

CHAPTER 7

DISCUSSION

How well has shade tolerance been quantified in Scottish native woody species in relation to physiological responses?

The first aim of the thesis was to quantify shade tolerance in Scottish native woody species in relation to growth, allocation and morphological responses. This aim has largely been achieved even though it was challenged by a number of factors, which will be discussed.

Seedlings of 15 woody species displayed different degrees of growth, allocation and morphological responses to different levels of irradiance in the nursery trial (Chapter 3). Differential responses enabled the distinction of shade tolerants, intermediates and shade intolerants as described by Veneklaas and Poorter (1998). Generally variation in relative growth rate (RGR) between species in low light could be explained by leaf area ratio (LAR) and variation in RGR in high light could be explained by net assimilation rate (NAR). Hence, shade intolerants could be distinguished from shade tolerants by their faster rates of growth in both low and high light explained by higher LAR and NAR respectively.

Classification based on the size and efficiency of the photosynthetic apparatus was backed up further by biomass allocation patterns, which aided the further identification of in/tolerant traits as well as specific shade tolerant strategies. *Quercus petraea* and *Fraxinus excelsior*, for example, were identified as having a shade tolerant strategy involving slow growth in the shade with the storage of carbohydrates in large root systems "in preparation" for rapid exploitative growth when exposed to higher irradiance. Generally, the greatest RGR response to irradiance occurred between 2.5% and 14% PAR, which indicates how species within this boreal group all require, enhanced light for further growth.

The quantification of shade tolerance of species from the nursery trials was specific to one-year-old seedlings and based on differential responses to irradiance alone. It is well known that many temperate species tend to be more tolerant in the juvenile phase (often due to a link with the seed reserve) but this changes as they grow older (Peterken, 1996; Spurr & Barnes, 1998). *Quercus* is a classical example where survival in the shade decreases with time as reserves run out (Jones, 1959; Shaw, 1974; Lorimer *et al.*, 1994; Vera, 2000). It is very possible that the tolerance ranking would be modified in following years. Furthermore, the ability to tolerate shade depends on an ability to tolerate other limiting resources besides low light.

Research revealed how growth, allocation and morphological responses of seedlings to irradiance was modified when subjected to an array of environmental factors in the field. The trade-off between precision and reality, which occurs between nursery and field trials, was also clearly illustrated.

In the field, one-year-old seedlings were planted in pole, old-growth and open stands of *Pinus sylvestris* woodland which had irradiance regimes (in terms of both light quantity and quality) comparable with the medium shade, low shade and high light treatments of the nursery (Table 7.1). Light regimes under old-growth and open stands in the natural regeneration study (Chapter 6) were slightly higher than under similar stand types in the main field trial but still comparable. The difference in the distribution of light beneath shade houses and tree canopy is duly recognised. It is possible that the initial rapid height gain of all stems under the pole stand in the first season was due to sunflecks penetrating the canopy.

Table 7.1 Comparisons in mean daily PAR% (direct measurements recorded in July/August between 11:00-15:00 hrs) and seasonal R:Fr ratios between irradiance regimes in the nursery and stand types in the field.

Trial	Medium shade / Pole		Low shade / Old-growth		High light / Open	
	PAR	R:Fr	PAR	R:Fr	PAR	R:Fr
Nursery	14	0.85	33	0.92	up to 100	1.02
Field: planted	12	0.85	36	0.98	65	1.05
Natural regeneration	-	-	46	-	87	

Generally seedlings grew much faster in the nursery than in the field with a 3 to 4 fold difference in absolute annual height and diameter increments for all light regimes in the first year of establishment (Table 7.2). Differences in RGR between species under low (pole) and high (open) light were not as clearly defined by differences in LAR or NAR as in the nursery. Other factors apart from the size and efficiency of the photosynthetic system were thus controlling growth in the field. The expression of phenotypic plasticity was generally lower in the field for most species than in the nursery, a possible consequence of the abiotic environment, neighbouring plants and herbivory (Callaway *et al.*, 2003).

The percentage of biomass allocation to roots was much higher in the field and allocation to the leaves much lower compared with the nursery (Table 7.3). It is possible that these differences in allocation are due to a lower level of nutrient acquisition in the field exacerbated by limiting below ground conditions such as poor soil aeration and lower pH. Chapin *et al.* (1987) explain how plants tend to allocate new biomass to the organs that acquire the most strongly limiting resource to maintain a favourable C:N balance (Section 5.1).

Table 7.2 Mean absolute height and diameter increments over the main growing season (April-Sept) (18 weeks) in 2000 (nursery trial) and in 2001 (field trial) for four broadleaved seedlings of planted stock. †Annual growth increments for 2001 of naturally regenerating *S. aucuparia* ten-year-old seedlings have also been included.

	Nursery trial				Field trial	
	14% PAR	33% PAR	Full daylight	Pole	Old-growth	Open
	Height increment (cm)					
<i>I. aquifolium</i>	20	25	26	11	8	7
<i>A. glutinosa</i>	30	41	29	16	13	11
<i>S. aucuparia</i>	63	71	44	33	26	23
<i>B. pubescens</i>	71	77	60	16	13	10
<i>S. aucuparia</i> †	-	-	-	-	7	9
	Diameter increment (mm)					
<i>I. aquifolium</i>	2.45	4.26	6.64	1.27	1.79	2.12
<i>A. glutinosa</i>	4.47	7.47	9.24	1.74	2.96	3.29
<i>S. aucuparia</i>	3.98	6.76	7.55	1.45	2.16	1.95
<i>B. pubescens</i>	4.87	7.67	8.26	0.89	1.79	1.58

Table 7.3 Percentage biomass allocation to plant components (leaf:stem:root) for comparable light regimes in the nursery trial and field trial for four broadleaved species.

	Nursery trial				Field trial	
	14% PAR	33% PAR	Full daylight	Pole	Old-growth	Open
<i>I. aquifolium</i>	46:39:15	42:42:16	39:34:19	37:33:30	32:31:37	26:37:37
<i>A. glutinosa</i>	27:54:20	25:52:23	19:49:33	19:46:35	13:42:45	14:42:44
<i>S. aucuparia</i>	19:63:18	16:61:23	19:52:30	7:61:33	8:52:40	7:57:37
<i>B. pubescens</i>	23:61:16	71:62:22	17:54:29	8:56:37	7:50:43	4:53:43

Ilex aquifolium displayed a shade tolerant strategy maintaining a positive carbon budget in the shade in both the nursery and the field: LAR and SLA were higher in the shade and less carbon was allocated to roots and more to leaves. Although, biomass allocation responses to irradiance were similar between trials, allocation of biomass between different plant components was more evenly balanced in the field (Table 7.3). This response was not shared by the other species. A more balanced allocation regime may reflect a superior ability of *I. aquifolium* to maintain a favourable C:N balance under dual carbon and nitrogen limiting conditions.

In the nursery, *I. aquifolium* responded positively to an increase in irradiance, maximising growth rates in full daylight. In contrast to this, *I. aquifolium* generally performed and grew better at the lowest light level (15% PAR) in the field. Lower growth rates at higher irradiances were associated with a higher percentage cover of *Calluna vulgaris* and a greater susceptibility to frost and the leaf miner, *Phytomyza ilicis*. A range of light indicator values from 4-7 were assigned to *I. aquifolium* in the nursery reflecting its more generalist behaviour but in the field it was only assigned a 4 to reflect its intolerance of high light conditions.

The physiology of *Alnus glutinosa* was reflective of a light demanding intolerant species in both the nursery and the field; where growth, allocation and morphological responses to different light regimes remained relatively similar. As a consequence, its light indicator values of 6-7 did not differ between trials.

A. glutinosa generally grew fastest at the two higher irradiances in the nursery which corresponded to higher growth rates in old-growth and open stands in the field. It maintained high levels of morphological plasticity in the field where relatively high RGRs in low light (15% PAR) could be explained by relatively high levels of LAR. Similar responses were found at 14% PAR in the nursery. Higher RGR in old-growth and open stands was not clearly explained by higher levels of NAR unlike in the nursery. Instead high RGR could be explained more by the maintenance of relatively high LAR. Savill (1998) notes how the rapid early growth of *A. glutinosa* can be related to the speedy development of a large area of leaves.

B. pubescens was classified as a light demander in the nursery on account of its fast growth, particularly in high light, its high level of plasticity and high etiolation rates in deep shade. In the field, however, growth rates were lower across all stands than in the other deciduous species. It retained high rates of etiolation in the shade, similar to *A. glutinosa*, but lower levels of plasticity were expressed. In the nursery, at 14% PAR, *A. glutinosa* and *B. pubescens* shared relatively high RGR explained by relatively high LAR. However, in the field, *B. pubescens* had a much lower LAR than *A. glutinosa* in 15% PAR explaining in part, its much lower RGR there.

B. pubescens achieved equally high RGRs at both 33% PAR and in full daylight in the nursery. In the field, RGR was maximised in old-growth but at higher light, growth was substantially reduced. Slow growth in the open stands was associated with high levels of soil moisture. It is possible that *B. pubescens* may have achieved faster growth rates, had it been planted on well drained soils in the open which were not subjected to drought. In the nursery, *B. pubescens* was assigned a light indicator value of 7 but this has been reduced to 6 in the field.

Sorbus aucuparia did not express the same level of plasticity in the field as in the nursery: LAR and leaf mass ratio (LMR) remained constant across stand types and there were only small differences in NAR. Growth rates in the field remained relatively constant in the second year of growth across stand types, unlike those in the nursery where faster rates of growth were generally found at 33% PAR and/or full daylight. The lack of differences in growth rate of planted *S. aucuparia* seedlings between stand types conformed partially with growth patterns of naturally regenerating *S. aucuparia*. Few differences were found in basal diameter growth between old-growth and open stands. However, height increments were much higher

in the open than in old-growth stands. Natural regeneration also had much lower diameter:height ratios in the open than in the shade in contrast to other results.

Generally, *S. aucuparia* displayed traits indicating a more intermediate degree of shade tolerance in all trials with an assignment of a light indicator value of 6. Intermediate behaviour was clear in the nursery, with intermediate growth rates in low and high light explained by intermediate LAR and NAR respectively. Similar growth rates under different stands in the field also hint at intermediate or even generalist behaviour. Individuals tended to put on steady diameter growth over time in semi-shade conditions where stems were more robust compared with the open.

The natural regeneration study was fruitful in clearly revealing facultative shade tolerance behaviour in *S. aucuparia*. Results indicated that seedlings could survive in the shade of old-growth *P. sylvestris* trees for up to 14 years but higher irradiance levels in gaps were required for further height growth. In the nursery, there were signs of this behaviour: *S. aucuparia* seedlings displayed a strong response in RHG, RDG and RGR to a small increase in irradiance from 2.5% PAR to 14% PAR.

Modification in species light demand or degree of tolerance when subjected to an array of limiting environmental conditions including water-shortage, frost, pests and disease have been illustrated (Chapter 5). Shade tolerance also can be modified from site to site in the field due to fluctuating environmental conditions (Coomes & Grubb, 2000, Spurr & Barnes, 1998). This was illustrated to some extent in Glen Affric.

Differences in growth responses between naturally regenerating and planted *S. aucuparia* seedlings can be partially explained by site differences. The naturally regenerating *S. aucuparia* were growing on a well-drained ridge dominated by peaty podzols whereas the planted seedlings were subjected to less well drained conditions in the glen. It is possible, that height growth was hindered in the open stands in the glen due to anaerobic conditions impairing root function. However on well-drained open sites on the ridge, seedlings were able to "shoot up". *S. aucuparia* could be perceived to be more light demanding on well drained sites but less so on water logged sites. There are many examples in the literature, which illustrate how tolerance can change from one site to another depending on site conditions. In central New England, for example, eastern white pine is more tolerant on dry sandy soils than on moister sandy loams (Spurr & Barnes, 1998).

Differences in growth response to stand types between natural regeneration and planted stock could also be due to differences in their growth form. Sprouts with well-developed root systems, such as occur in oaks, hickories and tuliptree, appear more tolerant than seedlings of the same species, at least in part, because sprouts are

better able to absorb water and nutrients from the well-established root system of the parent (Spurr & Barnes, 1998).

Some of the natural regeneration on the ridge may have been a collection of epicormic shoots. It is possible that the ability of naturally regenerating *S. aucuparia* seedlings to persist for 14 years under the shade of old-growth pine would not occur to the same extent amongst planted seedlings (especially cell-grown stock) due to less healthy root establishment.

Shade tolerance is known to differ across regional climates (Spurr & Barnes, 1998). In more oceanic climates with more persistent cloudy conditions, species can appear more intolerant than they are in sunnier climates. On the European continent, for example, *Q. petraea* is stated to have a higher level of tolerance than in the British Isles (Kelly, 2002). In Scotland, and particularly in Glen Affric, sky conditions are generally very cloudy so species may seem more intolerant than they would be further south or east.

Typical responses of shade tolerants, intermediates and tolerants have been tabulated but there are always exceptions to any rule and ecologists need to remember this regarding all types of "strategy" (Grime, 1982; Grubb, 1992). Not all species conform to typical combinations of traits which distinguish intolerant pioneers from tolerant climax species. Some climax species, for example, have a wide ecological range and do exhibit high levels of plasticity. This is true of gap dependent species which are subjected to a whole range of light conditions throughout their life cycle (Popma *et al.*, 1992). The Malaysian dipterocarp *Dryobalanops lanceolata* can tolerate a great range from deep shade to high light conditions (Scholes *et al.*, 1997). Although this climax species cannot adjust its maximum photosynthetic rate to higher light levels, it still survives due to a different mode of plasticity in the form of photoprotection. Wide species plasticity is also found in the following late successional species: Australian *Acmena ingens*, the neotropical *Carapa gluanensis* (Mulkey *et al.*, 1996) and the subtropical Chinese *Castanopsis fargesii* (Cornelissen, 1994).

A reduction in root mass in deep shade can be seen as a measure that conserves carbon in the shade due to the high respiration rates of roots. However, some species such as the northern red oak of North America have very large tap root systems that resist drought in the shade but also have very low root respiration rates (Walters *et al.*, 1993b; in Spurr & Barnes 1998). Other factors, which can confuse tolerance differentiation, are species specific strategies of shade tolerance that are not necessary linked to growth potential or biomass conservation (e.g.: defence, seed dispersal and seedling establishment).

Some species combine characteristics of both shade tolerant climax and intolerant pioneer types, which can confuse classifications. *F. excelsior* is tolerant as a seedling, as a sapling and in its rapid response to release from shade, but it casts a light shade and has the dispersal capabilities of an intolerant (Peterken, 1996). *I. aquifolium* and *Taxus baccata* are very long-lived, tolerant species, but their fruits are widely dispersed by birds and this enables them to act as pioneers in some situations. *Populus tremula* is a typical intolerant species, except that it can prolong site occupation by reproducing copiously from root suckers.

Seed size is often used as a shade tolerance parameter due to the positive relationship found between seed size and shade tolerance or successional stage (Salisbury, 1942; Grime & Jeffrey, 1965; Grime, 1979; Schupp *et al.*, 1989; Grubb *et al.*, 1996). However, this relationship does not always hold true due to other evolutionary influences on seed traits besides light demand (Grubb & Metcalfe, 1996; Grubb, 1998; Hewitt, 1998). A significant relationship between seed size and shade tolerance (Ogilvy rank) of the Scottish woody species was found but only when the evergreens were removed.

Greene *et al.* (1999) warn against assigning high shade tolerance to species from observations made in the initial years due to the seed reserve which eventually runs out. Although there was some evidence to suggest that the deciduous species with larger seeds grew more in their initial season (at the native tree nurseries), there was no effect of seed reserve on growth in the second season. Coomes & Grubb (2003) point out that seedlings with larger seeds often lead to larger seedlings which can be more tolerant of hazards in the understorey such as drought or herbivory. This may have relevance to the field situation but not when quantifying shade tolerance under controlled nursery conditions.

Both the nursery and field trial lacked mortality data. Mortality has been characterised as an important component of shade tolerance (Kitajima, 1994; Kobe *et al.*, 1995; Walters & Reich, 1996; Kobe & Coates, 1997; Kobe, 1999). It is argued that growth responses can only be reconciled with traditional notions of shade tolerance if measurements of light availability, growth and survival are integrated. Without mortality data, it is difficult to know about the long term survival of a species in the shade which essentially defines shade tolerance. In the nursery trial, it is likely that survival data would have been obtained if the trial had been run into a second season (Walters & Reich, 1996) or if the light regime in deep shade was even lower (<1.6% PAR) (Grubb *et al.*, 1996; Walters & Reich, 1996). Species that were identified as shade intolerants (*Betula* and *Salix* species) grew fast at both low and high light as a consequence of high degrees of morphological and physiological

plasticity. This contributed to a lack of the cross-overs of ranks of growth in high and low light conditions.

Although, the shade intolerant species did not die in the first trial season, higher mortality rates are predictable in a second season. Generally, in the longer term, species that have the highest LAR values (the light demanders) will have the lowest NARs in the shade due to high respiratory costs and short leaf lifetimes (Walters & Reich, 1999) leading to eventual death. Furthermore, as plants grow bigger, LAR values decline corresponding to an increase in the whole-plant light compensation point, and a slowing of RGR, especially in shade and especially for the most fast growing species (Givnish, 1988).

It is possible, that there was a lack of mortality in the nursery due to the application of fungicide and insecticide. Fungal attack is commonly reported as a very important cause of death in shaded habitats (Grime, 1966; Vaartaja, 1962; Hutchinson, 1967). Damping off, for example, is believed to be a major cause of mortality in low light for *Betula* species (Miles & Kinnaird, 1979). Mildew is believed to reduce the amount of light reaching the photosynthetic system of *Quercus* seedlings thus reducing their survival rates (Rackham, 1980). In support of this, Jarvis (1964) found that mildew on *Quercus* leaves in low light raised their compensation point from 2% to above 8% daylight.

In the field, where seedlings were subjected to pests and disease, mortality still remained very low and rather random across plots. A greater number of dying seedlings were actually associated with the open treatment than the shade treatment due to anoxic water-logged ground conditions preventing recovery from frost (*I. aquifolium*) as well as general root functioning. It is possible that the low light treatment at 15% PAR was not low enough to cause mortality over this time period. The use of one-year-old plants cultivated in tree seedling nurseries probably also contributed substantially to the lack of mortality. Mortality is often high at the germination and initial establishment stages which were bypassed in the nursery and main field trial. Nursery grown one-year-olds are probably more sturdy and larger than plants which naturally germinate and establish in the field. This is because cultivation procedures protected them from fungi, insects, water and nutrient stress.

Although, there was little mortality in the shade, performance class and damage recordings enabled an assessment of species vigour under shade and thus an assessment of tolerance. *I. aquifolium*, for example, was least susceptible to damage (caused primarily by *Phytomyza ilicis*) and had the greatest number of apparently healthy seedlings in the pole stand compared to the other stand types. The more

shade intolerant *B. pubescens*, however had a very low percentage (12%) of apparently healthy seedlings in the pole stage, lower than all other species.

Shade tolerance quantification would have benefited from the addition of ecophysiological measurements alongside growth analysis. Jabowa-Foret models which parameterise species specific responses of tree growth to light availability are based on the theory that the leaves of shade tolerant species tend to have higher photosynthetic rates at low light levels and lower photosynthetic rates at high levels than shade intolerants (in Pacala *et al.*, 1994). Some argue that it is not possible to explain the absence of sun plants in shaded habitats in terms of efficiency of utilisation of light energy. This is because similar photosynthetic rates between species types have been found in low light. Dark respiration rates, however, are proving to be a more successful and consistent determinant of shade tolerance in many studies (Loach, 1967; Reich *et al.*, 1998b; Walters & Reich, 2000b).

Shade tolerants are believed to survive in shade due to their low dark respiration rates which result in small respiration losses. The inherently high respiration rates of leaves of shade intolerants are a consequence of selection for rapid photosynthesis and growth in productive environments. Bazzaz (1979) explains how the photosynthesis to respiration ratio (P/R) of a species in the shade and in a gap reflect the level of its shade adaptation and successional position. Shade tolerants tend to have a high P/R in the shade as this produces a more favourable carbon balance. When grown in low light, shade intolerants tend to suffer from higher mortality because reserves are rapidly expended during periods below the compensation point. *Populus tremula* has been found to have much higher respiration losses when grown at low PPF compared to more shade tolerant trees (Loach, 1967; Walters & Reich, 2000b). Lower respiration rates have also been linked to the maintenance of a higher soluble carbohydrate content, which gives the plant a higher resistance to fungal attack.

How well do native broadleaved species establish and grow under different developmental stages of *P. sylvestris* woodland?

The second aim of this thesis (which is closely linked with the first) was to understand how broadleaved species establish and grow under different development stages of *P. sylvestris* woodland. All species grew slowly in the field particularly in the second season. *B. pubescens*, for example, had a mean height increment of 13 cm across stand types in the first year but in the second season this was reduced to 4 cm.

Slower rates in the second season could be explained by a reduction in nutrient acquisition. In the second season, the growth of roots further outside their pots would have exposed them to more acidic (pH 3.8) soil conditions. The presence of other competing vegetation (e.g.: *C. vulgaris*) is likely to have reduced nutrient availability, particularly nitrogen (Evans, 1984) (see below). Furthermore, *C. vulgaris* produces allelopathic chemicals which may have slowed down the formation of mycorrhizal associations (Miles & Kinnaird, 1979). Even if nutrients were not limiting, acquisition was probably hindered by failure of the root system in anaerobic soil conditions (Evans, 1984) on the more water-logged sites.

Most seedlings suffered from leaf chlorosis, which can indicate nutrient deficiency. A strong positive linear relationship has been demonstrated between percentage leaf nitrogen and percentage leaf chlorophyll in tree species (Ichie *et al.*, 2002, Chang & Robison, 2003). In the first growing season, efforts were made to calibrate leaf nitrogen% (concentration in leaves as a percentage of oven-dry mass) against leaf chlorophyll% to obtain a measure of nitrogen availability for all trial seedlings. However regressions for individual species for each stand type were not good with very poor relationships found particularly for *B. pubescens*. This was probably due to a high level of disease on the leaves which altered chlorophyll readings.

Although, leaf nitrogen data were not analysed statistically, means of sub-samples generally revealed higher leaf nutrient contents (mg g^{-1}) in the pole stand than in either the open or old-growth stands, conforming with mean Wilson values for the sites (Table 7.4). *A. glutinosa* was an exception with similar levels found across stand types. As vascular vegetation cover, especially *C. vulgaris*, was much higher in the open and old-growth stands than in the pole stands, it is feasible to suggest that it is the surrounding vegetation which is limiting nitrogen availability to the seedlings. The mean leaf nitrogen content (mg g^{-1}) of the four broadleaves was much lower (three fold difference) than means pooled for broadleaved trees and shrubs species across the Americas (Reich & Walters, 1998c). Furthermore mean percentage of leaf nitrogen for the broadleaved species were much lower than critical values provided by Evans (1984) to indicate possible deficiency.

Table 7.4 Leaf nitrogen content of four broadleaved species growing in pole, old-growth and open pinewoods sites. Leaf nitrogen is expressed on a leaf mass basis (Leaf N_{mass} (mg g^{-1})).

	Pole	Old-growth	Open
<i>I. aquifolium</i>	6.9	4.3	5.4
<i>A. glutinosa</i>	9.9	7.7	9.2
<i>S. aucuparia</i>	8.2	4.9	4.8
<i>B. pubescens</i>	10.0	6.2	5.8

A. glutinosa was the most successful grower across pinewood sites compared with the other broadleaves. This can be attributed to its roots that can penetrate anoxic water-logged conditions as well as their relatively high level of plasticity. It is also possible that it grew better than the other species due to an ability to fix atmospheric nitrogen in association with bacteria (*Frankia* spp.) in large root nodules (Savill, 1998). It did have a slightly higher leaf nitrogen content across all stand types compared with other species (except for *I. aquifolium* in pole) which was not reduced substantially in open and old-growth stands (Table 7.4). However, its leaves did show signs of chlorosis across sites. It is very possible that nodule formation has been retarded by the very acidic soils (pH 3.8) as formation is known to proceed best in the pH range 5.4 to 7.0. In a new native woodland project at Kirton Farm, Crianlarich, *A. glutinosa* is growing very well in relation to other species (M. Pollock, personal communication). In contrast to Glen Affric, leaves are very green perhaps reflective of the less acidic soils (water pH 5).

The Ecological Site Classification Decision Support System (ESC DSS) output did not recommend *A. glutinosa* as a species to grow on pinewood sites in Glen Affric probably due to the acidity (Hart, 1998, Anderson, 2002). *B. pubescens*, however was recommended for most sites. Conventionally, it is believed to tolerate acidic water-logged sites (Savill, 1998; Anderson, 2002) and is apparently the least exacting species of all the Caledonian broadleaves (Malcolm, 1957). The growth and performance of *B. pubescens*, however, was particularly poor across all sites compared with *A. glutinosa* and *S. aucuparia*.

There was little direct evidence to prove that the *C. vulgaris* cover actually did affect seedling growth. Naturally regenerating *S. aucuparia* were not “affected by” low or high percentage cover of *C. vulgaris* in old-growth and open stands. Results from the main field trial were inconclusive due to the effect of the percentage cover of *C. vulgaris* being confounded with stand treatment effects.

There was some evidence in the field, to support the theory that it is the drainage conditions associated with *Calluna* which have a more influential effect on seedling establishment (Pears, 1988; French *et al.*, 1997). Naturally regenerating

S. aucuparia seedlings were found in far lower densities in radial plots around stand treatments in the glen (Table 7.5) than on the ridge. Furthermore, in the glen, the majority of individuals were found in Block 4 which was characterised by better drainage.

The research focused mainly on the juvenile establishment stage of broadleaves. Hence, little information was obtained on other stages of regeneration which have equally important roles to play in successful establishment (Grubb, 1977; Greene *et al.*, 1999). The use of one-year-old seedlings by-passed important dispersal, germination and initial establishment stages (see Miles & Kinnaird, 1979). Furthermore, as the field trial was only run for two years, little is known about how the broadleaves will grow and survive on pinewood sites in the longer term.

The project involving temporal and spatial distribution patterns of natural regeneration was able to provide a more holistic understanding of the regeneration ecology of broadleaves in Caledonian Forest. *S. aucuparia* dominated the type of natural regeneration found on the ridge as well as in the glen with *B. pubescens* and *P. sylvestris* found in far lower numbers (Table 7.5). Its abundance could be explained by a number of factors specific to its regeneration ecology including seed dispersal, shade and browsing tolerance.

Ring core analysis provided a picture of the growth and survival of *S. aucuparia* over time. Seedlings were able to persist in shade cast by old-growth trees for up to 14 years. Furthermore temporal growth patterns revealed sensitivity to particularly cold dry years, where ring widths on more exposed open sites dipped below widths in the shade. There was much variation in growth patterns over time as well as space. Abundance of seedlings also varied between blocks on the ridge and in the glen (Table 7.5). This variation highlights the nature of regeneration which is sensitive to appropriate microsite conditions which also fluctuate in time and space.

Table 7.5 Total number (no.) of all naturally regenerating seedlings within radial plots (5.6 m) centred around pole, old-growth and open stand types. Means pooled across blocks are included with standard deviations (STDEV) in brackets (n = 7).

	Pole		Old-growth		Open	
	No.	Mean no.	No.	Mean no.	No.	Mean no.
<i>S. aucuparia</i>	233	33.3 (\pm 87.6)	87	12.4 (\pm 27.9)	26	3.7 (\pm 8.2)
<i>P. sylvestris</i>	2	0.29 (\pm 0.76)	4	0.57 (\pm 1.13)	28	4.0 (\pm 7.2)
<i>B. pubescens</i>	7	1.0 (\pm 2.7)	0	-	4	0.57 (\pm 1.13)

What role does shade tolerance and the broadleaf component have to play in Caledonian forest dynamics?

The Caledonian Forest should be viewed holistically to include not only the pinewoods but also the other associated woodland and non-woody (mostly heath and mire) communities. In Glen Affric, associated woodlands include birch-oak woodland types (W11 and W17), wetter birchwood, (W4), and ashwood (W9) (see Chapter 2). Alder and *Salix* communities surround the lochs and other watercourses and pine-birch mixtures occur predominately in the east. A close link between all these communities can be drawn when reviewing theories on successional change in the Highlands (Rodwell, 1991; Miles, 1988).

Understanding of the natural successional status and the dynamics of woodlands within the Caledonian Forest remains theoretical due to anthropogenic interference. In the absence of other species, *Pinus sylvestris* has been described as forming climax forest, and *B. pubescens* replaces it as a climax in more northerly latitudes (Miles & Kinnaird, 1979). *Betula* within the natural range of *P. sylvestris* has been described as forming a quasi-climax forest type, but it has also been described as successional to pine-dominated or mixed broadleaved woodland. Alternations in *Pinus* and *Betula* dominance have also been mentioned in association with disturbance caused by fire (Miles, 1985; 1988). *Betula* can also occur within mixed stands with *P. sylvestris* but the successional status of these stands are unknown. It is likely that pinewoods always had a proportion of *Betula* species and other broadleaves, the proportion varying with site type and climatic region.

There is a theory that the pine and birch and oak woodlands of the Highlands are naturally a cyclo-climax, in which tree cover alternates with grassland or dwarf shrub heath (Yapp, 1953; in McVean, 1964). The lack of internal regeneration within these woodlands and the more common occurrence of regeneration on adjacent unwooded ground is regarded as evidence to support the theory. While this may be true for the pioneer species, it is doubtful if it can be applied to shade tolerating species as well. Often secondary successions involve an intermediate phase of predominance of another species. Although *Pinus* and *Betula* are known to regenerate directly themselves, this may be a reflection of the non-availability of seed of those tree species that would naturally succeed them (Miles & Kinnaird, 1979; Miles, 1985). High levels of grazing also can suppress the regeneration of other species. Birchwoods fenced against sheep and deer often exhibit an understorey of rowan saplings (McVean, 1964). Alternations of predominance of species are important because they produce alternating influences on the soil which are important in the perpetuation of the system (Miles, 1985).

The general removal of all trees within the Caledonian Forest has led to decreased interception of precipitation and increased soil wetness, run-off, leaching, organic matter accumulation, erosion and paludification (Malcolm, 1957; Worrell, 1996). Where birch dominated woodland has been replaced by heather moorland on acidic geology, podzolisation and acidification increases, iron pans frequently develop and soil fertility decreases. Reduction of the broadleaved component in many pinewoods has probably promoted acidification and podzolisation of soils (Miles, 1986). These conditions are unfavourable for pine germination, which prefers well-drained mineral soils (Carlisle & Brown, 1968), and do not seem to encourage broadleaf establishment either. Soil degradation may make regeneration of woodlands more difficult (Malcolm, 1957) particularly in high rainfall areas. Podzolisation, however, is believed to be reversed by broadleaf tree establishment (Miles, 1985; 1986).

In the absence of burning and grazing, the development of woodland from mire, heath and grassland communities is often described (Miles, 1974b; Miles, 1985; Miles, 1988; Rodwell, 1991; Hester *et al.*, 1991). Transitions can also occur between woodland types and their sub-communities (Rodwell, 1991). Edaphic factors are often reported to play an important role in these transitions. In Deeside pinewoods, for example, transitions between sub-communities (W18b to W18d) can be seen as one moves from drier podzols to peaty podzols. The acidic birch-oak woodland type (W17) tends to be found on less base-poor soils than W11 but when soils "alternate in acidity", transitions between the two occur. Furthermore, both these birch-oak woodlands can give way to ashwood (W9) on more calcareous rocks with base-rich mull brown earths. In non-woody communities, Miles (1988), has shown that sowing a variety of field layer species at one site showed a sequence of species progressively able to establish as the soil changed towards mull conditions.

It is argued, however, that it is difficult to segregate the effects of differences in shading and competition from those of soil change. Reductions in light intensity has been found to be the major factor driving changes in the ground vegetation during succession from heather moorland to birch woodland (Hester *et al.*, 1991). It was postulated that species that are more shade tolerant in the heathland will have a competitive advantage during the development of birch woodland.

In open grass and heathland, seedlings can be subjected to deep shade under tall vegetation such as *C. vulgaris*. At the pioneering stage, the species which will have the competitive advantage amongst all intolerants will be the ones with the higher stem extension rate or higher LAR that enables growth out of the sward.

The different woodland types within the Caledonian Forest can include many different tree species. For example, the patch of *Fraxinus excelsior-Sorbus*

aucuparia-Mercurialis perennis woodland (W9), in Glen Affric has *F.excelisior*, *Q. petraea*, *U.glabra*, *S. aucuparia* and *B. pubescens* in the main canopy and *C. avellana* in the understorey (Averis, 1994). All these species differ in their degree of shade tolerance or light demand (as shown in this thesis) which would likely contribute to the dynamic processes determining the structure and composition of the woodland.

Successional transitions are commonly reported to be influenced by alternations in grazing pressures, burning regimes, soil type and seed source availability, microclimate and topography (Miles, 1988; Rodwell, 1991; Hester *et al.*, 1996b). Shade tolerance is hardly mentioned. Although British tree species on the whole are light demanding they still differ in shade tolerance which has its part to play in woodland dynamics.

What are the practical implications of the research?

Many of the concepts of forest restoration practice in the tropics can be applied to native woodland restoration in Scotland (Hardwick *et al.*, 1997; Ashton *et al.*, 2001; Elliot *et al.*, 2003). Tropical restoration approaches can be ranked in order of the amount of human input needed, which is linked, closely to reliance on natural regeneration. The "framework species method" is an example of an approach which involves much human input, planting tree species with high field performance (high survival and growth rates) in open degraded sites (Elliot *et al.*, 2003). The idea is that these species 'capture' the site, re-establish a multi-layered canopy and restore forest productivity and nutrient cycles. Another approach, with less human input involves accelerated natural regeneration (ANR) and enrichment planting. ANR involves assisting natural regeneration by counteracting particular limiting factors such as removal of excessive weed competition. It can be supported with enrichment planting of native tree species which have been totally removed by deforestation leaving behind no parent tree seed sources (Ashton *et al.*, 2001).

A combination of ANR and enrichment planting would seem most appropriate for broadleaf establishment in Glen Affric. The use of ANR would be particularly beneficial in exclosures on more open sites where unchecked over-topping vegetation could be clipped back to release *B. pubescens* and *P. sylvestris* seedlings and reduce etiolation in *S. aucuparia* seedlings which makes them more susceptible to drought and insect attack (Chapter 6). Enrichment planting of *S. aucuparia* would probably be unnecessary on account of its abundance in the Glen, particularly on well-drained sites subjected to low browsing pressure. Natural regeneration of

S. aucuparia, however, should be encouraged under semi-shade conditions such as on the fringes of old-growth, where it was found to establish well.

Enrichment planting of other native broadleaves (with deer browsing protection), is recommended on appropriate sites. Research revealed that *I. aquifolium* seedlings are best grown under shade (15% PAR) where the growth of *C. vulgaris* is restricted (Chapter 5). Open sites should be avoided due to potential frost damage and susceptibility to *Phytophthora ilicis*. Both old-growth and open sites are favourable for *A. glutinosa* seedlings. *B. pubescens* seedlings are best grown away from open sites on perhaps the fringes of old-growth where they can benefit from more favourable drainage conditions. Planted seedlings would also benefit from ANR. If cell-grown seedlings from native tree nurseries are to be used it is strongly recommended that soil should be aerated around the planting spot to aid root establishment (such as by hand turfing). Seedling plugs that were planted with a small amount of garden peat and perlite outgrew basic plugs by 40% (Chapter 5). Furthermore, patch scarification or the use of low mounds maybe also be appropriate where *C. vulgaris* growth is aggressive.

Soils under *P. sylvestris* sites within Glen Affric were found to be very acidic and dominated by very poor soil nutrient regimes. Broadleaf planting and establishment is preferable to help reduce this soil acidity and mineralise the soils but was found to be hindered by nutrient deficiency. Initial establishment does require a kick-start of some kind and, once started, podzolisation problems could then be alleviated naturally. The use of spot nitrogen fertilisers probably would be inappropriate as they encourage weeds and exacerbate the nutrient deficiency problem (Evans, 1984; Anon, 2003a). *A. glutinosa*, however, could be used as a natural alternative, if planted on a less acidic base which would encourage more successful nodule formation and nitrogen fixation. Its ability to fix nitrogen, tolerate anaerobic soil conditions, produce a shady canopy (high LAR) and grow well (relative to the other three broadleaves) across pinewood sites, highlights it as a potential ‘framework species’ in Caledonian pinewood restoration. Once established, it has the potential to improve soil conditions for other native tree species. If sustainable broadleaved ‘nodes’ are produced this will aid integration and connectivity on the landscape scale.

It is acknowledged that a balance is required in terms of planting or encouraging broadleaves within pinewoods. Broadleaves have relatively fast transpiration rates which retard the downward spiral of paludification. However the wet and boggy areas are also seen as integral components of the pinewood ecosystem providing diverse habitat for wildlife and variety to the scene (Anon, 2003a). Also fast

growing broadleaves such as *A. glutinosa* have the potential to suppress conifers as reported in intimate mixtures within plantations (Kerr *et al.*, 1992).

The research has much practical implication for Continuous Cover Forestry (CCF) involving alternative silvicultural systems to patch clear felling. These alternative systems are increasing in popularity in the UK as they are now recognised as the best way of enhancing within stand structural diversity as well as aesthetic, conservation and environmental benefits (Malcolm *et al.*, 2001). In the past, alternative silvicultural techniques have not been developed due to constraints associated with lack of natural regeneration, general forest cover and shade tolerant species and risk of wind damage as a consequence of stand opening. However, there are many UK case studies emerging now which reveal how CCF works well where browsing is controlled and on 'windfirm' sites and especially where there are free-draining soils. Group selection and irregular shelterwoods have been recommended to be the most suitable systems for the UK, primarily due to the predominance of light-demanding conifers (Malcolm *et al.*, 2001). However, now that differential degrees of shade tolerance and light demand in native broadleaves has been recognised, perhaps other systems could be considered.

In Glen Affric, there is potential for CCF on windfirm sites (all plantation sites in this study had relative low DAMS scores between 11-14). Alternative silvicultural techniques are already being implemented in a sense with the naturalisation programme which involves the thinning of local origin *P. sylvestris* plantations at different intensities to encourage the development of a naturally regenerating understorey (Wield, 2001). Canham (1989) explains how it is the frequency of disturbance and duration of periods of release that determines the rate of regeneration more than initial gap sizes or light level *per se*. Under optimal conditions in the shadehouse trial, all one-year-old tree seedlings responded most dramatically to an increase in irradiance between 2.5% and 14% PAR in terms of growth (Chapter 3). This highlights the importance of a relatively small increase in irradiance to promote growth for this boreal set of species. Species, however, differed in the magnitude to which they responded and in their shade adaptive potential which has implications for thinning regimes.

Generally, broadleaved species that displayed a greater response to the smallest increase in irradiance, such as the *Betula* and *Salix* species and *A. glutinosa*, also displayed shade intolerant traits. At an early stage, more frequent longer opening of the canopy to maintain a steady growth as plants increase in size would seem appropriate for these species. In the *P. sylvestris* plantations, the growth rate of

B. pubescens seedlings continued to increase from 9%-23% PAR, suggesting a minimum light regime necessary for more successful establishment (Chapter 5).

Species that displayed a lower response to a small increase in irradiance, such as *Q. petraea*, *F. excelsior* and *I. aquifolium* displayed shade tolerant traits. These species could be left to established as ‘advanced regeneration’ under a canopy for the first year or so, due to an ability to tolerate longer term suppression. Thinning could be done later for release and at less frequent shorter intervals due to slower rates of growth. It should be noted, that, with time, the frequency and duration of periods of release will need to be increased for these species as their shade tolerance ability diminishes with age. *U. glabra* and *S. aucuparia* displayed degrees of response between 2% and 14% PAR comparable with the light demanders but they also revealed shade tolerant attributes. They, thus could be left to establish as advanced regeneration under the canopy, initially, followed by a similar thinning regime for the faster growers.

Generally all species were found to grow best at intermediate light levels rather than in full daylight conditions in both the nursery and in the field. As overhead canopy is progressively removed in shelterwood systems, for example, light regimes of say more than 50-60% PAR should be avoided due to associated conditions limiting successful tree seedling growth such as aggressive *C. vulgaris* competition, anaerobic soil conditions and exposure to frost (Malcolm *et al.*, 2001).

Further research

This research has highlighted the complex nature of shade tolerance. Tolerance is not constant for a given species: it varies with genetically different individuals and races, with different regional climates, with different local site conditions, with different plant and pathogenic associates and with different growth forms and especially with age (Spurr & Barnes, 1998). The new light indicator values or shade tolerance ranks based on physiological responses must therefore be interpreted with great care and with these points in mind. Shade tolerance quantification in British native tree species has begun but it needs to be continued.

The following questions arose from the research:

- i/ How does ontogenetic drift affect shade tolerance quantification?
- ii/ Would more species change rank in terms of growth between low and high irradiance if the trial was run into a second season? What about mortality?

- iii/ Would it be possible to predict the specific irradiance at which species changed rank in terms of both growth and mortality with a different experimental design?
- iv/ How would growth and survival responses differ in newly germinated seedlings?
- v/ How is shade tolerance modified across soil moisture and soil nutrient gradients under controlled conditions?
- vi/ How do species differ in their dark respiration rates in low and high light?
- vii/ How would the growth and survival of broadleaved species differ when grown under different types of woodland canopy (e.g.: pine, mixed and broadleaf canopy), and swards of different plant communities?
- viii/ How does genotype modify shade tolerance?

Answers to these sorts of questions would help build the foundations of a model for predicting shade tolerance of a given species. Model parameters would include: location (co-ordinates); climatic and edaphic inputs (similar to ESC); competition indices (above & below ground); tree canopy type and amount of shade cast; disturbance agents; disease and pest susceptibility; physiological traits, age, size (height, diameter), architecture and growth form / vegetative condition of the individual.

Work on shade tolerance or differential light demand is particularly relevant at the present time due to current forest policy promoting sustainable forest management and biodiversity. Information on shade tolerance is important for restoration schemes as well as continuous cover forestry and plantations on ancient woodland sites.

A forest landscape dynamics model (FLMD) has been developed for Glen Affric (Glen Affric Landscape Dynamics Reconstruction) (Hope, 2003a, b). It involves the simulation of landscape dynamics of semi-natural pine (*P. sylvestris*) and birch (*B. pubescens*, *B. pendula*) dominated woodland. It is able to predict change in species composition and forest structure over large spatial extents and long timescales. By simulating the effects of natural processes such as seed dispersal, regeneration, growth, wind disturbance and herbivory, the model will be used to investigate the relationship between emergent landscape pattern and process as well as predicting potential effects of management strategies. At the moment, it does not involve other native woodland species and thus the shade tolerance parameter box has been left redundant (J.C.E. Hope, personal communication). However, in the future, shade tolerance predictions for many species will be required.

