only the cotyledons and no first leaf-pair, or a bitten off leaf-pair). Fungal infection has most impact on smaller leaves and wilt mostly affects leaves of intermediate size, but this is a consequence of the frequency distributions existing at the time most of those mortalities occurred. Most rot occurred when the leaves were small (hence the distribution of Figure 20b), leaving a population of intermediate-sized leaves which were subsequently exposed to drier conditions, hence the large number of intermediate-sized leaves dying from wilt (Figure 20a).

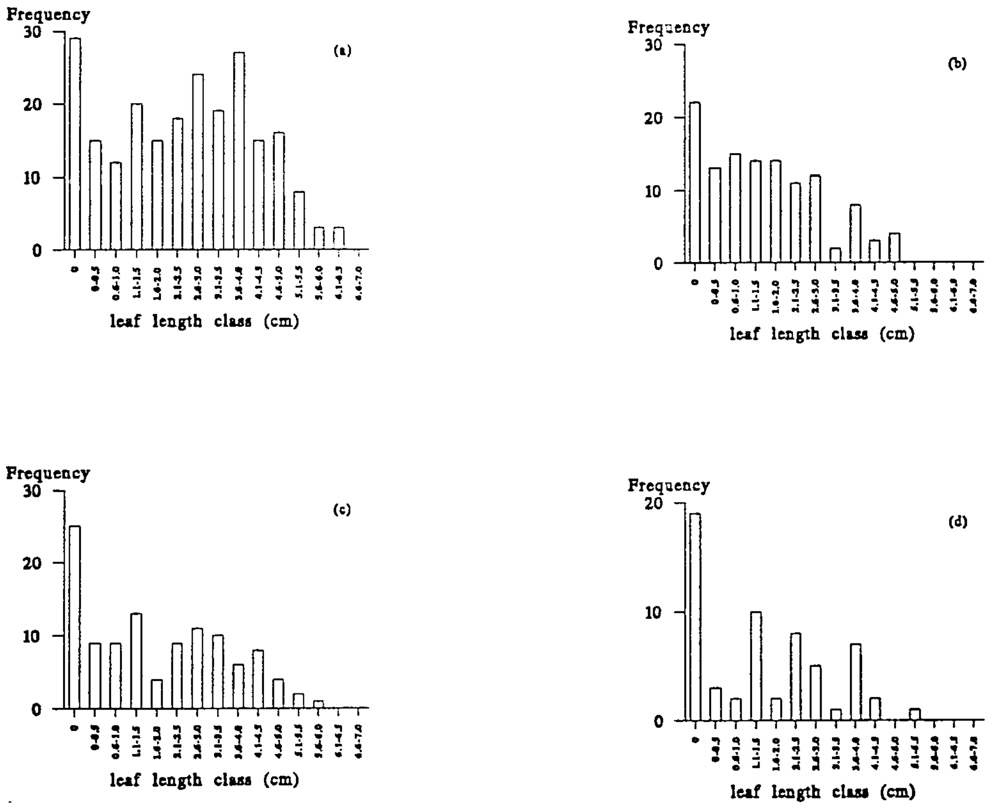


Figure 20: The relationship between leaf length and cause of mortality: Frequency distribution of leaf lengths of seedlings dying from: (a) wilt; (b) fungal infection; (c) unknown cause; (d) animal predation.

The influence of animals (Figure 20d) has been analysed further in an attempt to overcome the problems described above. The mean length of primary leaves at the time of each predation was determined, and the length of the predated leaf regressed against that of the mean leaf-length available in the quadrat in which the predation occurred (Figure 21). The significant correlation (P<0.001) suggests that animals predate seedlings with a leaf-length similar to that of the mean available, i.e. they do not select the biggest leaves.

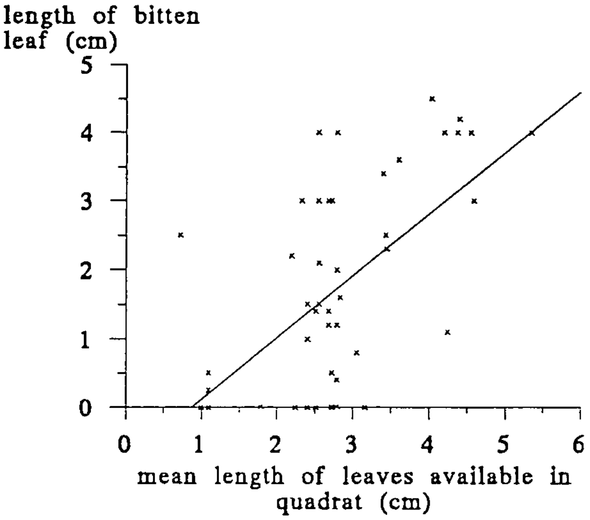
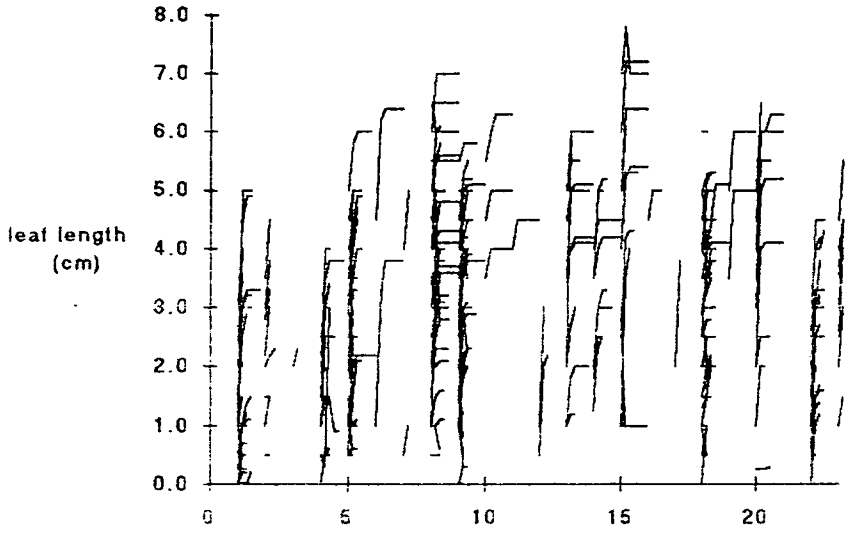
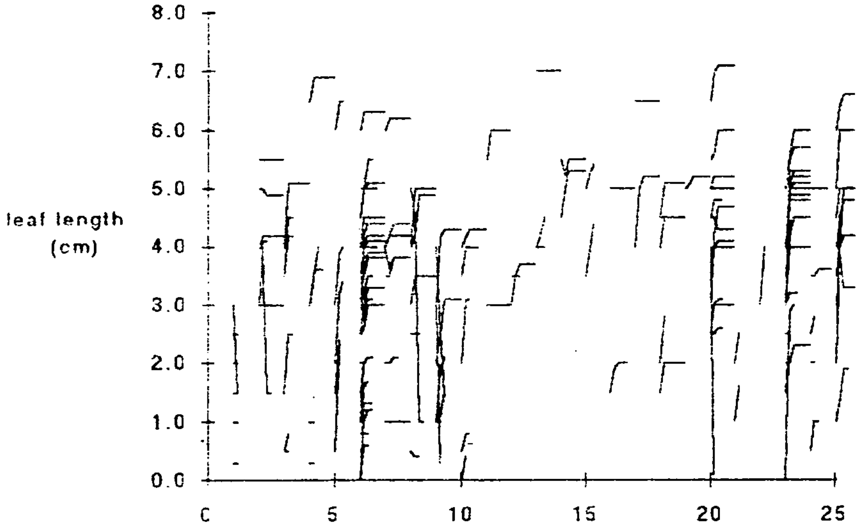


Figure 21: The relationship between leaf-length and predation by animals over the whole period.

The growth of seedlings' primary leaves is shown in Figure 22. It should be noted that these curves terminate upon death, therefore the decline in growth rate towards the end of the period may not be evident.

Figure 22: Growth of primary leaves in Moorhouse Wood from census 1 to 7. Each curve is for one leaf of the primary-pair, for all seedlings in the quadrat. Sets of curves are ranked from 0 (shaded) to 25 (open habitat), according to the value of PAR in the quadrat. Top: Quadrats (0,1) to (25,11); bottom: Quadrats (25,16) to (43,31).





DISCUSSION

Transplant study

The results of the experiment in Hollingside Wood suggest that grouping plants together at high density has several physiological effects on the plants. The differences between the two treatments may indicate the causes of the differential growth of the plants under the two treatments. The differences between the treatments are mainly those of light levels, root competition and soil moisture, the latter being not a deliberately imposed condition, but a consequence of the size of the pot.

The two treatments received the same irradiance of PAR, but the competing plants are self-shading which will result in some plants' leaves receiving irradiance of a lower intensity and a reduced R/FR ratio. Measurement of the light microclimate within competing plants was not recorded at the time of the experiment, but subsequent measurements found the R/FR ratio beneath seedlings' leaves to be 0.63 compared to 0.93 above the leaf, in blue sky conditions. It is assumed that a similar reduction would have occurred in the woodland where the R/FR ratio above the leaf was approximately 0.73 during the course of the experiment. Fitter (1987) describes the competition by plants for PAR, competition being governed by the nature of the incident photons, which may be absorbed, transmitted or reflected by a leaf. Live leaves absorb 85% of visible PAR and scatter 85% of NIR wavelengths (Norman and Campbell 1989). Transmitted light has an enhanced far-red component due to leaves being opaque to light below 700 nm and transparent to light above 700 nm.

There was a significant difference (approximately 2.5%) between the moisture levels in the two treatments. This was sufficient to cause a difference in SI within treatments, but not sufficient to influence dry matter allocation, suggesting that SI is more sensitive to water conditions in the plant or soil than the mechanism which determines dry matter allocation. Schoch *et al.* (1984) propose that phytochrome influences global plant morphology, suggesting that the allocation ratios are less responsive to soil moisture than light or other factors. The levels of soil moisture were insufficiently stressful to test this.

The plants in the two treatments all had the same volume of soil to grow in, but those planted in groups were free to exploit a larger pool of soil resources (water and nutrients) and influence the root chemistry of neighbouring plants.

The influence of these differences on SI and plant morphology will now be considered in turn.

The influence of light on rates of photosynthesis of sun and shade plants has been determined by several authors, but less study has been done on the influence of light on SI. However the two are related and the findings of the former aid an understanding of the mechanism of the latter.

The light saturation curves of sun and shade plants in general have been studied by (Boardman 1977, Dale 1982), and those of birch (*Betula*) and sycamore have been determined by Taylor and Davies (1988). All studies showed the sun-adapted plants to have higher light saturated curves.

Numerous studies indicate the positive relation between light intensity and stomatal density (Fetcher *et al.* 1983; Dean *et al.* 1982; Abrams & Kubiske 1990; Carpenter & Smith 1975; Fernandez 1973; Schoch *et al.* 1984; Young & Yavitt 1987).

Several studies have related the two observations. Holmgren (1968) studied the light saturation curves of sun and shade ecotypes of *Solidaga virgaurea*. Sun plants had both higher light saturation curves and higher SD. Willmot and Moore (1973) studied the rates of CO_2 exchange in sun and shade leaves of the sun and shade species *Silene alba* and *S.dioica*. Rates were higher for the sun leaves, and this was more marked in the light adapted species. In addition the differences in leaf area and stomatal density between the species (smaller leaf, higher SD in *S.alba*) were consistent with the idea that *S.alba* is physiologically and anatomically adapted to grow under higher light levels. The relationship between net photosynthesis and stomatal conductance (related to SD) has been demonstrated for *Atriplex triangularis* (Björkman 1981). Although differences in stomatal conductance between sun and shade plants cannot account for the differences in photosynthesis between plants, an increased stomatal conductance in response to increased light levels is an important factor since it allows the plant to express its increased intrinsic photosynthetic capacity. More importantly the differences in stomatal conductance between light regimes were accompanied by corresponding differences in stomatal frequency, the leaves under higher light levels having 2-3 times the stomatal density of shade plants. These findings suggest that the positive relation between light intensity, light saturation and SI can be applied to other species.

An additional observation in studies of sun and shade-leaves is the reduction in size of guard cells at higher light intensities (Young and Yavitt 1987). Theoretically, smaller guard cells should have increased CO_2 diffusion per unit area and reduced water loss compared to larger guard cells (Bidwell, 1974). However other studies of tree species have found no consistent differences in guard cell length between sun and shade-leaves (Abrams and Kubiske 1990; Fetcher *et al.* 1983).

Björkman (1981) suggested that obligate shade plants have very limited capacity for adjustments to increase the capacity for light-saturated photosynthesis in response to increased light intensity. Sycamore seedlings are not obligate shade plants, but shade-tolerant, therefore they will have some capacity for response to higher light intensities. Taylor and Davies (1988) showed that in sycamore photosynthesis became light-saturated at approximately 300 μmol m^{-2} s^{-1}, but below 200 μmol m^{-2} s^{-1} had a higher rate of net photosynthesis than birch. It is suggested therefore that the observed response of raised SI at higher light levels is the same as that seen by Björkman (1981) in *A. triangularis*; the increase in SI increases the diffusive transport of CO_2 and therefore the rate of photosynthesis of the seedling; as a result the plant is able to express its increased intrinsic photosynthetic capacity, within the range over which a response is possible. Since sycamore does not respond to light intensity above 300 μmol m^{-2} s^{-1} it would be of interest to determine whether SI is also unresponsive. It is assumed that the light intensity in Hollingside Wood was always below 300 μmol m^{-2} s^{-1}, (the maximum light intensity recorded was 122 μmol m^{-2} s^{-1}), i.e. within the range of light intensities at which a response might be expected.

The studies described above concern the influence of light intensity on SI. The effect of the spectral quality of light, i.e. shade, on SI has been determined for *Vigna sinensis* (Schoch *et al.* 1984). The study indicates that phytochrome plays a role in stomatal differentiation, thereby influencing SI.

The influence of soil moisture on SD has been shown in several studies, each indicating that a reduction in soil moisture is associated with a higher SD (Gindel 1969; Abrams 1986). Studies of the leaves of xeric and mesic trees (Tobiessen & Kana 1974; Carpenter & Smith 1975) found that in addition to a lower SD xeric species had smaller guard cells. However a mesic tree will exhibit xeric leaf characters under enough stress. A study of poplars (*Populus*) growing under severe drought conditions found leaves with high SD and small guard cell lengths, xeric characters in a normally mesic tree (Larsen 1961). The smaller stomata may be able to respond more quickly to low leaf water potential than the large stomata of mesic species. It has been suggested that the ranking of species from xeric to mesic results in a ranking similar to that of shade-tolerant to sun-adapted plants (Abrams & Kubiske 1990).

The differences in leaf morphology between sun and shade leaves have been found to be consistent with differences between mesic and xeric species, respectively (Tobiessen & Kana 1974; Abrams 1986). This suggests that the peculiar leaf structure of a sun leaf serves the dual purposes of increased CO_2 uptake and improved water conservation. However this assumes that plants in a sunny environment are also in a xeric environment, and since this is not always the case the stomata will not always be serving this dual purpose. This is evident in a study of SD in hardwood trees (Carpenter & Smith 1975) in which stomatal density was lower for the xeric species but unrelated to the shade-tolerance of the species.

The results of the experiment in Hollingside suggest that soil moisture has an influence within treatments, i.e. when light levels are similar. However when all plants are considered independent of light there is no significant change in SI with moisture level. Since the competing plants are all at a lower moisture level than the isolated plants, they might be expected to have a higher SD and therefore a higher SI. The fact that the competing plants exhibit a lower SI yet at a lower moisture suggests that the influence of light is more dominant, and that the difference in soil moisture is too small to cause an opposing change in SI.

The discussion of environmental influences on SI has been limited to the two factors, namely light and moisture, about which an assessment can be made. Since stomatal frequency is sensitive to a number of environmental variables including light, water relations and temperature, caution should be used when assessing the adaptive significance of stomatal frequency and SI. Indeed the third difference between the two treatments highlights the complexity of the mechanism. The difference in soil volume available for exploitation may result in the competing plants having altered water relations. Other factors discussed below have resulted in different allocation ratios between the two treatments. Differences in root density, leafiness and plant water relations in general can all influence the plant's rate of photosynthesis and need for water conservation measures, and therefore will have an influence on SI. The roots of competing plants do not appear to exhibit any morphological signs of competition, being of similar density as those of the isolated plants. However they may have modified root chemistry as a result of their proximity to neighbouring conspecific roots, and root chemistry has been suggested as another factor which influences SI. In this situation the change in SI is presumably not of adaptive significance but a consequence of the influence of the roots on the rate of stomatal differentiation (J.A.

Pearson, pers. comm.). A mechanism by which light influences leaf morphology and thereby SI has been suggested by Schoch *et al.* (1984), that phytochrome may direct global plant morphogenesis. An increased export of assimilates away from leaves in shade might decrease the energy supply to the leaves, and thereby alter the stomatal differentiation and SI.

The influence of environmental parameters on resource partitioning in the plant has been determined particularly in terms of the effect of the light environment (Evans & Hughes 1961; Hiroi & Monsi 1963; Björkman 1981). Plant morphology may be influenced more by light than other factors (Schoch e*t al.* 1984). The observed increase in LWR in the competing plants may be the result of competition with neighbouring plants for PAR. Harper (1977) notes that plants grown at high density or in shade tend to adjust their root: shoot ratio in favour of shoot, and develop a shallower root system. Evans & Hughes (1961) noted that an increased LWR in *Impatiens parviflora* grown in shade was largely at the expense of root growth, but soil conditions were not ideal. A reduced RWR may not be harmful in shaded environments with adequate nutrient levels and favourable water relations. It is assumed that the levels of moisture and nutrients in were adequate in both treatments in Hollingside, and therefore that any responses of LWR and RWR are not at the expense of other organs but due to a change in the absolute weight of the organs. There is an indication that this was the difference between the two treatments, because root density appears to be similar in both treatments, the main difference lying in the leafiness of the plants. It is suggested that the grouped plants are competing not for soil resources but for light. Evidence of competition for light is required and this can only be obtained from an analysis of the ratios.

Shade results in a reduced RSR (Dowell 1956; Helliwell & Harrison 1979; Fetcher *et al.* 1983), increased LWR, and leaves are commonly thinner and larger (Fitter 1987). LWR is more labile in plants adapted to high light intensity than in shade-adapted plants. Generally woodland species show little response to increased shade whereas plants of open conditions have a very plastic response. Therefore the response of LWR in shade should indicate the shade-tolerance of sycamore. Fitter & Ashmore (1974) found the LWR of the shade-tolerant *Veronica montana* to be unaltered by shade stress. But Loach (1970) found that the shade-tolerant tree species *Acer rubrum* and *Quercus rubra* showed a substantial increase in LWR in response to shade. A series of studies by Taylor and Davies (1985, 1986a, 1986b,

1988) showed that a low photon fluence rate at a low R/FR ratio and higher humidity resulted in increased leaf turgors favourable for the growth of sycamore leaves. This demonstrates that sycamore is not unresponsive to shade, but does not indicate the influence of shade on resource partitioning.

However there are indications that resource partitioning is influenced by plant maturity. This would suggest that sycamore's responsiveness to light as demonstrated above is not the only factor affecting resource partitioning. Correlations have been demonstrated between total plant dry weight and allocation ratios (Table 3). A correlation between LWR and total dry weight has been found in *Impatiens parviflora* (Evans 1972) and *Helianthus annuus* (Hiroi & Monsi 1963). It is concluded that resource partitioning in sycamore responds to both light and total dry weight, but the relative importance of light cannot be determined from the experimental data due to the additive effects of these factors in the treatments. Therefore it would be of value to determine the influence of light independent of total dry weight, by using seedlings of similar total dry weight. However if the different light treatments result in plants of different total dry weights at the end of the experiment, which is entirely possible, then the influence of light will still be uncertain. Such an investigation may therefore be impossible.

An interesting observation concerning the effect of age is shown in *Helianthus annuus* (Hiroi & Monsi 1963). Plants were observed to become increasingly shade-intolerant with age. If this conclusion holds for plants other than obligate sun species then this implies that sycamore will become less shade-tolerant as it matures. Saplings might be expected to have higher demands for light to enable them to support their increased biomass. However sycamore seedlings have been observed to survive for many years in a stunted state in conditions of deep shade, growing very slowly, then growing faster when light intensity increases (Okali 1961). Sycamore saplings have similar shade-tolerances to seedlings (Grime *et al.* 1988) suggesting that conclusions based on obligate sun-plant species cannot be applied to shade-tolerant species.

The measurements of leaf length from the seedlings in Moorhouse Wood provide an interesting record of the response of naturally regenerated seedlings to environmental variables (Figure 22). There is no clear correlation between light intensity and leaf length. However light levels were only measured once and are probably not representative of the light climate during the whole season. There is substantial variation in leaf length of seedlings which presumably germinated at the same time, and this is worthy of further investigation. Taylor and Davies (1988) concluded that leaf growth in sycamore is controlled by changes in leaf turgor. It is therefore possible that water supply to growing seedlings may limit growth. In areas of lower rainfall reduced leaf turgor may lead to reduced leaf growth and this may be particularly harmful as the yield turgor for sycamore is high (Taylor & Davies 1985).

Most of the growth curves in Figure 22 indicate an abrupt termination of growth at around the fifth census. If leaf growth is under genetic rather than environmental control then the leaves may have ceased growing because they had reached a predetermined size within a certain time. But if the leaves are responsive to environmental changes then these may have caused the cessation of growth. Possible causes are canopy closure, photoperiod and reduced soil moisture. The abrupt nature of the termination seems to preclude photoperiod as a cause. It might also preclude canopy closure but this can be remarkably rapid. However the amount of shade cast by the canopy would have to be great to reduce the growth of leaves to such an extent. The lengths and rates of leaf extension of sycamore leaves grown at 25 μmol m^{-2} s^{-1} at a R/FR of 0.26 were similar to those grown at 250 μmol m^{-2} s^{-1} at a R/FR of 1.65 (Taylor & Davies 1988). Therefore it is suggested that leaves have gone into a period of dormancy induced by a water deficit, such as that demonstrated by Charles-Edwards *et al.* (1987) in *Liriodendron.* A criticism of this is the simultaneity of the cessation of growth, which could only occur if the same water deficit was experienced by all seedlings throughout the wood. The likelihood of the soil becoming dry throughout the wood is uncertain. This could be investigated by measuring soil depth beneath each seedling to determine its chances of experiencing water deficit during periods of low rainfall.

Survivorship study

Density

The non-randomness of the initial and final frequency distributions (Figure 4) suggests that seedlings are clumped. This is expected to some extent in a wind-blown seed, but an observation suggests that there may be another cause. Seedlings often germinated in pairs approximately 2 cm apart obviously from the same unseparated samara. Unseparated fruits will not windmill away from the tree increasing the density directly beneath the seed-tree above that expected if all seeds were to separate.

The leptokurtic curve shown in Figure 4a is not a smooth distribution but it demonstrates that density is generally higher closer to the tree. This has been observed in other trees, for example beech

(*Fagus grandifolia*) (Harcombe *et al.* 1982). There are many quadrats with low initial density closer than expected to a parent tree. This is a result of overlapping seed-shadows, the consequence of the seed-trees being less than 25 m apart. However these quadrats highlight a feature of the seedling distribution. If seed-shadows overlap, which they certainly do in Moorhouse Wood, the seeds from one tree should artificially increase the density beneath a neighbouring seed-tree resulting in an increased density but not altering the overall shape of the density distribution around a tree. This has not occurred in this study. Instead of adding to the seedlings already there the seeds from a neighbouring tree are raising the density above zero. This occurs because some of the trees have a distribution that is either extremely flattened or extremely clumped. Both of these are likely to have occurred in the wood. Some of the trees had no apparent seed shadow, and others had seed shadows that were very clumped. This explains how seeds blown into a neighbour's seed shadow can raise the density above zero, and why seedling density can be low very close to the parent tree.

The density-dependent nature of the mortality as illustrated in Figures 7 and 12 suggests that density is the major influence over the future distribution of the seedlings, at least until the end of the first year. This is supported by the findings of Van Miegroet *et al.* (1981). In a two year study of seedlings from germination, mortality during the growing seasons was demonstrated to be density-dependent. In contrast, Hibbs (1979) observed the mortality of seedlings of *Acer pensylvanicum* to be density-independent. This was due to the first-year seedlings being spaced many plant-diameters apart and therefore not likely to have been competing.

The survival of seedlings both at lower density and further from the parent tree (Figure 9 and 10) has also been observed in a study of seedlings of beech (*Fagus grandifolia*) (Harcombe *et al.* 1982).

The regression of initial and final densities (Figure 11) suggests that the final density is attained in either of two ways. If the initial density is at or below 10 m^{-2} it may be maintained at that density, or decline. If the initial density is above 10 m^{-2} it either declines to zero or near zero or declines to 10 m^{-2}. This seems to hold for some of the quadrats with higher initial density but the validity of this is less certain for the quadrats with low initial density, where there is much variation in the final density attained. A similar pattern was observed for seedlings of beech (*Fagus grandifolia*) (Harcombe *et al.* (1982).

The regression of total deaths versus initial density (Figure 12) suggests that the density-dependent mortality fits a simple model whereby the mechanism reducing numbers operates equally at all densities, rather than a fixed percentage of the seedlings being killed, although the two mechanisms would produce much the same result below densities of about 1000 seedlings m^{-2}. The minimum level sustainable is particularly low suggesting that the causes of mortality are very efficient at killing not only dense clumps of seedlings but also less dense groups which might have been considered reasonably isolated but were in fact still too densely packed for them all to survive. There is probably an annual variation in the minimum density sustainable since very high densities of young sycamore saplings occur in other similar sycamore woods in Durham with probably similar opportunities for natural regeneration to occur. The minimum density sustainable is probably a product of the peculiarities of the weather during the year, the light environment of the woodland and the population size of seedling predators. Since all of these will vary from year to year the densities sustainable will also vary. Van Miegroet *et al.* (1981) found that sycamore seedlings had no minimum initial density below which it could not survive in competition with ash (*Fraxinus excelsior*). In comparison ash seedlings apparently required a minimum initial density of 30 seedlings m^{-2} in order to survive competition with sycamore. Although there was little evidence of competition from other tree seedlings in Moorhouse Wood this is indicative of the ability of sycamore to sustain populations at very low densities.

Sycamore seedlings are apparently very tolerant of competition from vegetation in the quadrat, percentage survival being independent of percentage vegetation cover in the quadrat (Figure 13). This is contrary to the finding of Jones (1945), and confirmation of the finding of Helliwell (1965).

Causes of mortality

Seedlings died from wilt, fungal infection or predation by animals. Seedlings which disappeared without trace were not allocated to one of these groups since there was an equal chance that they had died of any of the causes. These are the same causes of mortality observed in a survivorship study of *Acer pensylvanicum* seedlings (Hibbs 1979), except in that study seedling disappearance was attributed to predation.

The causes of mortality varied over the period studied with fungal infection being most important at the start of the period. There was a very high level of rainfall between census 1 and 2 which resulted in a week-long period of high humidity before the wood dried out. This provided ideal conditions for fungal infection, which accounted for 23% of all deaths by the end of the period. Deaths due to wilt occurred throughout the period, and can be split into stages. Initially wilt was due to dry soil conditions. Later, fungal infection weakened a large number of seedlings, which subsequently wilted. These seedlings should perhaps have been classified as dying from rot but since it was difficult to distinguish between seedlings weakened through infection and those weakened simply through poor rooting, they were all classified as having wilted. If they had been distinguishable then fungal infection may have accounted for 43% of all deaths, if the 23 that wilted by census 3 and 89 by census 4 were reclassified.

Animals (assumed to be slugs and voles) seem to have been most active earlier in the period, but the lower rate of predation later may be due to their ignoring the subsequently lower density of seedlings. There is no evidence of selection of leaves of particular lengths. The predation observed is probably the combined effect of slugs, voles and other unknown predators, therefore no conclusion can be drawn of the relevance of specific predators. However of more significance is the finding that predators in general are no more important than any other cause of mortality.

The seedlings that disappeared without trace, classified as "gone" in Table 7, were probably a result of the other causes, seedlings either wilting to an unidentifiable state, rotting completely or being completely eaten. If these deaths were equally distributed between the three causes it indicates the rapidity of the recycling of dead plants, and the need for close attention to seedlings over time. The interval between censuses, ten days, was sufficiently long enough for a reasonable number of deaths to occur, but too long to allow all the processes to be observed accurately.

The conclusion drawn from the analysis of seedling deaths (Figures 14, 15 and 16) is that mortality is density-dependent and distance-independent. Invertebrate leaf damage, the only potential cause of mortality showing any indication of distance-dependence has no influence over the fate of seedlings. The frequency distribution of percentage leaf damage, similar to those seen for other tree species (Edwards & Wratten 1983) suggests that leaves have some defence mechanism to prevent excessive defoliation, but there is no mention of this in the literature (Jones 1945; Grime *et al.* 1988). This may be due to the wet weather which occurred at the peak of the invertebrate's feeding period. However the ephemerality of invertebrates on sycamore in spring is well known (pers.comm. Tim Waters).

As a consequence the main factor influencing a seedling's chances of survival is its proximity to neighbouring seedlings. Mechanisms are understood by which all three causes of mortality, wilt, fungal infection and predation can act in a density-dependent manner. Harper (1977) describes the positive correlation between the rate of advance of the damping-off fungus *Pythium* and the density of seedlings in a variety of plant species. Harper (1977) reviews the behaviour of seedling predators and concludes that well dispersed seed escapes predation more effectively clumped seeds. It is assumed that this also holds for seedlings. The density-dependence of wilting may be due to the cumulative effect of the seedlings' exploitation of the same soil resources, in particular water. In a dense group a consequence of seedlings rooting in the same soil horizon may be that the water resource is insufficient to provide the needs of all the plants. The importance of high leaf turgor in growing sycamores has been stressed (Taylor & Davies 1985).

The lack of distance-dependence in the three causes of mortality can also be explained. The distance-independence of opportunistic predators such as slugs and voles is obvious. Fungal infection by generalist pathogens such as species of *Pythium* and *Fusarium* will occur wherever there are suitable conditions for the pathogen to overcome the seedling's defences. Seedlings weakened by excessive defoliation or excessive shade will be susceptible to infection from such organisms, and since this can occur anywhere, this cause of mortality will be distance-independent. Although the levels of light and humidity prevailing beneath the canopy of a parent sycamore provide an environment unsuitable for growth and suitable for fungal infection this is true beneath any adult tree, so no pattern will be seen by assessing the distance from sycamore adults, but might be seen if the distance to any trees was considered. The distance-independence of wilt occurs for similar reasons with levels of light and soil moisture probably being the important factors, and these too are unrelated to distance to adult sycamores.

Janzen (1970) proposed that a combination of "distance-responsive agents", herbivores which normally feed on adult trees, and density-responsive predators or pathogens would cause disproportionately high seedling mortality close to adult trees. It is concluded that in Moorhouse Wood it is only the density-responsive agents that are the cause of the distribution of seedlings being less clumped around adults than was the initial postdispersal seed shadow (Figure 4b). Clark and Clark (1984) evaluated Janzen's (1970) model and noted that the higher progeny mortality closer to the parent tree could result from factors other than predators or pathogens. There could be interference from the parent tree, such as allelopathy or destructive litterfall. There was evidence of the latter in Moorhouse Wood. The week of high rainfall was also a week of very high wind-speeds, which blew leaves from the adults onto seedlings beneath which provided a humid environment suitable for fungal infection to occur. Competition between seedlings for light, water and nutrients could be the dominant cause of density-dependent seedling mortality, as described above for wilting. Clark & Clark (1984) state that if such self-thinning occurs then the influence of predators and pathogens cannot be demonstrated.

The only support for Janzen's (1970) hypothesis is the evidence of density-dependence of the seedling predators and pathogens. The seedlings will survive anywhere where density is low enough to prevent density-dependeny mortality. Since this is usually furthest from the tree, this is where the best survival is most commonly observed, but as demonstrated it is not the only place.

Although survival over the first few months has been demonstrated to be density-dependent rather than distance-dependent, this may not be the case in subsequent years. Mortality in the second growing season may be distance-dependent, a seedling's requirements for water, light and nutrients being higher than that of a first-year seedling. Distance-dependent mortality, with higher mortality adjacent to the parent tree will then result in recruitment tending to "drift" further from the tree as it ages. The importance of external factors should not be ignored in the study of mortality. Van Miegroet *et al.*(1981) demonstrated that seedling deaths over winter were more important than those occurring during the growing season. Bolton (1949) observed 90% survival of first-year sycamore seedlings to mid-July, but only 5% of the initial germination survived to mid-September and 2% to January.

The evidence on seedling leaf length seems to suggest that larger leaves improves the survival of seedlings. This may indicate a general relation between seedling size and survival. The height of the surviving seedlings was not analysed, but Collins (1990) found no relation between survival and seedling height or the number of leaves per seedling for *Acer rubrum* and *Betula lutea.*

A number of other causes can influence the survival of seedlings, but these have not been studied in detail here. Measurements of the abundance and types of litter in each quadrat were recorded, but since vegetation had such an insignificant effect on survival, the data on litter was not analysed. The litter layer may assume more importance in a site with little vegetation. The depth and composition of the litter layer has been shown to be of importance to seedling survival in several studies (Yamamoto & Tsutsumi 1985; Collins 1990). Light can also have a profound influence on seedling survival. However the influence of light in Moorhouse Wood has not been clearly determined since measurements were only taken on one day. The influence of light has been demonstrated in similar studies (Yamamoto & Tsutsumi 1985; Perkins *et al.* 1988; Collins 1990).

Ecology

In conclusion, the results of this study confirm the shade-tolerance of sycamore, and suggest that there are a number of physiological and ecological adaptations which contribute to its success in a variety of growth conditions, and when subjected to a variety of potential mortality factors. However the influences of environmental parameters have been considered in isolation. The growth and survival of seedlings is influenced by the cumulative response of the seedling to all environmental factors, therefore future studies should attempt to determine the influence of stomatal index and growth form on leaf damage, and *vice versa*. Conclusions from isolated physiological and ecological studies might then provide a greater understanding of the ecology of sycamore.

BIBLIOGRAPHY

Abrams, M. D. (1986). Physiological plasticity in water relations and leaf structure of understory versus open-grown *Cercis canadensis* in northeastern Kansas. *Can. J. For. Res.* **16**: 1170-1174.

Abrams, M. D. & Kubiske, M. E. (1990). Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: Influence of light regime and shade-tolerance rank. *Forest Ecology and Management* **31**: 245-253.

Ashby, K. R. (1959). Prevention of regeneration of woodland by field mice (*Apodemus sylvaticus* L.) and voles (*Clethrionomys glareolus* Schreiber and *Microtus agrestis* L.). *Quart. J. For.* **53**: 228-236.

Bidwell, R.G.S. (1974). *Plant Physiology.* Macmillan, London.

Björkman, O. (1981). Responses to different quantum flux densities In: *Physiological Plant Ecology I, Encyclopedia of Plant Physiology*, vol. 12A (Ed. by O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler), pp. 57-107. Springer-Verlag, Berlin.

Boardman, N. K. (1977). Comparative photosynthesis of sun and shade plants. *Ann. Rev. Plant Physiol.* **28**: 355-377.

Bolton, Lord (1949). The growth and treatment of sycamore in England. *Quart. J. For.* **43**: 161-167.

Carpenter, S.B. & Smith, N.D. (1975). Stomatal distribution and size in southern Appalachian hardwoods. *Can J. Bot.* **53**: 1153-1156.

Charles-Edwards, D. A., Doley, D. & Rimmington, G. M. (1986). *Modelling plant growth and development.* Academic Press, London.

Clark, D. A. & Clark, D. B. (1984). Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *American Naturalist* **124**: 769-788.

Collins, S. L. (1990). Habitat relationships and survivorship of tree seedlings in hemlock-hardwood forest. *Can. J. Bot.* **68**: 790-797.

Dale, J. E. (1982). *The growth of leaves.* Edward Arnold, London.

Dean, T. J., Pallardy, S. G. & Cox, G. S. (1982). Photosynthetic responses of black walnut (*Juglans nigra*) to shading. *Can. J. For. Res.* **12**: 725-730.

Dowell, M.H.D. (1956). The influence of shade on certain trees seedlings, with particular reference to the regeneration of beech. *J. Oxf. Univ. For. Soc.* Ser. **4**, No.4, 32-42.

Edwards, P. J. & Wratten, S. D. (1983). Wound induced defences in plants and their consequences for patterns of insect grazing. *Oecologia* **59**: 88-93.

Evans, G. C. (1972). *The quantitative analysis of plant growth.* Blackwell Scientific Publications, Oxford.

Evans, G. C. & Hughes, A. P. (1961). Plant growth and the aerial environment. 1: Effects of artificial shading on *Impatiens parviflora. New Phytol.* **60**: 150-180.

Fernandez, O. A. & Mujica, B. (1973). Effects of some environmental factors on the differentiation of stomata in *Spirodela intermedia* W.Koch. *Bot. Gaz.* **134**: 117-121.

Ferris, R. (1991). *A study of stomatal patterns in* Plantago lanceolata *L.*, Acer pseudoplatanus *L.*, Sesleria caerulea *L. in relation to environmental parameters.* MSc. Thesis, University of Durham.

Fetcher, N., Strain, B. R. & Oberbauer, S. F. (1983). Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. *Oecologia* **58**: 314-319.

Fitter, A. H. (1987). *Environmental physiology of plants.* 2nd edition. Academic Press, London.

Fitter, A. H. & Ashmore, C. J. (1974). Response of *Veronica* species to a simulated woodland light climate. *New Phytol.* **73**: 997-1001.

Gindel, I. (1969). Stomatal number and size as related to soil moisture in tree xerophytes in Israel. *Ecology* 50: 263-267.

Grime, J. P., Hodgson, J. G. & Hunt, R. (1988). *Comparative plant ecology.* Unwin Hyman, London.

Harcombe, P. A., White, B. D. & Glitzenstein, J. S. (1982). Factors influencing distribution and first-year survivorship of a cohort of beech (*Fagus grandifolia* Erh.). *Castanea* **47**: 148-157.

Harper, J. L. (1977). *Population biology of plants.* Academic Press, London.

Helliwell, D. R. (1965). Factors influencing the growth of seedlings of sycamore and Norway maple. *Quart. J. For.* **59**: 327-337.

Helliwell, D. R. & Harrison, A. F. (1979). Effects of light and weed competition on the growth of seedlings of four tree species on a range of soils. *Quart. J. For.* **73**: 160-171.

Hibbs, D. E. (1979). The age structure of a striped maple population. *Can. J. For. Res.* **9**: 504-508.

Hiroi, T. & Monsi, M. (1963). Physiological and ecological analyses of shade tolerance of plants. 3: Effects of shading on growth attributes of *Helianthus annuus. Bot. Mag.* **76**: 121-129.

Holmgren, P. (1968). Leaf factors affecting light-saturated photosynthesis in ecotypes of *Solidago virgaurea* from exposed and shaded habitats. *Physiol. Plant.* **21**:676-698.

Janzen, D. (1970). Herbivores and the number of tree species in tropical forests. *Amer. Nat.* **104**: 501-525.

Jones, E. W. (1945). Biological Flora of the British Isles. *Acer* L. *J. Ecol.* **32**: 215-252.

Larsen, C. M. (1961). Developpement des stomates de peupliers au cours d'une année seche. *Physiol. Plant.* **14**: 877-889.

Larsen, C. M. (1968). Development of stomata in the genus *Populus* during the course of leaf growth. *Silvae Genet.* **17**: 73-82.

Loach, K. (1970). Shade tolerance in tree seedlings. 2: Growth analysis of plants raised under artificial shade. *New Phytol.* **67**: 273-286.

Norman, J. M. & Campbell, G. S. (1989). Canopy structure. In: *Plant Physiological Ecology.* (Ed. R. W. Pearcy, J. Ehleringer, H. Mooney & P.W. Rundel), pp. 301-325. Chapman & Hall, London.

Okali, D. (1966). A comparative study of the ecologically related tree species *Acer pseudoplatanus* and *Fraxinus excelsior*: Analysis of seedling distribution. *J.Ecol.* **54**: 129-141.

Perkins, T. D., Klein, R. M., Vogelmann, H. W., & Badger, G. J. (1988). *Betula* seedling establishment in response to forest decline induced canopy degeneration. *Eur. J. For. Path.* **18**: 250-252.

Pigott, C. D. (1984). The flora and vegetation of Britain: ecology and conservation. *New Phytol.* **98**: 119-128.

Pyke, D. A. (1986). Statistical analysis of survival and removal rate experiments. *Ecology* **67**: 240-245.

Schoch, P. G., Jacques, R., Lecharny, A. & Sibi, M. (1984). Dependence of the stomatal index on environmental factors during stomatal differentiation in leaves of *Vigna sinensis* L. 2. Effect of different light quality. *J. Exp. Bot.* **35**: 1405-1409.

Schoch, P. G., Zinsov, C. & Sibi, M. (1980). Dependence of the stomatal index on environmental factors during stomatal differentiation in leaves of *Vigna sinensis* L. 1. Effect of light intensity. *J. Exp. Bot.* **31**: 1211-1216.

Taylor, G. & Davies, W. J. (1985). The control of leaf growth of *Betula* and *Acer* by photoenvironment. *New Phytol.* **101**: 259-268.

Taylor, G. & Davies, W. J. (1986a). Yield turgor of growing leaves of *Betula* and *Acer*. *New Phytol.* **104**: 347-353.

Taylor, G. & Davies, W. J. (1986b). Leaf growth of *Betula* and *Acer* in simulated shadelight. *Oecologia* **69**: 589-593.

Taylor, G. & Davies, W. J. (1988). The influence of photosynthetically-active radiation and simulated shadelight on the control of leaf growth of *Betula* and *Acer*. *New Phytol.* **108**: 393-398.

Tobiessen, P. & Kana, T. M. (1974). Drought stress avoidance in the pioneer tree species. *Ecology* **55**: 667-670.

Van Miegroet, M., Verhegghe, J. F. & Lust, N. (1981). Trends of development in the early stages of mixed natural regenerations of ash and sycamore. *Silva Gandavensis*. No. 48.

Willmot, A. & Moore, P.D. (1973). Adaptation to light intensity in *Silene alba* and *S. dioica*. *Oikos* **24**: 458-464.

Woodward, F. I. & Bazzaz, F. A. (1988). The responses of stomatal density to CO_2 partial pressure. *J. Exp. Bot.* **39**: 1771-1781.

Yamamoto, S. & Tsutsumi, T. (1985). The population dynamics of naturally regenerated hinoki seedlings in artificial hinoki stands. V. The development and survivorship of seedlings on the various kinds of forest floors. *J. Jap. For. Soc.* **67**: 427-433.

Young, D. R. & Yavitt, J. B. (1987). Differences in leaf structure, chlorophyll, and nutrients for the understorey tree *Asmina triloba*. *Amer. J. Bot.* **74**: 1487-1491.

Appendices

Appendix 1: Stomatal index of the third and fourth leaf for each site and treatment.

Site	SI, 3rd leaf				SI, 4th leaf	
	Competing	2x s.e.	Isolated	2x s.e.	Competing	Isolated
1e	0.0687	0.016	0.0734	0.0055	0.0698	0.0891
4e	0.0729	0.0074	0.0687	0		
5e	0.0724	0.0074	0.0838	0	0.0804	0.0994
6e	0.0636	0	0.0938	0		
1w	0.0467	0.0128	0.0792	0.001		
2w	0.06	0.007	0.0743	0		
3w	0.0583	0.0063	0.0749	0.0124		
4w	0.0588	0.0068	0.091	0.0376	0.0577	0.0788
5w	0.0629	0.0019	0.1005	0		
6w	0.0607	0.0014	0.0735	0.0027	0.0649	0.0903

Appendix 2: Mean total plant dry weight, and mean resource allocation ratios for each treatment and site. Abbreviations as for Table 2.

Site Competing	Mean total dry weight	2x s.e.	RWR	2x s.e.	SWR	2x s.e.	LWR	2x s.e.	L:R	2x s.e.
1e	0.139	0.016	0.257	0.045	0.158	0.041	0.586	0.029	2.325	0.458
2e	0.379	0.051	0.209	0.02	0.217	0.051	0.573	0.062	2.752	0.484
4e	0.398	0.049	0.248	0.053	0.172	0.019	0.58	0.038	2.469	0.78
5e	0.384	0.031	0.207	0.034	0.187	0.032	0.605	0.008	2.986	0.526
6e	0.124	0.021	0.264	0.157	0.223	0.08	0.514	0.153	2.584	2.004
1w	0.094	0.009	0.292	0.114	0.153	0.019	0.554	0.098	2.021	0.967
2w	0.403	0.052	0.242	0.049	0.175	0.016	0.584	0.055	2.531	0.718
3w	0.301	0.039	0.209	0.086	0.236	0.167	0.555	0.245	3.039	2.849
4w	0.538	0.125	0.219	0.057	0.168	0.022	0.613	0.045	2.921	0.821
5w	0.237	0.027	0.255	0.066	0.171	0.034	0.574	0.055	2.437	0.98
6w	0.263	0.020	0.286	0.075	0.136	0.039	0.578	0.061	2.121	0.719
Isolated										
1e	0.257	0.052	0.282	0.072	0.164	0.033	0.554	0.039	2.026	0.671
2e	0.104	0.047	0.413	0.628	0.203	0.007	0.384	0.635	1.717	4.146
4e	0.156	0.044	0.31	0.133	0.156	0.052	0.534	0.081	1.777	1.026
5e	1.336	0.000	0.218	0	0.222	0	0.56	0	2.568	0
6e	0.305	0.000	0.304	0	0.154	0	0.542	0	1.781	0
1w	0.197	0.079	0.308	0.165	0.154	0.063	0.538	0.111	2.075	1.834
2w	0.093	0.069	0.368	0.205	0.265	0.296	0.367	0.501	1.135	1.994
3w	0.19	0.013	0.293	0.149	0.145	0.029	0.562	0.178	2.02	1.636
4w	0.157	0.016	0.352	0.096	0.186	0.039	0.462	0.073	1.369	0.639
5w	0.173	0.000	0.264	0	0.135	0	0.6	0	2.274	0
6w	0.289	0.080	0.301	0.024	0.181	0.024	0.518	0.045	1.727	0.289

Competing	L:S	2x s.e.	R:S	2x s.e.	Lprop	2x s.e.	Sprop	2x s.e.	RSR	2x s.e.
1e	3.841	0.91	1.715	0.673	1.42	0.175	0.189	0.059	0.348	0.083
2e	2.712	0.969	0.98	0.236	1.359	0.338	0.28	0.083	0.265	0.032
4e	3.385	0.261	1.475	0.428	1.396	0.218	0.208	0.028	0.335	0.093
5e	3.295	0.498	1.153	0.352	1.533	0.052	0.232	0.049	0.264	0.054
6e	2.484	0.984	1.373	1.323	1.175	0.677	0.294	0.135	0.397	0.322
1w	3.609	0.375	1.944	0.995	1.277	0.46	0.181	0.026	0.426	0.246
2w	3.377	0.559	1.388	0.278	1.435	0.314	0.212	0.024	0.323	0.088
3w	3.213	3.844	0.97	0.36	1.548	1.669	0.33	0.296	0.27	0.133
4w	3.688	0.474	1.337	0.504	1.606	0.294	0.202	0.032	0.284	0.099
5w	3.498	0.883	1.611	0.809	1.383	0.35	0.207	0.047	0.351	0.118
6w	4.416	1.171	2.27	1.28	1.396	0.361	0.159	0.053	0.41	0.158
Isolated										
1e	3.412	0.456	1.772	0.808	1.25	0.2	0.197	0.047	0.397	0.141
2e	1.912	3.202	2.026	3.027	0.873	1.931	0.254	0.011	0.988	2.127
4e	3.439	0.634	2.046	1.537	1.153	0.374	0.186	0.074	0.456	0.281
5e	2.516	0	0.98	0	1.271	0	0.286	0	0.279	0
6e	3.529	0	1.981	0	1.184	0	0.182	0	0.437	0
1w	3.619	1.111	2.227	1.692	1.21	0.562	0.184	0.09	0.47	0.322
2w	1.95	4.066	1.516	0.919	0.713	1.355	0.389	0.56	0.604	0.521
3w	3.917	2.001	2.003	0.631	1.329	0.946	0.17	0.039	0.423	0.3
4w	2.52	0.554	1.955	0.856	0.871	0.262	0.229	0.058	0.555	0.216
5w	4.432	0	1.949	0	1.503	0	0.157	0	0.359	0
6w	2.881	0.649	1.665	0.137	1.079	0.201	0.222	0.035	0.431	0.05

Appendix 3: Light levels in Hollingside Wood.

Site	PAR µmol s^{-1} m^{-2}	R/FR ratio
1e	25	0.80
1w	122	0.75
2e	19	0.75
2w	21	0.74
3e	20	0.75
3w	22	0.75
4e	18	0.73
4w	36	0.76
5e	67	0.85
5w	22	0.75
6e	25	0.74
6w	24	0.74

Appendix 4: Distance scores, vegetation cover and seedling densities in quadrats in Moorhouse Wood.

Quadrat (north,east)	Seed-tree distance score	Canopy (15m) distance score	Canopy (25m) distance score	Percent vegetation cover	Initial density	Final density	Percent survival	Total deaths
(0, 1)	3.4	2.1	1.6	25	3	0	0	3
(0, 4.6)	4.0	2.7	2.0	0	1	0	0	1
(0, 11)	5.8	4.8	3.0	78	0			
(0, 16)	9.7		4.4	30	0			
(0, 21)	21.2		8.7	80	0			
(0, 26)				80	0			
(5, 1)	0.6	0.3	0.3	0	14	0	0	14
(5, 5)	2.9	1.5	1.4	0	13	0	0	13
(5, 10.7)	4.0	4.2	2.4	50	3	3	100	0
(5, 16)	4.9		3.1	80	0			
(5, 21)	7.3		3.7	90	0			
(5, 26)	21.4		12.5	100	0			
(10, 1.4)	2.3	1.3	1.1	0	27	0	0	27
(10, 5)	2.4	1.6	1.2	15	12	4	33	8
(10, 11)	3.6	2.8	2.3	60	2	0	0	2
(10, 17)	4.5		2.7	0	0			
(10, 21)	5.0		3.0	70	0			
(10, 26)	16.5		5.0	75	0			
(15, 1)	1.6	1.1	0.9	100	47	0	0	47
(15, 5)	2.0	1.5	1.1	90	22	0	0	22
(15, 11)	2.8	2.5	1.6	50	12	2	17	10
(15, 16)	3.3	14.9	1.8	70	5	3	60	2
(15, 20)	3.1	13.4	2.0	15	1	0	0	1
(15, 26)	5.7	7.5	2.9	75	1	0	0	1
(20, 1)	0.8	0.6	0.5	5	50	2	4	48
(20, 5.5)	1.7	1.2	1.0	25	70	2	3	68
(20, 11)	2.5	3.0	1.4	50	11	5	45	6
(20, 16)	2.3	9.8	1.4	3	2	2	100	0
(20, 21)	2.4	7.2	1.6	50	2	1	50	1
(20, 26)	3.0	5.4	2.0	75	2	0	0	2
(24, 1)	1.0	0.8	0.7	0	66	2	3	64
(25, 5)	1.8	1.2	1.0	15	40	15	38	25
(25, 11)	2.1	1.7	1.2	10	11	6	55	5
(25, 16)	1.9	6.8	1.4	15	8	2	25	6
(25, 21)	0.8	1.2	0.7	0	6	1	17	5
(25, 26)	2.1	2.3	1.6	100	5	0	0	5
(30, 1)	1.8	0.7	0.7	90	58	16	28	42
(30, 4.3)	2.1	0.9	0.9	25	19	13	68	6
(30, 11)	2.1	2.0	1.3	0	5	3	60	2
(30, 16)	2.0	8.3	1.4	0	3	1	33	2
(30, 21)	1.6	2.6	1.2	70	0			
(30, 26)	1.9	1.9	1.2	100	0			
(30, 31)	2.1	1.5	1.4	40	0			
(34, 2)	0.7	0.2	0.2	5	11	0	0	11
(35, 4.3)	1.9	0.8	0.6	0	5	0	0	5
(35, 11)	2.1	2.2	1.0	0	5	1	20	4
(35, 16)	2.0	2.4	1.1	0	3	0	0	3
(35, 21)	2.0	2.6	1.4	25	3	0	0	3
(35, 26)	1.5	1.6	1.1	95	0			
(35, 30)	0.6	0.6	0.5	100	0			
(39, 2)	2.6	1.5	0.8	0	6	4	67	2
(40, 4)	2.5	1.8	0.9	30	8	6	75	2
(40, 11)	2.2	3.1	1.1	15	2	2	100	0
(40.5, 16)	2.3	6.9	1.3	10	2	2	100	0
(40, 21)	2.1	2.7	1.2	55	0			
(40, 26)	1.7	1.7	1.5	100	8	1	13	7
(38, 31)	0.8	0.8	0.7	100	3	1	33	2
(45, 1)	4.5	1.2	1.2	10	10	9	90	1
(45, 3)	3.8	1.2	1.1	90	2	2	100	0
(45, 11)	2.6	1.5	1.1	5	1	0	0	1
(45, 16)	2.7	12.7	1.3	100	1	1	100	0
(45, 21)	2.2	3.3	1.3	100	6	4	67	2
(45, 26)	1.2	1.3	1.3	85	15	10	67	5
(43, 31)	1.6	1.8	1.5	95	11	1	9	10

Appendix 5: Details of mortalities, light levels and invertebrate damage in quadrats in Moorhouse Wood.

Quadrat (north,east)	Numbers of seedlings killed by each mortality				Light levels		Mean percent invert. leaf damage	Percent seedlings damaged
	Wilt	Gone	Animal	Rot	PAR μmol $s^{-1} m^{-2}$	R/FR ratio		
(0, 1)	2	1	0	0	9	0.83	0.0	0
(0, 4.6)	1	0	0	0	16	0.77	2.5	0
(0, 11)					25	0.74		
(0, 16)					13	0.77		
(0, 21)					11	0.79		
(0, 26)					19	0.76		
(5, 1)	9	5	0	0	5	0.73	5.5	29
(5, 5)	1	12	0	0	32	0.94	9.9	46
(5, 10.7)	0	0	0	0	21	0.77	0.7	33
(5, 16)					13	0.74		
(5, 21)					5	0.79		
(5, 26)					8	0.80		
(10, 1.4)	14	9	4	1	31	0.97	13.0	39
(10, 5)	6	2	0	0	21	0.80	11.1	50
(10, 11)	0	1	1	0	12	0.69	25.0	50
(10, 17)					11	0.76		
(10, 21)					6	0.78		
(10, 26)					10	0.77		
(15, 1)	24	9	5	17	3	0.80	14.2	27
(15, 5)	12	6	1	4	6	0.75	12.2	35
(15, 11)	2	4	1	3	13	0.75	4.0	25
(15, 16)	1	0	1	0	11	0.77	2.8	40
(15, 20)	0	0	0	1	6	0.80	12.5	100
(15, 26)	1	0	0	0	29	0.76	5.0	100
(20, 1)	15	8	2	24	8	0.77	12.0	47
(20, 5.5)	31	9	7	21	16	0.75	16.6	53
(20, 11)	7	0	0	0	12	0.69	16.0	50
(20, 16)	0	0	0	0	8	0.80	48.5	100
(20, 21)	0	1	0	0	11	0.77	6.3	50
(20, 26)	1	0	1	0	14	0.79	0.0	0
(24, 1)	21	9	10	25	9	0.75	8.1	33
(25, 5)	21	2	2	1	9	0.77	13.6	54
(25, 11)	2	1	1	1	14	0.76	14.5	64
(25, 16)	0	0	3	3	10	0.76	17.9	38
(25, 21)	3	0	0	2	5	0.76	3.9	50
(25, 26)	2	1	1	1	7	0.77	20.5	40
(30, 1)	19	11	11	3	7	0.80	6.9	33
(30, 4.3)	1	0	2	3	16	0.77	16.7	68
(30, 11)	0	1	1	0	14	0.79	59.8	80
(30, 16)	0	1	0	1	12	0.76	13.0	100
(30, 21)					12	0.78		
(30, 26)					16	0.78		
(30, 31)					6	0.80		
(34, 2)	4	4	1	2	3	0.83	11.6	18
(35, 4.3)	3	0	1	1	20	0.79	34.4	80
(35, 11)	3	0	0	1	6	0.79	4.3	60
(35, 16)	1	1	1	0	15	0.77	1.7	33
(35, 21)	2	1	0	0	13	0.77	0.0	0
(35, 26)					9	0.77		
(35, 30)					7	0.77		
(39, 2)	2	0	0	0	9	0.82	23.1	67
(40, 4)	1	1	0	0	8	0.78	12.7	50
(40, 11)	0	0	0	0	14	0.77	2.5	50
(40.5, 16)	0	0	0	0	12	0.80	3.0	50
(40, 21)					7	0.77		
(40, 26)	5	2	0	0	12	0.77	15.8	38
(38, 31)	1	1	0	0	14	0.77	17.3	100
(45, 1)	1	0	0	0	22	0.80	17.8	70
(45, 3)	0	0	0	0	12	0.74	34.5	100
(45, 11)	0	0	0	1	15	0.78	55.0	100
(45, 16)	0	0	0	0	14	0.77	0.0	0
(45, 21)	0	1	1	0	4	0.92	18.8	50
(45, 26)	4	0	0	1	14	0.77	26.7	73
(43, 31)	1	7	2	1	11	0.73	9.5	25