CHAPTER 3

Growth, biomass allocation and morphological responses of 15 Scottish woody species to irradiance

3.1 Introduction

The aim of this study was to quantify shade tolerance in one-year-old seedlings of 15 Scottish native tree species, by analysing their growth, biomass allocation and morphological responses to different degrees of irradiance. A simple definition of shade tolerance involves the ability of trees to survive and maximise carbon gain in the understorey environment (Spurr & Barnes, 1998) or persist in deep shade for a period of time (Grime, 1966; Greene *et al*., 1999). Variation in shade tolerance is believed to be a key factor underlying forest successional dynamics, whereby slow growing shade tolerant climax trees replace relatively shade intolerant pioneers in the absence of major disturbance (Shugart, 1984; Spurr & Barnes, 1998).

Traditional notions of shade tolerance in British tree species have been described but much is based on subjective observation with very little quantitative support (Savill, 1998; Hill *et al*., 1999). Hence the quantification of shade tolerance in British tree species has received very little attention in the literature to date. Most current studies involving cold temperate woody species have been mainly based in North America (Bourdeau & Laverick, 1958; Grime & Jeffrey, 1965; Loach, 1970; Walters *et al*., 1993a, 1993b; Pacala *et al*., 1994; Kobe *et al*., 1995; Messier & Puttonen, 1995; Kobe & Coates, 1997; Walters & Reich, 1996, 1997, 1999, 2000a, 2000b; Delucia *et al*., 1998; Reich *et al*., 1998a, 1998b; Kaelke *et al*., 2001; Sack & Grubb, 2002) or continental Europe (Nygren & Kellomaki, 1983; Niinemets *et al*., 1997; also see review in Vera, 2000) with few studies based in Britain involving native tree species (McVean, 1956a; Jarvis, 1964; Shaw, 1974; Kelly, 2002). Most studies are comprehensive but lack the benefits of comparability between a large number of different tree species. A considerable effort in research is thus required to bridge this gap.

Initial work on shade tolerance quantification has often begun with the analysis of growth and survival responses to different levels of irradiance. Light is not only fundamental to plant growth but also the difference in the light required by different species of trees is considered by many authors as the most important factor for regeneration (Woodward, 1990; Denslow *et al*., 1990; Pacala *et al*., 1994; Vera, 2000). The sub-division of tree species into shade intolerant pioneers and shade tolerant climax species with descriptions of their specific morphological and physiological adaptations which enable them to survive extremes of light are well documented (Swaine & Whitmore, 1988; Spurr & Barnes, 1998; see Section 1.2.5). Responses to different degrees of irradiance of representatives of species from across the tolerance spectrum, have also been reported. All the above studies provide a framework for shade tolerance quantification.

As continued growth and survival in shade implies a net gain in carbohydrates, the ability of a species to tolerate shading has commonly been linked to photosynthesis, viz in the efficiency of the utilisation of light energy (in Pacala *et al*., 1994). Differences between species in their relative ability to tolerate shade may therefore be explained by: i) adaptations involving the efficiency of their photosynthetic system (i.e.: high photosynthetic rates at low light intensities) or (ii) morphological adaptations, involving change in the size of their photosynthetic system (in Loach, 1970).

There is an argument that the size or efficiency of the photosynthetic system in shade-grown plants cannot be used successfully as a shade tolerance parameter as neither clearly differentiates between tolerant and intolerant species (Loach, 1970; Corre, 1983a). However the lack of differences in growth between these two species types in low light can be explained by morphological adaptations, which plants generally express to counteract the potentially deleterious effects of reduced irradiance on growth (Loach, 1970; Read & Hill, 1985; Latham, 1992; Grubb *et al*., 1996). For example, light interception per unit plant biomass may be increased by an augmented biomass allocation to leaf material (Leaf mass ratio (LMR)) and the production of relatively thin leaves with a high specific leaf area (SLA) which leads to a high leaf area per unit plant mass (Leaf area ratio (LAR)) (Veneklaas & Poorter, 1998). Although species show similar responses to shade, the magnitude of response is often very different between shade intolerant and shade tolerant species which enables a distinction to be made between them.

Shade intolerants have been found to be more plastic in their response to irradiance whereby greater morphological adjustments (higher SLA, LAR) in shade have led to initially higher rates of growth compared to shade tolerants (Grime, 1965; Canham, 1989; Reich *et al*., 1998a). Shade tolerants, with their less flexible growth form, tend to maintain lower SLAs and LARs and lower RGRs in shade. The summary of typical morphological and physiological responses of shade tolerant, intermediate and shade intolerant tropical tree species growing under low, medium and high light conditions by Veneklaas and Poorter (1998) illustrates the differences in plasticity and its influence on RGR. Shade tolerants are reported to be distinguished by lower LMRs with the highest ratios found amongst pioneers. The same pattern is found for SLA leading to a considerably higher LAR for the pioneer species, especially under low-light conditions. The largest differentiation for LAR can be seen at the lowest light intensities, whereas the largest differentiation for NAR occurs at the highest light intensity. The patterns in both NAR and LAR lead to predictable ranking in growth rates of species groups, with the pioneer species realising the highest RGRs at low and high light. Largest interspecific differentiation in photosynthetic rates (reflected in NAR) in high light occur because shade tolerant species will be constrained by an inherently low photosynthetic capacity, whereas pioneer species can realise high light-saturated photosynthetic rates.

Changes in leaf morphology and physiology are not the sole determinants of growth. The relative proportion of other plant components to total plant mass can also alter the photosynthesis / respiration ratio and thus growth rates. This is why it is important to evaluate plant responses to shade with a whole plant perspective (Givnish, 1988). Givnish defines shade tolerance as a product of complex combinations of whole seedling responses including biomass allocation, morphological changes, leaf orientation and leaf level photosynthetic changes emphasising this point.

The whole plant approach also helps distinguish different shade tolerant growth strategies. Traits such as high SLA, LAR and lower root to shoot ratios tend to increase the ratio of photosynthesis to respiration at the whole plant level, thus contributing to the maintenance of a positive carbon budget and maximisation of growth in shade (Givnish, 1988). There are some species, though, which do not maximise growth in the shade but have a strategy to persist in shade which involves traits to minimise mortality (Delucia *et al.*, 1998). Where the relative cost of carbon loss to herbivores and pathogens is high and recovery from tissue loss is difficult due to energy limitation, natural selection tends to favour traits such as a high defence and storage allocation in the shaded environment (Coley, 1993). Traits include smaller, thicker leaves (low SLA, LAR) to confer resistence to pests (Burns & Honkala, 1990; Kitajima, 1994) and high root:shoot ratios to provide support and aid survival during periods of transient water limitation (Spurr & Barns, 1998). Large stores of carbohydrate in the root also suggest facultative behaviour where the plant is preparing itself for rapid growth following gap formation (Peterken, 1996; Delucia *et al.*, 1998).

Other traits that help to distinguish degrees of tolerance include shade avoidance responses (Grime, 1965; 1966). Shade intolerant species tend to have higher rates of etiolation in the shade. Furthermore, they will eventually start to display higher mortality rates (especially at < 2% PAR, Grubb *et al.*, 1996; Walters & Reich, 1996) where unadjusted sun-adapted traits (such as high rates of dark respiration) can lead to carbon exhaustion and eventual death (Grime, 1966).

In this experiment, one-year-old seedlings of 15 woody species native to the Caledonian Forest of the Scottish Highlands were grown in pots in an outdoor environment under three simulated forest shade regimes and a treatment open to full daylight. The objective was to determine whether one-year-old seedlings of these native species differ from one another with respect to shade tolerance, and/or responses to different irradiance levels. Specifically, the study documents the effects of different fluxes of Photosynthetic Active Radiation (PAR) on growth, biomass partitioning and morphology.

The following questions were asked:

i) Do species display classical responses to shade in accordance with the literature?

ii) Are morphological (leaf area ratios) or physiological (net assimilation rates) variables more important in driving RGRs at low and high irradiance levels?

iii) How can differences in growth, biomass allocation and morphology distinguish different degrees of tolerance or light demand between species?

v) How do physiological responses match traditional notions of shade tolerance and Ellenberg light indicator values?

3.2 Methods

3.2.1 Study site and species

The experiment was conducted over one growing season from mid-April to mid-August 2000 (18 weeks) in an open nursery site on the Bush Estate, Forestry Commission Northern Research Station, Roslin, Edinburgh (Figure A1.2). The tree species included in this study are native to the Glen Affric Caledonian Forest Reserve, Highland Region, Inverness-shire. The 15 species used are listed in Table 3.1, together with their original Ellenberg light indicator values (Ellenberg, 1988) as well as revised values for British saplings (Hill *et al*., 1999) (see Section 1.2.6). Species come from a range of habitats with different light regimes encompassing shade-tolerant intermediates (shade to semi-shade plants found in more than 5% relative illumination) to intolerant species (light loving plants rarely found where relative illumination in summer is less than 40%) (Ellenberg, 1988). It should be noted that these indicator values are based more on the distribution of plants in the field rather than physiological responses to irradiance. However as Ellenberg’s ranking scheme is the only one available which is based specifically on species preference for light, it provides a good baseline for comparison.

3.2.2 Seedling stock

One-year-old cell-grown tree seedlings of all 15 species were ordered from a Scottish native tree nursery (Christie Elite Nurseries Ltd (Forres, Moray). Unfortunately, due to unforeseen circumstances, three species had to be obtained from two other Scottish native tree nurseries: *Populus tremula* and *Prunus padus* from Cheviot Trees Ltd. (Berwick upon Tweed) and *Quercus petraea* from Alba Trees Ltd (Gladsmuir, East Lothian). All individuals were hand selected to ensure uniformity in stem height and provenance. Most seedlings were grown from seed which was collected from Strathconon Forest, 24 km north of Glen Affric in the UK Seed Collection Zone 201 (Herbert *et al*., 1999).

Table 3.1 Species used in the shade house trial with their type, original Ellenberg light indicator value (Ellenberg, 1988) and revised values for British saplings (Hill *et al*., 1999) in brackets. The scale ranges from 1(plants in full shade) to 9 (plants in full light).

Species	Type	Ellenberg's Light Indicator Values (British saplings)	Shade Tolerance Classifications
Juniperus communis	Evergreen conifer	8 (8)	Very Intolerant
Betula pubescens	Deciduous hardwood	7 (7)	Intolerant
Betula pendula	Deciduous hardwood	7 (7)	Intolerant
Pinus sylvestris	Evergreen conifer	7 (7)	Intolerant
Salix caprea	Deciduous hardwood	7 (7)	Intolerant
Salix cinerea	Deciduous hardwood	7 (7)	Intolerant
Populus tremula	Deciduous hardwood	6 (6)	Intermediate
Quercus petraea	Deciduous hardwood	6 (6)	Intermediate
Sorbus aucuparia	Deciduous hardwood	6 (6)	Intermediate
Corylus avellana	Deciduous hardwood	6 (4)	Intermediate
Alnus glutinosa	Deciduous hardwood	5 (5)	Intermediate
Prunus padus	Deciduous hardwood	5 (5)	Intermediate
Ilex aquifolium	Evergreen hardwood	4 (5)	Tolerant Intermediate
Ulmus glabra	Deciduous hardwood	4 (4)	Tolerant Intermediate
Fraxinus excelsior	Deciduous hardwood	4 (5)	Tolerant Intermediate

3.2.3 Experimental soils

All seedlings were potted up in a Hardwood Base Mix Standard pH compost mix (Alba Trees Ltd., Glasmuir, East Lothian) (pH 5.5 ± 0.3). Seedling cells were a mix of Sphagnum moss and 10% bark compost containing N:P:K (Christie Elite:10:18:24; Alba Tree Ltd; 10:24:27) base nutrients and slow release Sincrocell 12. As Sincrocell starts to have an effect 12-16 months after germination, it is feasible that it may have aided initial establishment of roots in trial pots. No extra fertiliser was added to the potting compost to simulate natural soil conditions found under Caledonian *P. sylvestris* forest.

3.2.4 Experimental design

The trial was set up following a hierarchical factorial design. The top stratum consisted of four light treatments (open, low, medium and deep shade) placed in a randomised Latin Square (one replicate per treatment placed in each of the four rows and columns) (see Appendix 1). Treatments were spaced two metres apart from each other on all sides. Each light treatment was divided up into three group areas, each containing one seedling per species (15 species x 3 replicates per light treatment). Each seedling was randomly placed, 0.02 m apart from each other. A buffer zone of 0.02 m between pots and the frame edge was also maintained. Seedlings were re-randomised every two weeks within groups to counteract any edge effects.

3.2.5 Light

The four light regimes were created with the construction of shade houses (1.34 m x 2.14 m x 1.5 m). Wooden frames were covered with different layers of green nylon shade cloth (Titan netting, LBS group, Lancashire) of 50% density so as to create the different light environments of approximately 2% PAR (4 layers), 15% PAR (2 layers), 30% PAR (one layer), and 100% PAR (no layers). The three latter light regimes were comparable with gap and shade microsites in *Pinus sylvestris* woodland (see Chapter 7). The deep shade treatment (2%) was comparable with light conditions found under *Calluna vulgaris* or *Pteridium aquifolium* vegetation (Peterken, 1966; Humphrey & Swaine, 1997). When the shade houses were being built, a portable meter with a Photosynthetic Active Radiation (PAR) sensor (SKP 200 0300 20498, Skye Instruments Ltd, Wales) was used to quickly establish the different light transmittances within an appropriate range. In June and August, data loggers with PAR sensors (SDL 2512, 15450, version DH / MM 63, Skye Instruments Ltd.) were used to obtain more accurate measures of daily transmittance. This involved placing one data logger on a 1 m high platform at the centre of each of the four treatment plots within a single column. There were only four loggers, so PAR was recorded in one column of the Latin Square at a time. In June, readings for each treatment plot were taken over one day. A more thorough record of day to day PAR variation was achieved in August with readings for each treatment plot taken over a period of four consecutive days. The sensor was set to record measures of PAR at every 30 s intervals and record values as an integrated mean over each 30 minute period in µmol m^{-2} s^{-1}. The percentage of light transmittance (PAR) in each of the three different shade houses was calculated as a percentage of total PAR in the open treatment[1]. An estimate of total daily PAR for each light treatment was calculated by summing the PAR readings for each light treatment pooled over 16 days.

As well as measuring PAR within the light treatments, an estimate of seasonal light quality was also obtained. A 660-730 nm sensor (SKR 110 0797 15447, SK3, Skye Instruments Ltd, UK) measuring instantaneous red:far-red (R:FR) ratio in µmol m^{-2} s^{-1} was placed on the platform in the centre of each treatment at 12 noon on a continuous cloud cover day approximately every two weeks during the growing season. To ensure constant positioning, the sensor was also mounted on a removable metal platform. An average of the recordings for each treatment throughout the experimental period was calculated.

3.2.6 Temperature and humidity

At the same time that PAR loggers were placed in the treatments, data loggers with temperature and humidity sensors (HOBO H8 Pro Series H08-032-08, Onset Computer corporation, Bourne, MA) were attached underneath the PAR platforms. There were only four loggers so temperature and humidity were recorded in one column of the Latin square at a time. The sensor was set to record measures of ambient air temperature (°C) and relative humidity (%) at 30 s intervals and record values as an integrated mean over each 30 minute period. For June, data were recorded over a single day period from 9.30am to 6pm. For August, data were recorded over 24 hours (18:00 18:00) each day for four consecutive days.

3.2.7 Establishment

At the beginning of the trial period, a considerable effort was made to minimise the potential effect of seedling size on growth. Nursery selection provided a level of uniformity in height. This was refined further by dividing individual species into four different size rank groups of very small, small, medium and large (based on height measurement). Each size rank group across species was then allocated a

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[1] Normally PAR% is calculated as a percentage of total PAR measured in a shade free open area. However with the lack of a fifth logger and shade-free conditions in the nursery, the open treatments had to suffice. Daily PAR was calculated from 11:00 –15:00 hrs to omit readings potentially affected from shade cast from adjacent buildings and shelter-belts.

specific column in the Latin Square design to integrate size variation effects with column effects. Seedlings were potted up into 2 litre black rose pots (10.5 cm in diameter, 18.5 cm in height) (Aeroplas Ltd) early in February to allow for an adjustment period before transfer to the different light treatments in March before leaf flushing. In June, all seedlings were hand-sprayed with Provado, a systematic insecticide, due to the presence of aphids (particularly on *P. padus*). In August, *Q. petraea* contracted powdery mildew so it was treated with Systane, a systematic fungicide. Seedlings were hand watered when the soil in pots started to dry following rain-free periods. During hot dry summer periods, pots were watered everyday.

3.2.8 Survival & growth measurements

Seedling survival was recorded after the first week of the trial and then every month over the growing season. Stem height (from stem base to apical bud), basal diameter and internode number were measured for all trial seedlings at the beginning and end of the growing season. Such measurements were obtained with a metre rule and digimatic caliper (ABSolute, RS 432-025 Mitutoyo (UK) Ltd).

3.2.9 Harvesting

After 18 weeks of growth (t_2), the seedlings within the treatments were harvested to obtain total dry mass and dry mass values of the leaf laminas (broadleaves) / needles (conifers), stems (including leaf petioles and rachis) and roots. Plants were divided up into their separate components and oven dried until a constant dry mass was obtained (48 hrs @ 80 °C). Methodology from Evans (1972) was followed. The samples were then weighed using a digital top balance (± 0.001 g). Before the fresh leaves were placed in the oven, they were photocopied so that leaf area calculation (± 1 cm^2), could be measured at a later date with a leaf area meter (Delta T Devices Ltd.). The photocopier was checked for scale distortion using graph paper. All roots were washed free of soil by hand and with the aid of sieves and a lightly powered water spray. From these primary data, a number of growth parameters were calculated (Hunt, 1990). These were: leaf area ratio (LAR, leaf area /dry plant mass (m^2g^{-1})); specific leaf area (SLA, leaf area/dry leaf mass (m^2g^{-1})); leaf mass ratio (LMR, dry leaf mass/dry plant mass); stem mass ratio (SMR, dry stem mass/dry plant mass); root mass ratio (RMR, dry root mass/dry plant mass) and specific stem length (SSL, stem length/dry stem mass). Calculations have been modified slightly from descriptions in Hunt (1990) as lamina was used instead of leaf, and "stem" also included petioles or rachis. Henceforth, the term "leaf" is used to mean leaf lamina and "stem mass" is taken to include petiole and rachis. Relative growth rate (RGR) and net assimilation rate (NAR) were determined using the following equations:

$$RGR = (\ln W_2 - \ln W_1)/(T_2 - T_1) \qquad \text{Equation 3.1}$$

$$NAR = (W_2 - W_1).(\ln A_2 - \ln A_1)/(T_2 - T_1).(A_2 - A_1) \qquad \text{Equation 3.2}$$

in which W is total dry mass (g), A is leaf area (m^2), T is the time interval between harvests (weeks) and the subscripts refer to initial (1) and final (2) harvest.

In the calculation of RGR, plant mass was log-transformed before averaging; adopting the estimator 2 approach outlined by Hoffmann & Poorter (2002). This was done to avoid bias, which can occur if plant mass is averaged before log-transformation[2]. Total dry mass (W_1) was obtained by an initial harvest of 12 extra seedlings per species at the beginning of the experiment. Three seedlings per species were selected from each of the four size/height ranks in an endeavour to represent the whole size range of the plants. They were then paired[3] with trial seedlings from the same size group. Mean W_1 was then calculated from the means of each size group (ie: four means) after transformation. As the initial harvest was done before bud burst, initial leaf area for NAR calculation could not be obtained for broadleaves so a nominal value ($0.0001m^2$) was assigned.

The equation used for the calculation of NAR is only valid when total plant dry mass (W) and leaf area (A) are linearly related (Radford, 1967; Hunt, 1978). When leaf area was plotted against total plant dry mass, the scatter of data points was consistent with a linear relationship ($P < 0.001$) for all species. However, deciduous species at time 0 could not be included in this graph because they were leafless. Consequently NAR for these species should be viewed with caution.

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[2] a biased estimate of RGR is produced whenever the variance of the natural logarithm-transformed plant mass changes through time. This bias increases with an increase in the variance in RGR, in the length of the interval between harvests or in sample size.

[3] The simplest method of pairing is by unrestricted randomisation and has the advantage of statistical validity, but a randomised block / latin square design, in which similar sized plants are grouped together at the beginning of the experiment, also gives a valid statistical basis for pairing and would intuitively seem to be better than completely random pairing (Causton, 1991). Causton (1991) also found that there was no difference in mean RGR and no consistent difference in the standard deviations of RGR from three different ways of calculating RGR: non-pairing method (Venus & Causton, 1979), pairing by block and random pairing.

3.2.10 Statistics

ANOVA (Genstat/Windows Ed. 6, Rel. 6.1) was used to analyse growth and morphological responses of species to light treatments. Within Genstat, the treatment terms that were analysed by ANOVA included species, light and species-light interactions. The main experimental design involved a nested and crossed structure which was incorporated into the BLOCKSTRUCTURE model: (Row*Column)/Rep/Pots[4]. The ANOVA tables (Appendix 2) clearly illustrate how the design structure was incorporated into the analysis with sources of variation explained at each stratum level[4].

Before ANOVAs were interpreted, residual plots were drawn up for each parameter to check for normality and homogeneity of variance. Data were transformed where necessary using natural logs for plant mass and unconstrained ratios such as SLA and SSL. Square root transformation was used for counts such as number of leaves. Missing values in the orthogonal design were dealt with by substituting in estimated values generated by Genstat's missing value estimation function[4]. Least significant difference error bars (LSD) were attached to ANOVA plots (multiple comparison tests were found to be inappropriate) (see Appendix 2).

Spearman's rank correlations were used to analyse relationships between growth parameters due to non-normality in the dataset (Minitab, Windows Version 13). Parameters were also plotted against irradiance so comparisons could be made with the RGR light response. These plots also helped validate significant correlations between parameters sharing similar components in their calculation, thus accounting for possible autocorrelation effects (eg: RGR & NAR).

3.3 Results

3.3.1 Micro-climatic conditions in the shade houses

Daily PAR% from logged data for three shade compartments yielded 2.5% PAR (deep shade), 14% PAR (medium shade) and 33% PAR (low shade) for August (Table 3.2). PAR readings in June were slightly higher but not dissimilar in upper range. In August, very few differences in minimum air temperature occurred during the night between shade frames but maximum air temperature during the day was higher in the open than in deep shade by 1° C. Maximum humidity remained the same for all treatments but the minimum humidity was slightly higher in 2.5% PAR

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[4] See Appendix 2 for ANOVA tables (including degrees of freedom and F ratio calculations), explanation of directive terms, sources of variation at each stratum level and calculation of missing values.

than in the open by 3%. Maximum air temperature during the day was similar between June and July (i.e.:19-20°C) as was minimum humidity (55-59%) across light regimes. Seasonal R:Fr ratio was significantly reduced with increasing shade ranging from 1.01 in the open to 0.69 in deep shade.

Table 3.2 Microclimatic conditions in the shade houses compared with the open treatment. Means for each treatment have been summed across columns in the Latin Square design. Light values are means of total daily PAR or maximum PPFD for June (n = 4, ± Standard Deviation (STDEV)) and August (n = 16, ± STDEV). PAR have been calculated from readings taken from between 11:00 and 15:00 hrs. R/Fr readings reflect seasonal means taken between June and August (n = 32). Temperature and humidity means are daily readings (9:30 - 18:00 hrs) for June (n = 4, ± STDEV) and diurnal readings for August (n = 16, ± STDEV).

	Light treatment			
Period	Open	Low shade	Medium shade	Deep Shade
JUNE (20/6/00-26/6/00)				
Daily PAR (%)^	100	42 (± 5.3)	16 (± 1.4)	3 (± 0.89)
Max. PPFD†	1174 (± 146)	525 (± 139)	175 (± 38))	39.0 (± 16.6)
Max. air temperature (°C)	19.1 (± 1.8)	19.6 (± 1.6)	19.0 (± 1.8)	18.7 (± 1.6)
Min. relative humidity (%)	55.2 (± 6.9)	55.3 (± 6.5)	57.1 (± 7.5)	58.4 (± 5.8)
AUGUST (11/8/00-1/9/00)				
Daily PAR (%)^	100	33 (± 13.0)	14 (± 2.7)	2.5 (± 0.9)
Max. PPFD†	949 (± 273)	312 (± 143)	137 (± 56)	24.1 (± 12.4)
Min. air temperature (°C)	8.6 (± 2.0)	8.6 (± 1.8)	8.9 (± 1.9)	9.0 (± 1.9)
Max. air temperature (°C)	20.8 (± 3.0)	20.5 (± 3.0)	19.9 (± 2.8)	19.5 (± 2.6)
Min. relative humidity (%)	55.7 (± 10.8)	55.5 (± 11.6)	*	59.1 (± 10.7)
Max. relative humidity (%)	98.5 (± 2.8)	98.5 (± 2.5)	*	98.5 (± 2.6)
SUMMER (23/6/00-18/8/00)				
Red/Far-red ratio	1.02 (± 0.04)	0.92 (± 0.05)	0.85 (± 0.05)	0.69 (± 0.04)

^Daily photosynthetically active radiation as percentage of open conditions
†Photosynthetc photon flux density (µmol m^{-2} s^{-1})
*Sensor malfunction

3.3.2 Plant size (Primary data)

Number of leaves, stem and basal diameter increment, leaf area, leaf mass, stem mass, root mass and total plant mass were all significantly affected by light ($P < 0.001$) (ANOVA tables, Appendix 2). Values were generally lowest in deep shade (2.5% PAR) and highest at 33% PAR and or in full daylight (100% PAR) (see Appendix 6). However, significant species-light interactions for all growth parameters indicated that species responses at each light level varied ($P < 0.001$). In terms of total biomass, the relative effects of shade were most pronounced in *Alnus glutinosa*, *Betula pubescens*, *Betula pendula* and *Salix cinerea*. For these species, the final mass of the seedlings in full daylight were approximately 5-6 times those at 2.5% PAR. The effect was moderate (approx. 4 to 5 fold difference) in *P. tremula*, *P. padus*, *Sorbus aucuparia*, *Ulmus glabra*, *Salix caprea*, *Pinus sylvestris* and

Juniperus communis. The lowest effect (approx. 2 fold difference) was found in *Corylus avellana*, *Fraxinus excelsior*, *Q. petraea* and *Ilex aquifolium*.

Maximum relative height growth (RHG) was generally achieved at 33% PAR with similar[5] levels found at 14% PAR for nearly half of all species (Figure 3.1). At 33% PAR, *B. pubescens* had the highest RHG which was similar to that of *B. pendula*, *S. aucuparia* and *P. padus*. In deep shade (2.5% PAR), *S. caprea* had the highest RHG. Maximum relative diameter growth (RDG) was achieved in full daylight but for the majority of species RDG was also similar to 33% PAR (Figure 3.1). Exceptions included all evergreens and *P. tremula* which continued to increase RDG in full daylight. *Q. petraea* stood out amongst all species with the highest RDG of all, achieved at 33% PAR. In deep shade, there were few differences between species. *U. glabra* had the highest RDG sharing a similar value with *S. caprea*.

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[5] The term "similar" is used throughout the text to imply differences less than the calculated LSD.

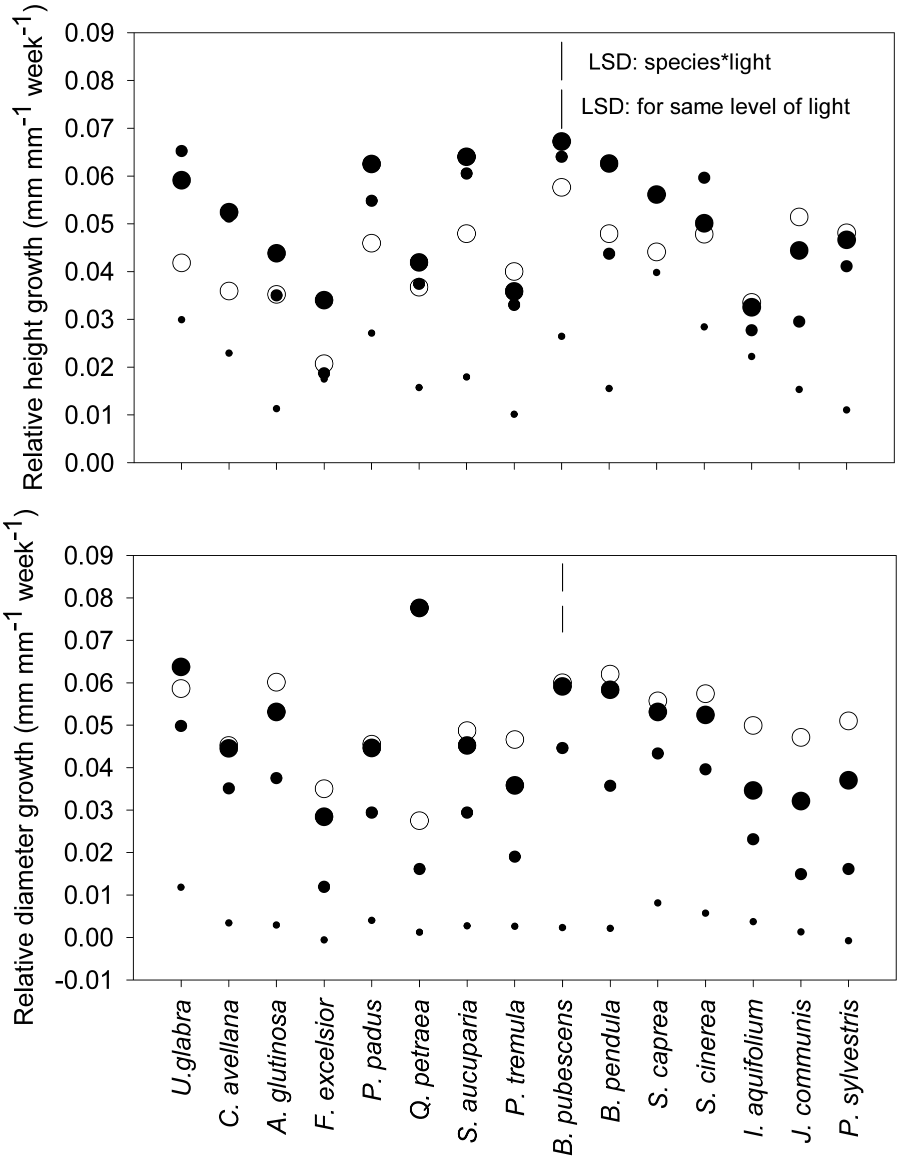

Figure 3.1 ANOVA plots displaying species.light interactions for relative height growth (mm mm^{1} week^{-1}) and relative diameter growth (mm mm^{-1} week^{-1}). Least significant different error bars have been appended to each plot; the first for the interaction between light and species and the second for the comparison of means with the same level of light: 100% PAR (○); 33% PAR (●); 14% PAR (•); and 2.5% PAR (·). Species have been put along the x axis in order of increasing Ellenberg light indicator value (decreasing shade tolerance) for British saplings (Hill *et al.*, 1999) segregating the evengreens so they appear as a group to the far right.

3.3.3 *Relative growth rates, morphology and physiology*

ANOVA results showed highly significant light, species and light-species interactions ($P < 0.001$) for relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR) and specific leaf area (SLA) (ANOVA tables, Appendix 2). RGR increased with increasing light availability in all species up to 33% PAR where further significant increases in growth in full daylight were found for approximately half of the trial species (Figure 3.2). They included *I. aquifolium, P. sylvestris*, *J. communis* plus *A. glutinosa, Q. petraea, P. tremula,* and *S. cinerea*. The size of response to irradiance was greatest between 2.5% PAR and 14% PAR for most species except the evergreens, *F. excelsior* and *Q. petraea* which displayed a lower more steady positive response. In full daylight, the fastest growers were *B. pubescens*, *S. cinerea*, *B. pendula*, *A. glutinosa*, and *U. glabra*. The slowest growers were *Q. petraea*, *I. aquifolium*, *F. excelsior* and *P. sylvestris*. In deep shade, the fastest growers were *U. glabra*, *S. caprea* and *C. avellana*. The slowest growers were the two conifers *P. sylvestris* and *J. communis* followed by *Q. petraea* and *F. excelsior*.

NAR showed a positive response to irradiance comparable with RGR but continued to increase beyond 33% PAR for all species except for *S. aucuparia* (Figure 3.2). In deep shade, there are no significant differences in NAR between species, however, at higher light levels, differences between species become more apparent. In full daylight, *S. cinerea* had the highest NAR of all species. *P. padus* had the second highest NAR but it was also similar to *S. caprea*, *U. glabra*, *B. pubescens*, *F. excelsior*, *B. pendula* and *P. tremula*. The evergreens had the lowest NAR followed by *Q. petraea*.

Generally LAR and SLA displayed an opposite response to irradiance, with higher values found at lower light levels (Figure 3.2). In full daylight, species generally maintained relatively low LARs which were similar to each other. Differences however became more apparent at lower light levels. In deep shade, *U. glabra* had the highest LAR of all species followed by *C. avellana*. *F. excelsior* had the lowest LAR similar to *P. sylvestris*. The evergreens displayed distinctively lower SLAs than deciduous species for all light levels. In deep shade, *S. aucuparia* had the highest SLA, similar to both *Betula* species, *U. glabra* and *C. avellana*. *Q. petraea* had the lowest SLA of all deciduous species.

All species responded to shading by producing etiolated stems, expressed by Specific Stem Length (SSL), measured as stem height divided by stem mass (Figure 3.3). Etiolation in deep shade was most marked in the two conifers; *J. communis* and *P. sylvestris* which both produced the longest thinnest stems of all species. Higher levels of etiolation amongst broadleaves was shared by both *Betula* and both *Salix* species plus *P. tremula* and *A. glutinosa*. *I. aquifolium*, *F. excelsior*, *P. padus*, *Q. petraea* and *S. aucuparia*, all shared lower levels of etiolation leaving *U. glabra* and *C. avellana* with a more intermediate response. The above grouping of species in relation to their SSL response in deep shade can be closely associated with Ellenberg light indicator values for British saplings (Hill *et al*., 1999).

3.3.4 *Biomass allocation and partitioning patterns*

ANOVA results showed highly significant light, species and light-species interactions ($P < 0.001$) for leaf mass ratio (LMR), shoot mass ratio (SMR), root mass ratio (RMR), and root shoot ratio (RSR) (ANOVA tables, Appendix 2). The one exception involved LMR with no significant difference found between light treatments ($P = 0.058$) (Figure 3.3). The evergreens were distinctly different from deciduous species with much higher LMRs at all light levels.

The SMR response to irradiance revealed slightly more differences than LMR but most were found with RMR (Figure 3.3). Generally evergreens had a higher SMR in high light (33% and 100% PAR) compared to deep shade and deciduous species showed an opposite response with a lower SMR in full daylight compared to at least one of the lower light levels. *Q. petraea* and *P. tremula* were exceptions where SMR remained similar between irradiance levels. A general trend revealed a decrease in RMR with shade down to 14% PAR for most broadleaves but further decreases were not apparent in deep shade except for *I. aquifolium*. Conifers displayed an opposite response with an increase in RMR with shade. In deep shade, *F. excelsior* and *Q. petraea* had the highest RMR compared with all other species. They also maintained relatively high RMRs in full daylight similar to *U. glabra* and both *Salix* species. *I. aquifolium* had the lowest RMR in deep shade as well as in full daylight.

All species changed their biomass partitioning pattern between light regimes (Figure 3.4). Deciduous species tended to allocate more carbon to the stem, followed by root and then leaves. Most reduced the amount of carbon allocated to roots down to 14% PAR with a subsequent increase in stem mass rather than leaf mass. In deep shade, carbon allocation to the roots increased root mass again but differed in degree between species:

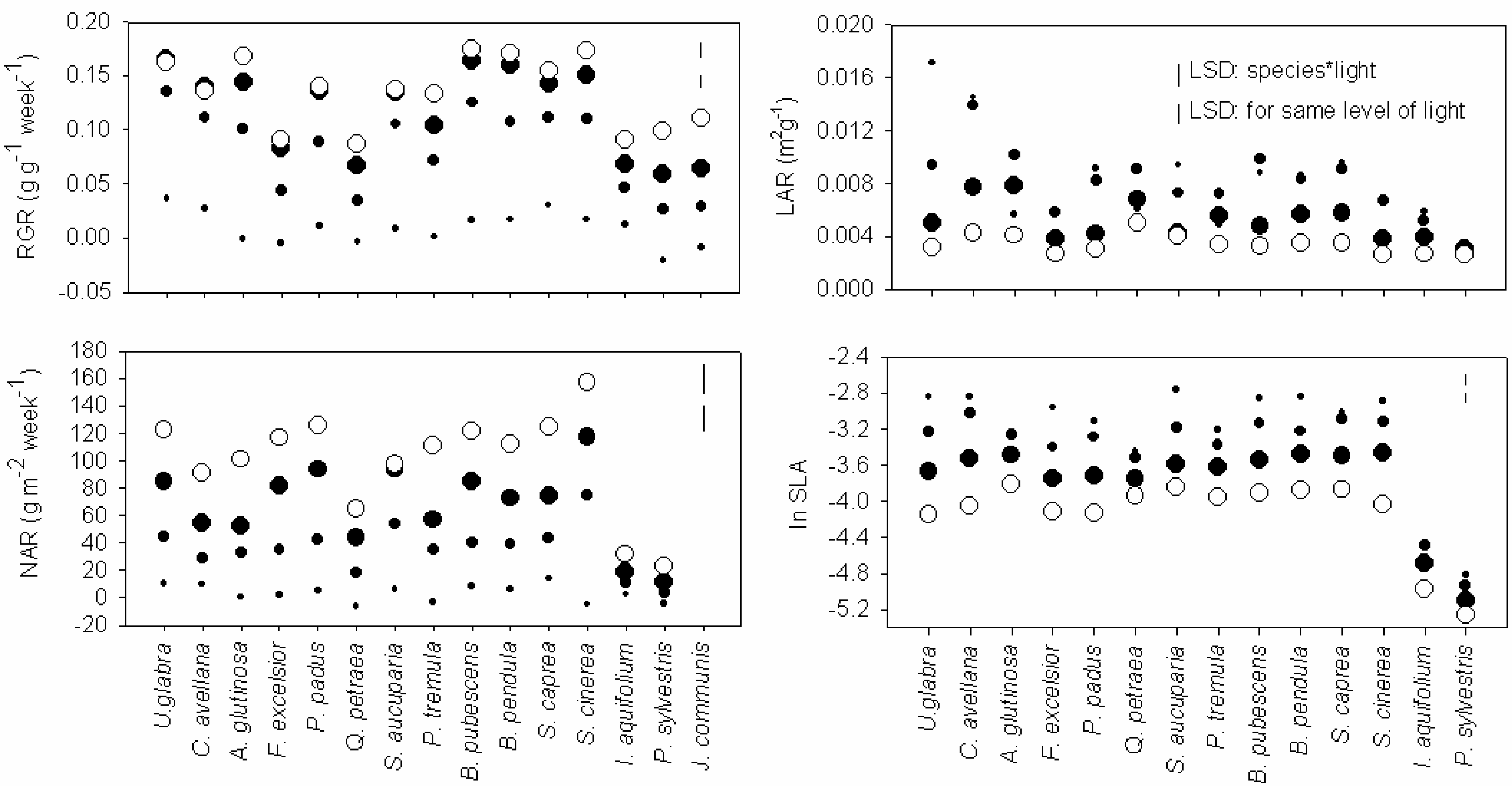

Figure 3.2 ANOVA plots displaying species.light interactions for relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR) and loge specific leaf area (SLA). Least significant different error bars have been appended to each plot; the first for the interaction between light and species and the second for the comparison of means with the same level of light: 100% PAR (o); 33% PAR (●); 14% PAR (•) and 2.5% PAR (•).

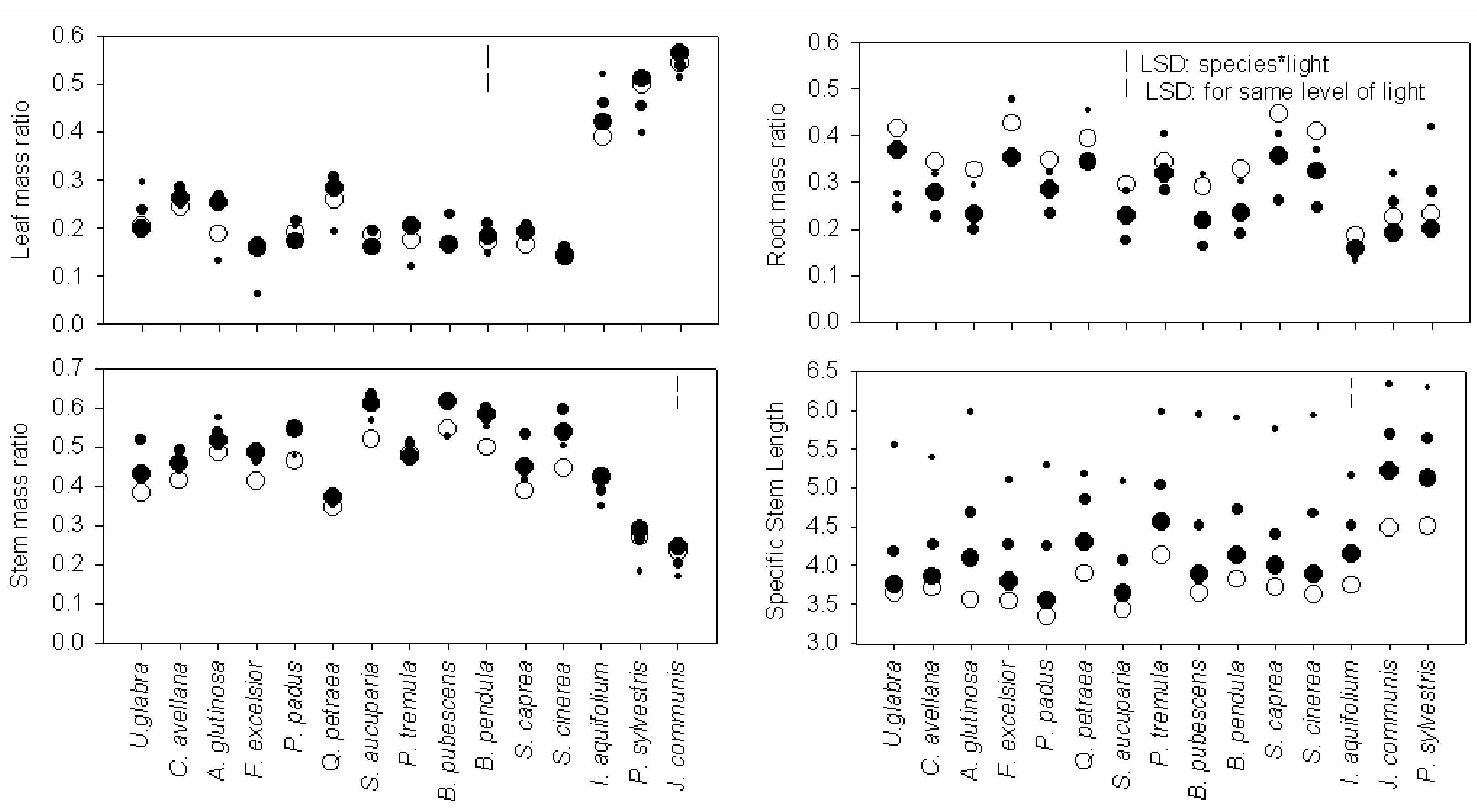

Figure 3.3 ANOVA plots displaying species.light interactions for leaf mass ratio, stem mass ratio, root mass ratio and specific stem length (mm g^{-1}). LSD error bars have been appended to each plot; the first for the interaction between light and species and the second for the comparison of means with the same level of light: 100% PAR (○); 33% PAR (●); 14% PAR (●); and 2.5% PAR (•).

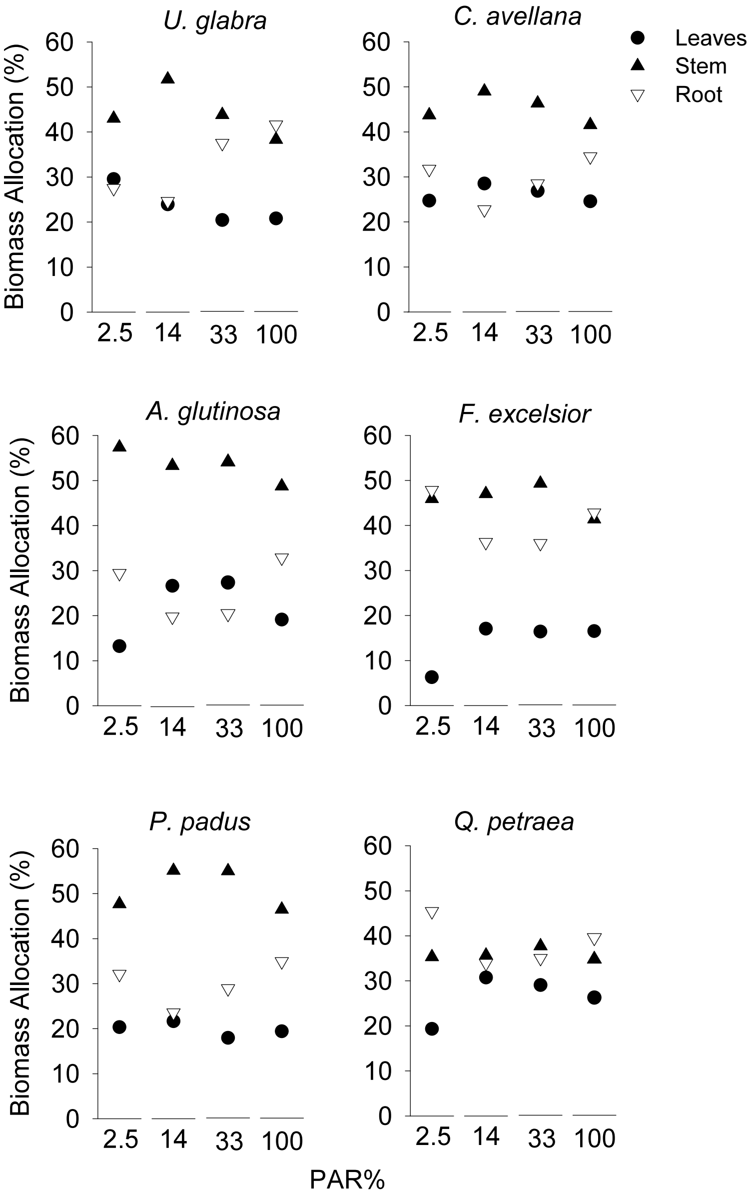

Figure 3.4 Biomass allocation patterns at four different light regimes of 2.5%, 14%, 33% and 100% PAR (open) for 15 Scottish native tree species.

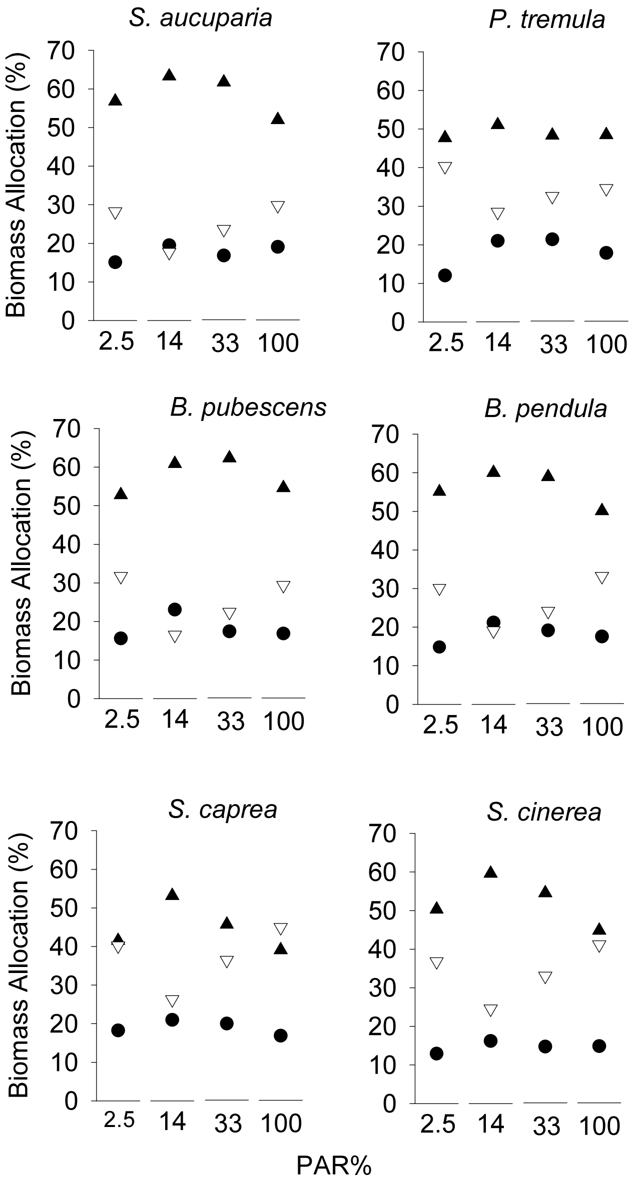

Figure 3.4 continued

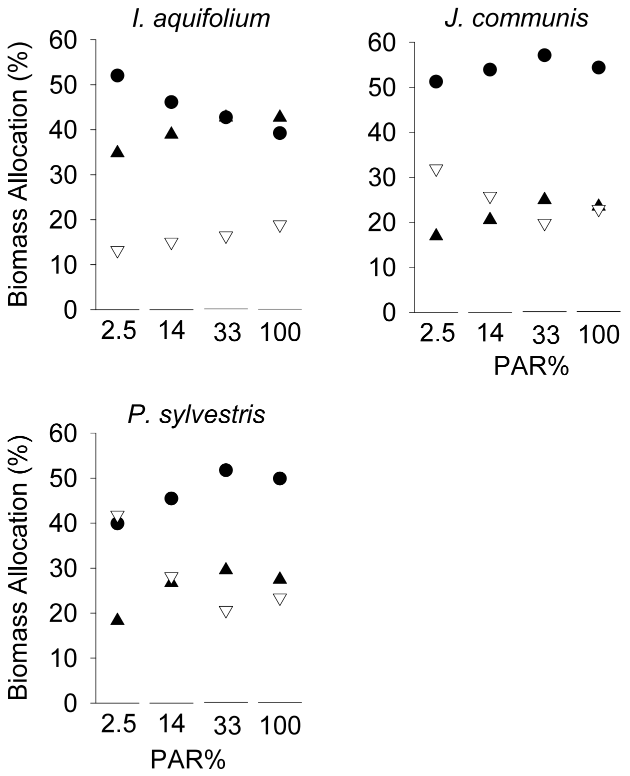

Figure 3.4 continued

C. avellana, *A. glutinosa*, *P. padus*, *S. aucuparia*, both *Betula* and both *Salix* species had similar root biomass to levels found in the full daylight whereas *F. excelsior*, *Q. petraea* and *P. tremula* increased root mass to its highest level. Carbon allocation to leaves did not change much across light regimes for some deciduous species. Others were subjected to substantial reductions in deep shade. *U. glabra* was the only deciduous species which displayed an increase in carbon allocation to leaves with increasing shade.

Evergreens allocated more carbon to the leaves / needles rather than stem or root. Both conifers allocated increasing amounts of carbon to roots in shade at the expense of the leaves and stem from 33% PAR. *I. aquifolium* showed the same trend of stem mass decline with shade as the conifers but in contrast, increasing amounts of carbon were allocated to the leaves with a subsequent decline in root mass down to 2.5% PAR.

3.3.5 Interrelationships between growth variables

The RGR of a plant is a product of a physiological component, NAR (the net increment of plant mass expressed per unit leaf area) and the morphological component, LAR (the leaf area relative to plant dry mass) (Evans, 1972). Both LAR and NAR were sensitive to changes in light availability (Figure 3.5-3.7). When analysis was restricted to individual light levels for all species, significant positive correlations between RGR and NAR were found at all individual light levels (Table 3.3). Significant positive correlations between RGR and LAR were only found at the two lower light levels (14% & 2.5% PAR). Similar patterns were found for just deciduous species.

Responses across light regimes (pooled data) revealed distinctive patterns: RGR was significantly positively correlated with NAR and significantly negatively correlated with LAR for both species groups (Table 3.3). Generally for all species, NAR was lowest at 2.5% PAR and highest (but with marked variation) in full daylight (Figure 3.2). In contrast, the LAR was generally lowest at the two higher light levels and highest (with marked variation) at 2.5% PAR (Figure 3.2). Thus it can be surmised, although the plants growing in high light had a lower LAR, the disproportionately high value of NAR more than compensated for this and resulted in higher growth rates.

The LAR of a plant is a product of SLA and LMR (Evans, 1972). When analysis was restricted to individual light levels for all species, significant strong positive correlations were found between LAR and SLA rather than LMR (Table 3.3). However for just deciduous species, a stronger correlation between LAR and SLA (rather than LMR) was found in full daylight. With increasing shade, LMR became increasingly more important with stronger positive correlations found between LAR and LMR rather than SLA . More consistent patterns were found across light regimes. Identical highly significant correlations were found between LAR and SLA for both groups of species. However, the presence of a weaker but significant correlation between LAR and LMR for just deciduous species suggests that LMR also played a role in driving LAR.

For all species across light regimes, no other growth parameters were significantly correlated with RGR apart from NAR and LAR (Table 3.3). However for just deciduous species, SLA and SSL were significantly negatively correlated with RGR. At individual light levels, for all species, SLA was significantly positively correlated with RGR at all levels except for full daylight and LMR was significantly negatively correlated with RGR in just full daylight. For just deciduous species, SLA was significantly positively correlated with RGR at the light levels of 14% PAR and 2.5% PAR.

Table 3.3 Spearman's rank correlations between growth variables (means) at final harvest for all species (except *J. communis*) and just deciduous species. Correlations are presented for individual light regimes (n = 14) as well as overall trends (n =56) *P < 0.05, **P< 0.01, ***P< 0.001.

		Growth variables					
		LAR	NAR	SLA	LMR	RSR	SSL
ALL SPECIES							
100% PAR	RGR	-0.03	0.65*	0.45	-0.54*	0.02	-0.33
	LAR	-	-0.26	0.70**	0.13	0.03	0.05
33% PAR	RGR	0.30	0.56*	0.72**	-0.47	0.23	-0.42
	LAR	-	-0.25	0.47	0.29	0.21	0.11
14% PAR	RGR	0.65*	0.65*	0.87***	-0.25	-0.42	-0.44
	LAR	-	0.14	0.59*	0.16	-0.25	-0.19
2.5% PAR	RGR	0.83***	0.75**	0.74**	0.22	-0.51	-0.03
	LAR	-	0.77**	0.70**	0.36	-0.49	-0.25
Across light regimes							
	RGR	-0.27*	0.89***	-0.25	-0.09	-0.08	-0.82
	LAR	-	-0.40**	0.81***	0.15	-0.30*	0.48
DECIDUOUS							
100% PAR	RGR	-0.26	0.54	0.25	-0.42	-0.31	-0.15
	LAR	-	-0.68*	0.61*	0.45	-0.18	0.32
33% PAR	RGR	0.01	0.31	0.56	-0.16	-0.15	-0.10
	LAR	-	-0.91***	0.24	0.89	-0.09	0.63*
14% PAR	RGR	0.49	0.49	0.82**	0.08	-0.50	-0.35
	LAR	-	-0.38	0.37	0.83**	-0.39	0.08
2.5% PAR	RGR	0.89***	0.75**	0.74**	0.57	-0.47	0.17
	LAR	-	0.84**	0.64*	0.81**	-0.62*	-0.12
Across light regimes							
	RGR	-0.45**	0.86***	-0.58***	0.09	-0.15	-0.81***
	LAR	-	-0.70***	0.81***	0.52***	-0.53***	0.67***

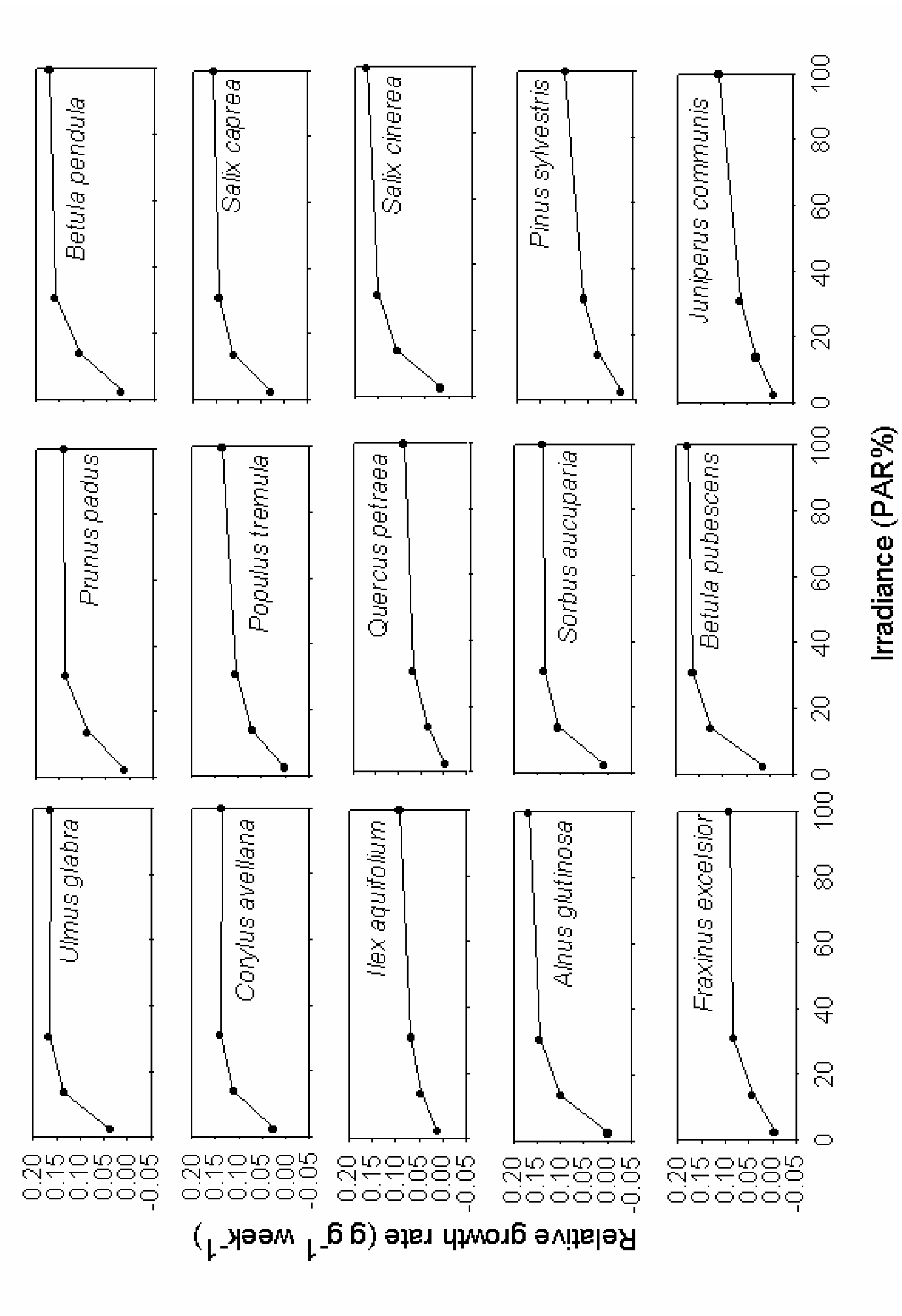

Figure 3.5 Relative growth rate (RGR) response to irradiance (PAR%) of 15 Scottish native tree species.

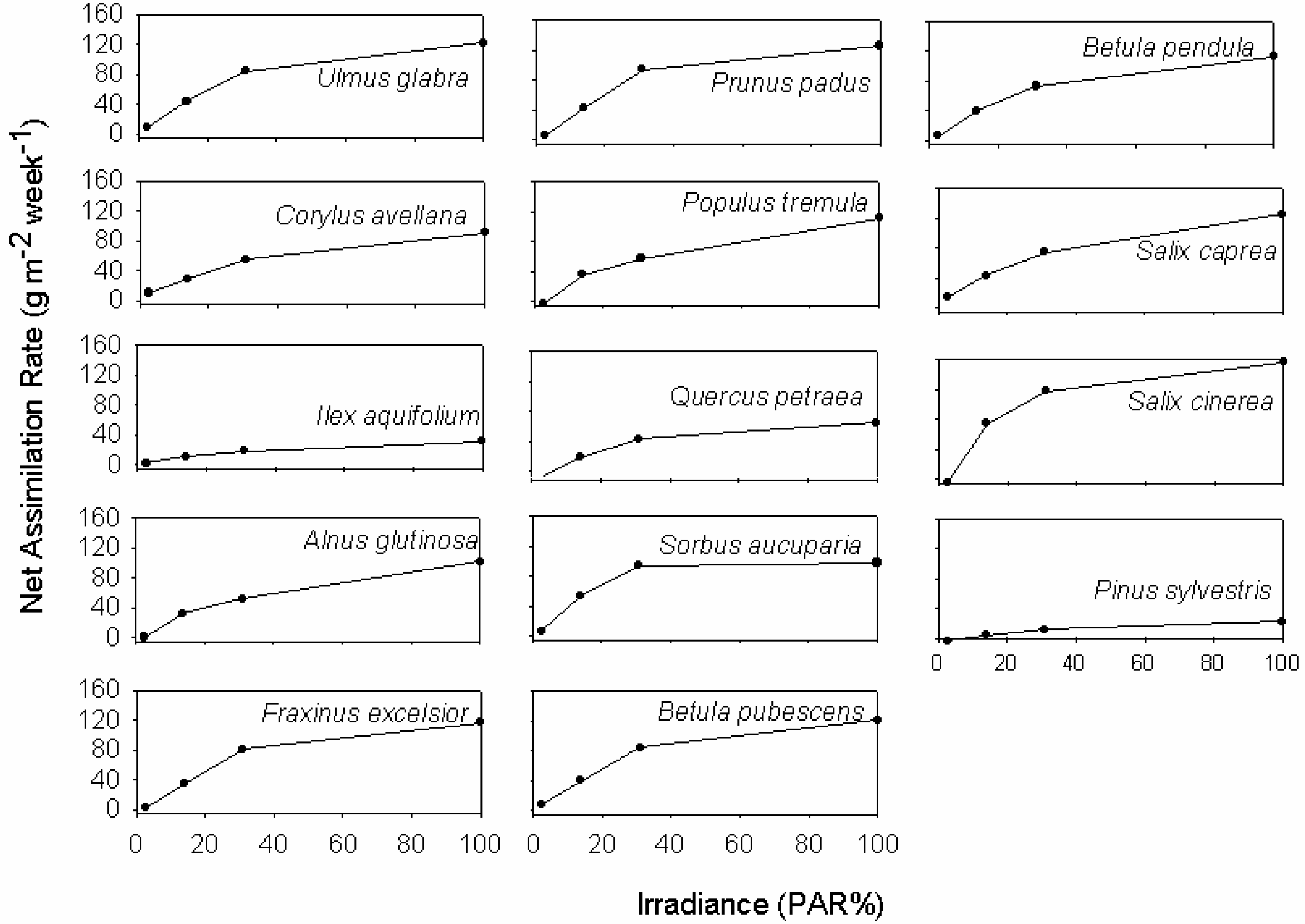

Figure 3.6 Net assimilation rate (NAR) response to irradiance (PAR%) of 14 Scottish native tree species.

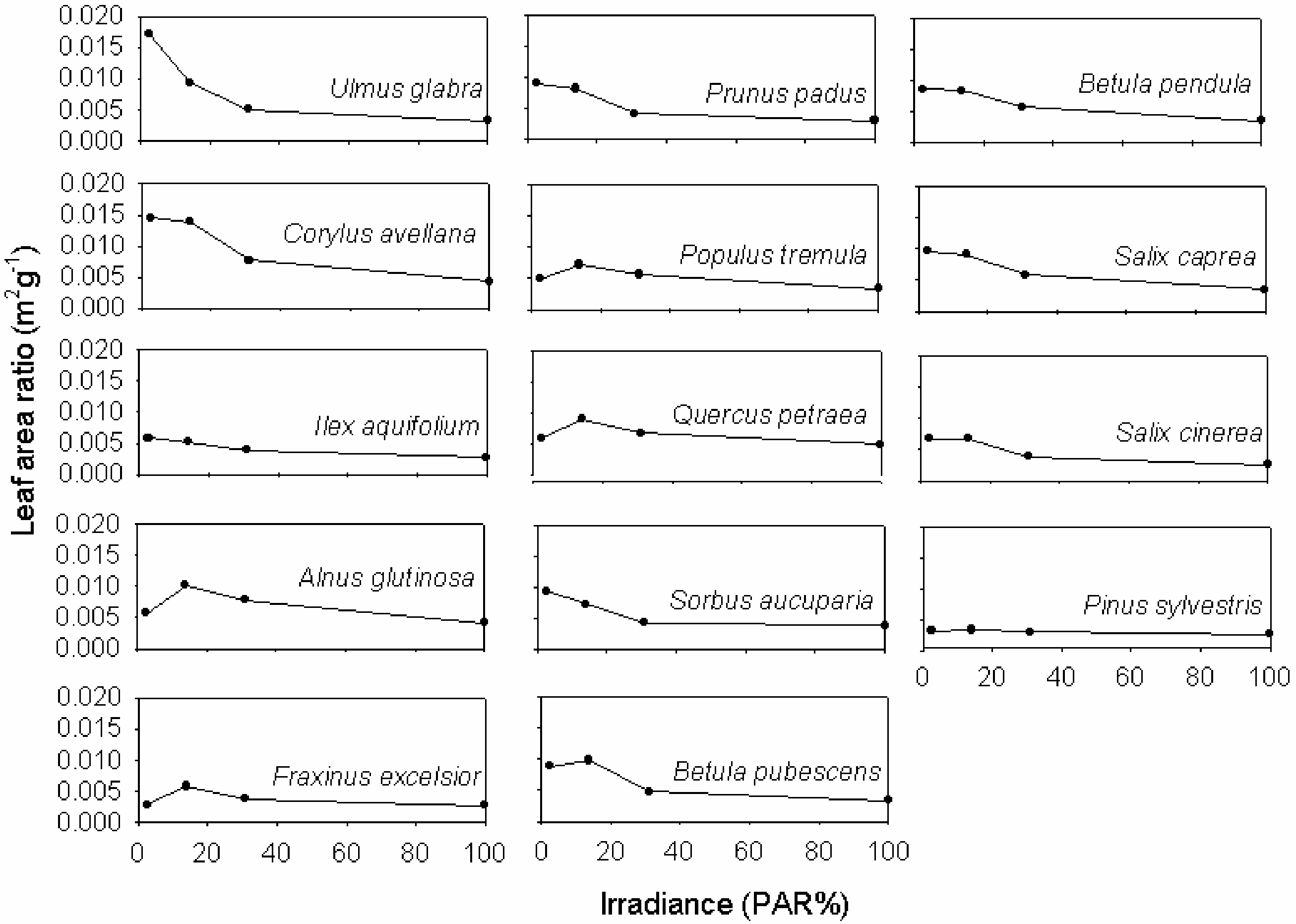

Figure 3.7 Leaf area ratio (LAR) response to irradiance (PAR%) of 14 Scottish native tree species.

3.4 Discussion

Do species display classical responses to shade in accordance with the literature?

Species displayed typical growth responses to shade: all reduced RGR and NAR but increased SLA and LAR (Figure 3.2). Morphological adjustments to shade such as the production of thinner leaves (higher SLA) and subsequent increases in LAR enhance light interception and are commonly reported for temperate woody species (Jarvis, 1964; Loach, 1970; Nygren & Kellomaki, 1983; Read & Hill, 1985; Latham, 1992; Ziegenhagen & Kausch, 1995; Grubb *et al*., 1996; Humphrey & Swaine, 1997; Reich *et al*., 1998a). A reduction in growth rate (RGR) with corresponding reductions in photosynthetic rate expressed in NAR due to light limitation has also been reported (Jarvis, 1964; Loach, 1970; Reich *et al*., 1998a; Veneklaas & Poorter, 1998).

Another typical response to shade when light is the most limiting factor involves a reduction in root mass (Ovington & McRae, 1960; Jarvis, 1964; Phares, 1971; Helliwell & Harrison, 1979) as more carbon is allocated to shoots to improve capture of photon energy (Chapin *et al*., 1987; Lambers & Poorter, 1992). Species (excluding the conifers) did show a general reduction in root mass but only down to 14% PAR rather than 2.5% PAR (Figure 3.4). Studies which report reductions specifically down to at least 2.5% PAR include Kitajima (1994), Walters & Reich (1996); Grubb *et al*. (1996) and Welander & Ottosson (1998). An unexpected response amongst deciduous species involved an increase in root mass, again in deep shade. Similar findings were revealed by McVean (1956a): the root:shoot ratio of potted *A. glutinosa* seedlings in a shade house trial was lowest in intermediate light (17% PAR) but increased again in deep shade (5% PAR). The response has also been reported in the field for *Betula* species (Messier & Puttonen, 1995; Humphrey & Swaine, 1997). Possible explanations for this response include: (i) increased competition for nutrients and water (Kolb *et al*., 1990; Grubb *et al*., 1996; Spurr & Barnes, 1998); (ii) strategy for facultative species which are released in gaps (Peterken, 1996; Delucia *et al*., 1998); (iii) leaf shedding leading to shifts in partitioning to the roots as well as stems (Kitajima, 1994), and (iv) light limiting shifts in allocation.

It would be surprising if shortage of nutrients or water was the reason for an increase in root mass in 2.5% PAR because the deep shade treatment tended to keep pots moist. Furthermore, seedlings grew the least in deep shade so were less likely to exhaust the existing nutrient supply. The other suggestions are possibly more feasible. Initial harvest root mass was found to be similar to final harvest root mass in deep shade for most species. Furthermore species with the highest root mass in deep shade (*F. excelsior*, *Q. petraea* and *P. tremula*) also showed definite signs of leaf shedding. Kitajima (1994) noted that plants which lost tissue tended to allocate more carbon to storage for recovery at the expense of growth. The three species mentioned had the lowest growth rates of all deciduous species in shade.

There are two opposing views as to where the carbon previously used in roots is reallocated in shade: Lambers & Poorter (1992) state that plants grown in shade show a shift in the allocation of biomass from roots and stem to leaves. However Corre (1983a) believes that the dry matter not used in root growth will benefit the stems and petioles and not the leaf blades, so this does not contribute to the relative size of the photosynthetic apparatus. The leaf mass is thus reported to remain constant over a wide range of light intensities. The only species which displayed the former pattern with both an increase in leaf mass and decrease in stem mass with shade was *I. aquifolium* (Figure 3.4). *U. glabra* also showed re-allocation to leaves but to the stem as well. Generally, most species revealed no consistent trends in LMR and SMR in response to light. A lack of change in leaf mass or LMR with shade is different from some studies with tree seedlings (Loach, 1970; Kwesiga & Grace, 1986; Walters *et al.*, 1993b; Kitajima, 1994; Grubb *et al.*, 1996; Walters & Reich, 1996) but conforms with others (Veneklaas & Poorter, 1998, Reich *et al.*, 1998a).

Are morphological (LAR) or physiological (NAR) variables more important in driving RGRs at low and high irradiance levels?

Variation in RGR in low light could be explained by LAR and variation in high light explained by NAR (RGR = LAR x NAR, Evans, 1972). Although plants at high light had significantly lower LAR than those at the two lower light levels, their RGR tended to be higher due to a proportionately greater increase in NAR. This indicates that at different light intensities, plants were able to make both physiological (NAR) and morphological adjustments. LAR is a product of LMR and SLA (Evans, 1972). Generally, SLA seemed to play a greater role is driving LAR when all species were included in the correlation analysis (Table 3.3). This result is often reported when the LMR tends to remain relatively constant across light regimes (Kwesiga and Grace, 1986; Reich *et al.*, 1998a). However, when only deciduous species were included in the analysis, LMR was also found to play a role in driving LAR even if to a lesser extent (Loach, 1970). Growth variables that were more important in driving RGR at different light regimes were related more to seedling leaf morphology and physiology (NAR, LAR, SLA) than to biomass allocation

(Table 3.3). This may be a reflection of the seedling's age where patterns of allocation as well as architecture become more important at a later development stage (Kuppers, 1985).

How can differences in growth, biomass allocation and morphology distinguish different degrees of shade tolerance between species?

Although species displayed similar responses to shade, species specific differences were clearly present as reflected in the highly significant species-light interactions for all growth variables. These differences aid shade tolerance quantification. Responses of evergreens to irradiance were found to be very different from deciduous species, clearly demonstrating their separate inherent physiologies (phylogenetic effects) (Cornelissen, 1996). Their responses in relation to shade tolerance will thus be discussed separately.

B. pendula, B. pubescens, *S. cinerea*, *S. caprea*, *A. glutinosa* and *U. glabra* all displayed a combination of responses which are indicative of light demanding, shade intolerant behaviour. These responses included high levels of plasticity, high levels of etiolation and fast growth rates particularly in high light.

High degrees of morphological plasticity often distinguish shade intolerants from shade tolerants (Grime, 1965; Canham, 1989; Reich *et al*., 1998a). Generally, shade intolerants with high degrees of plasticity differ from shade tolerants by their much higher RGRs in both low and high light driven by much higher values of LAR and NAR respectively (Veneklaas & Poorter,1998). *U. glabra* and both *Betula* and *Salix* species displayed high RGRs in low and high light explained by intermediate to high LAR and NAR respectively. *A. glutinosa* displayed a relatively low LAR in deep shade leading to a low RGR. Thus, it did not have the same high degree of morphological plasticity as *U. glabra*, and both *Betula* and *Salix* species but it did have a similarly high RGR in full daylight. Furthermore *A. glutinosa*, both *Betula* and both *Salix* species, all had similar relatively high rates of etiolation in deep shade producing long thin stems second only to the two conifers (Figure 3.3). McVean (1956a) also reported high rates of etiolation in *A. glutinosa* under deep shade (5% PAR) with more robust and healthier seedlings found in higher light.

Betula and *Salix* species shared very similar biomass partitioning patterns (Figure 3.4) which suggests these species are all from the same functional group. Root mass partitioning patterns across light regimes were also similar to *A. glutinosa*. This involved a reduction in root mass down to intermediate light levels (14% PAR) with an increase again in deep shade, returning values to similar levels found in full daylight. Allocation of carbon to the leaves remained fairly constant across irradiances for these species except for *A. glutinosa*. It suffered a dramatic reduction in carbon allocation to the leaves in deep shade reflective of substantial leaf shedding contributing to a low RGR.

U. glabra displayed very different biomass partitioning responses to its fast growing counterparts. It showed an ability to continually increase leaf mass with shade (Figure 3.4) and maintained a significantly lower RMR in deep shade compared to high light (Figure 3.3). *U. glabra* also displayed an intermediate etiolation response in deep shade in relation to other species. These responses suggest that *U. glabra* has shade-adaptive traits as well as light demanding ones. High LMRs in the shade coupled with high LARs and SLAs maximise carbon gain in deep shade and a low RMR aids carbon conservation.

Shade tolerant species with low degrees of plasticity differ from intolerants by their much lower RGRs in both low and high light driven by lower values of LAR and NAR respectively (Veneklaas & Poorter,1998). Deciduous species which displayed the slowest growth in both high and low light were *Q. petraea* and *F. excelsior*. Low RGR in deep shade could be explained by a relatively low LAR. It is possible that this low LAR is a consequence of substantial leaf shedding which occurred in both species in deep shade and not just reflective of poor morphological adjustment. Wardle (1959) also found that seedlings of *F. excelsior* suffered from a loss of leaves in weak light which offset an increase in LAR.

At higher light, the low RGR of *Q. petraea* could be explained by a relatively low NAR. However, low RGR of *F. excelsior* was puzzling as its NAR was not limiting in full day light achieving relative high rates similar to other faster growers such as the *Salix* and *Betula* species. It is known that *F. excelsior* tends to grow better on a pH between 7 and 8 (Kerr & Evans, 1993) rather than pH 5.5 and is very sensitive to over topping vegetation (Gardner, 1975). Both of these factors may have contributed to low growth rates in high light.

Both *Q. petraea* and *F. excelsior* displayed relatively low etiolation in deep shade conforming with other studies (Ovington & McRae, 1960; Jarvis, 1964) (Figure 3.3) which indicates a degree of shade tolerance. Biomass partitioning patterns suggested a specific type of shade tolerant strategy for both these species. They displayed the typical reduction in root mass down to 14% PAR followed by an increase again in deep shade like most deciduous species (Figure 3.4). However the increase in root mass in deep shade was substantial, rising above levels found in full daylight. As a consequence of this both *F. excelsior* and *Q. petraea* had the highest RMRs in deep shade compared with all other species (Figure 3.3) as well as the largest root systems pooled across light. *Quercus* species are commonly reported to have large root systems which aid nutrient and water acquisition especially when below ground resources are limiting (Spurr & Barnes, 1998; Newbold & Goldsmith, 1981; Savill, 1998; Vera, 2000). The well-established root system where starch is often accumulated in the first years of establishment (Ziegenhagen & Kausch, 1995) reflects a strategy to shoot up when light conditions are improved.

The large root system found in *F. excelsior* probably also supports a strategy to respond rapidly to enhanced light conditions which is commonly reported in the literature (Wardle, 1959; Gardner, 1975; Tapper, 1992; 1993). Both species definitely showed a positive growth response to an increase in light availability, maximising growth rates (including RGR, RHG, RDG) at the two higher light levels (33% PAR & full daylight). Other studies commonly report optimal growth at intermediate light levels for *F. excelsior* (Wardle, 1959; Helliwell & Harrison, 1979) and *Quercus* species (Ovington & McRae, 1960; Jarvis, 1964; Shaw, 1974; Igboanugo, 1990; Ziegenhagen & Kausch, 1995).

C. avellana, *S. aucuparia*, *P. padus*, and *P. tremula* generally displayed intermediate behaviour. Intermediate RGR in low light was explained by intermediate to low LAR for *S. aucuparia*, *P. padus*, and *P. tremula*. Intermediate RGR in high light was explained by intermediate NAR for *S. aucuparia* and *C. avellana*. *C. avellana* had a higher RGR in low light explained by a very high LAR, second only to *U. glabra* (Figure 3.2) which may suggest a higher degree of shade tolerance. However *C. avellana* had an intermediate etiolation response in deep shade whilst *S. aucuparia* and *P. padus* shared lower rates of etiolation similar to *Q. petraea* and *F. excelsior*.

P. tremula showed some signs of a higher degree of intolerance compared to its intermediate counterparts. It had a relatively high etiolation rate in deep shade similar to the *Betula* and *Salix* species and *A. glutinosa* and it maintained a relatively high NAR in full daylight. Responses of *P. tremuloides* in America strongly support a more shade intolerant classification. Reich *et al*. (1998a) found this species to have the highest RGR in low and high light as well as the highest NAR, SLA and LAR of all trial species. Furthermore, Loach (1970) found that the *P. tremuloides* had a negative NAR in deep shade (3% PAR) due to very high respiration rates (Loach, 1970).

Evergreens grew much more slowly than deciduous species displaying a steady rise in RGR up to full daylight (as in Reich *et al*. (1998a)). A significantly lower NAR and the combination of very high LMR and very low SLAs account for this slow growth (Figure 3.2). One explanation for the low rates of growth amongst gymnosperms involves the tracheidal system which has a low water conductivity which can constrain water and nutrient transport required for fast growth (Cornelissen *et al*., 1998).

Generally *P. sylvestris* and *J. communis* displayed light demanding shade intolerant responses to different irradiances. Maximum rates of growth were found in full daylight accompanied with high rates of NAR (as found by Grubb *et al.* (1996) for *J. communis*). Both conifers displayed the highest rates of etiolation of all species in deep shade consistent with other findings (Miles & Kinnaird, 1979). They allocated more carbon to the roots and less to stems and leaves resulting in a much higher RMR in deep shade (Figure 3.3) which does not aid carbon gain or conservation.

I. aquifolium displayed both shade tolerant and intolerant traits. It showed positive growth responses to irradiance, maximising RGR and NAR in full daylight (Figure 3.2). Peterken & Lloyd (1967) also found that NAR and RGR of second year old *I. aquifolium* seedlings was reduced by shading. Shade tolerant traits included relatively low etiolation rates in deep shade and a gradual decrease in carbon allocation to the root (resulting in the lowest RMR of all species) and stem with more carbon allocated to the leaves with increasing shade.

How do physiological responses match traditional notions of shade tolerance and Ellenberg light indicator values?

Both *Betula* and both *Salix* species displayed responses reflective of shade intolerant behaviour, which conforms with the literature. They are commonly classified as shade intolerant pioneers (Evans, 1988; Atkinson, 1992; Messier & Puttonen, 1995; Aas & Riedmiller, 1996; Hart, 1998; Savill, 1998) including at both the seedling (Miles & Kinnaird, 1979) and sapling stages (Hill *et al*., 1999). Both *Betula* and both *Salix* species have been assigned an Ellenberg light indicator value of 7 reflecting a relatively high light demand which corresponds well with physiological responses (Table 3.4).

Ulmus has been described as a strong light demander (Savill, 1998) which explains its fast growth rates in high light. It is also described as having a high tolerance of shade as a seedling showing a rapid growth in height when given more light (Vera, 2000). Others describe it as a shade to semi-shade species (Aas & Riedmiller, 1996; Hill *et al*., 1999). *U. glabra* as a one year old seedling acted more as a generalist in this trial. In deep shade, it reflected a shade tolerant strategy maximising carbon gain in low light but also grew well in higher light. A re-assignment of its Ellenberg light indicator value of 4 to a range between 4 to 7 is suggested.

A. glutinosa is described as a light demanding pioneer (Evans, 1988; Aas & Riedmiller, 1994; Tapper, 1996), very sensitive to shading so that regeneration within woodland is practically unknown (McVean, 1953; Tapper, 1993; Savill, 1998). Results support this classification with little evidence of any degree of tolerance when young (Hart, 1998; Hill *et al*., 1999). A re-assignment of the Ellenberg light indicator of 5 to a more light demanding value of at least 6 or 7 is recommended for *A. glutinosa*.

It is known that *F. excelsior* can persist with poor growth rates under the shade of a canopy for many years especially in the absence of understorey competition (14 years: Wardle, 1959; 7 years: Savill, 1998; 15 years: Vera, 2000). This is consistent with results of low RGR and low etiolation in deep shade. *Q. petraea* also displayed low growth rates which has been reported as characteristic of this species (Ovington & McRae, 1960; Shaw, 1974; Savill, 1998). Long term persistence in the shade after cotyledon reserves and root and stem reserves have been exhausted, however is questionable (Jones, 1959; Grime & Jeffrey, 1965; Vera, 2000). Savill (1998) actually describes it as a strong light demander.

Table 3.4 Original Ellenberg values (Ellenberg, 1988), Ellenberg light indicator values for British saplings (Hill *et al*., 1999) with revised indicator values based on physiology for the 15 trial species

Species	Original Ellenberg Light indicator values	Ellenberg light Indicator values for British saplings	Physiological light indicator values
U. glabra	4	4	4-7
C. avellana	6	4	6
A. glutinosa	5	5	6-7
F. excelsior	4	5	4
P. padus	5	5	6
I. aquifolium	4	5	4-7
Q. petraea	6	6	4
S. aucuparia	6	6	6
P. tremula	6	6	6
B. pubescens	7	7	7
B. pendula	7	7	7
S. cinerea	7	7	7
S. caprea	7	7	7
P. sylvestris	7	7	8
J. communis	8	8	8

At the one year old stage, low etiolation rates and slow growth promote a persistent stategy for both *Q. petraea* and *F. excelsior* seedlings in deep shade. An Ellenberg light indicator value of 4 thus seems appropriate for both species at this stage in their development (Table 3.4). In future years, a higher light indicator value (e.g.: 6) with become more appropriate as light is required for release and long term survival.

C. avellana, S. aucuparia, *P. padus* and *P. tremula* have original Ellenberg light indicator values of 5 or 6 (Ellenberg, 1988) which conform with intermediate responses to light. Both *C. avellana* and *P.padus* have been described in the literature as semi-shade species (Aas & Riedmiller, 1996). Some authors report *C. avellana* to be reasonably shade tolerant (Savill, 1998; Hart, 1998) surviving some shade for a long time (Rackham, 1980; Peterken, 1992). However Vera (2000) points out that *C. avellana* has only been characterised as shade tolerant as it is normally seen as coppice in woodland understoreys. In the first year, the reserve nutrients in the Hazel nut can contribute to strong growth but after the first season, the cotyledons become exhausted and seedlings tend to rely on assimilation for further growth. Both *S. aucuparia* and *P. tremula* had been described as strongly light demanding pioneers (Evans, 1988; Aas & Reidmiller, 1996; Findlay, 1998; Savill, 1998). It is possible they become more light demanding at later stages of development but at the one year seedling stage, an intermediate response is found to predominate. As there was little differential in intermediate responses between the above species, they have all been assigned the same light indicator value of 6 (Table 3.4).

Savill (1998) describes *I. aquifolium* as the most shade tolerant of all British tree species which is supported by a low compensation point of 1-3% PAR found by Peterken (1966). Biomass partitioning patterns support a shade tolerance strategy of maximising carbon gain in low light but it also maximised RGR in full daylight. Results thus support a more generalist nature and a re-assignment of the original Ellenberg light indicator from a 4 to a range between 4 and 7 is suggested.

Responses of *P. sylvestris* and *J. communis* to irradiance indicated shade intolerant behaviour which conforms with the literature (Fowells, 1965; Miles & Kinnaird, 1979; Barbour & Billings, 1988; Rodwell, 1991; Grubb *et al*., 1996; Hart, 1998; Savill, 1998). *J. communis* has a light indicator value of 8 (Ellenberg, 1988; Hill *et al*., 1999) where plants are classified as light loving, rarely found where there is less than 40% relative illumination. This rank also seems appropriate for *P. sylvestris*, which shared very similar responses.

Limitations

There were a number of limitations to this study with regards to the experimental design and methodology which would have influenced results. The main criticism of the use of shade houses regards the inability of shade cloths to reduce the ratio of R:Fr to a similarly low level to that found under forest canopies. Consideration of the R:Fr ratio is important because studies have shown that the spectral quality of light has a profound influence on tree seedling morphology and physiology (Kwesiga & Grace, 1986; Warrington *et al.*, 1989; Kamaluddin, 1991). However, the use of green nylon netting in this trial, did reduce the R:Fr ratio to levels comparable with the field (see Chapter 7).

The deep shade R:Fr ratio of 0.69 perhaps is not as low as found under dense understorey but it does falls into the range found under other conifer evergreen woodlands in overcast conditions (0.55-0.76) (Federer & Tanner, 1966). Typical responses to a reduction in R:Fr ratio include higher photosynthetic rates (Kwesiga *et al.*, 1986; Warrington *et al.*, 1989), higher SLAs (Kwesiga & Grace, 1986), reduced total leaf area (McLaren & Smith, 1978) and increased apical dominance, manifested in decreased branching, stem extension and internode elongation (Smith, 1982). As these responses are generally accentuated in more light demanding species, they probably aided the distinction between shade tolerants and intolerants.

Seedlings within the shade houses would have been subjected to other artificial microclimatic conditions such as a uniform distribution of light and enhanced temperatures and humidity levels due to reduced air-turbulence. These factors can influence the growth rate and morphology of plants and make field study comparisons difficult (Grime & Jeffrey, 1965; Brown & Jennings, 1998).

Unfortunately, seedlings in the higher light treatments were observed to wilt and lost a few leaves during hot dry periods in the summer despite watering everyday. The use of black pots most likely exacerbated the problem. A more frequent watering regime and use of mulch is recommended for future trials. The fast growers such as *Betula* and *Salix* species were most affected and it is predicted that these species would have continued to grow well in full daylight if well watered (Davies & Pigott, 1984).

Towards the end of the season, seedlings were outgrowing their space causing over-shadowing which can affect morphological responses (Grime & Jeffrey, 1965). Jarvis (1964) explained how mutual shading can lower the average light intensity experienced by the leaves so even more light is needed to reach maximum photosynthesis. Seedlings were re-randomised every two weeks but wider spacing should be considered in future trials. The astonishing rate of growth of the seedlings was unexpected.

Total biomass in plant components tends to increase with overall growth and the proportional distribution of biomass among these parts is rarely constant for extended periods (Coleman *et al*., 1994). As woody plants increase in height, less carbon is allocated to foliage and more to the stem for support (Givnish, 1988). Subsequently there is a decline in RGR because the proportion of the plant involved in energy capture (LMR or LAR) and/or biomass productivity per unit leaf (NAR) decrease (Walters *et al*, 1993a). These development changes are collectively known as ontogenetic drift. When plants are grown in different environments, such as in different light regimes, they often grow at different rates and thus will be of different sizes and developmental stages at a given age. Thus, plants of the same age, can frequently be ontogenetically dissimilar. This can confuse the interpretation of species specific growth responses. For example, it is difficult to know if typical increases in LAR shown with shade is not just a consequence of slow growth.

It has been suggested that multiple harvests are much better than single harvest studies for separating ontogenetic from species and treatment effects on measured plant traits than single harvest studies (Hunt, 1990; Coleman *et al*., 1994). However it was interesting to discover that Reich *et al.* (1998a) found that the application of either classical or functional approaches had little effect on treatment and species comparisons. Walters *et al*. (1993a) found that both RGR and LMR declined with plant mass (their principal scalar of ontogeny) and SMR increased with height reflecting classical ontogeny. However, the differences in the form of RGR versus mass relationships suggested that RGR rankings among species change little with size or age. Improvements to this study would involve multiple harvests and / or further analysis to establish whether ontogeny affects RGR rankings across different irradiances. This may have important ramifications for shade tolerance quantification.

It is well documented that the ability of species to tolerate shade is influenced by an array of environmental factors such as nutrients (Helliwell & Harrison, 1979; Latham, 1992; Canham *et al*., 1996; Grubb *et al*., 1996; Kobe *et al*., 1995; Veenendaal, 1996), soil moisture (Veenendaal, 1995, Walters & Reich, 1997; Sack & Grubb, 2002) and root competition (Watt & Frazer, 1933; Lutz, 1945; Jarvis, 1964; Putz & Canham, 1992; Coomes & Grubb, 2000) which interact with irradiance. Furthermore, shade tolerance can change with seedling age. The shade tolerance ranks assigned to the species in this trial are thus very specific to one year seedlings based on growth, allocation and morphological responses to irradiance alone. Trials are required to investigate how shade tolerance in modified in the field (see Chapter 5 and 6).

3.5 Summary

Differences in growth, allocation and the morphology of species at different irradiances enabled a distinction between shade tolerants, intermediates and shade intolerants. All species responded positively to an increase in light, optimising growth at the higher light levels of 33% PAR or in full daylight. Thus, none of the species in the trial seemed to conform to the shade tolerant type where seedlings grow slowly or steadily in shade with no response to periods of increased light. A few species showed signs of a shade tolerant strategy maximising carbon gain at low light such as *C. avellana*, *U. glabra* and *I. aquifolium*. The two latter species also showed signs of generalist behaviour, growing well in high light. *F. excelsior* and *Q. petraea* reflected a strategy which promotes the maintenance of a high potential for exploiting canopy gaps with little net growth in deep shade coupled with the development of substantial root systems. *J. communis*, *P. sylvestris*, *Betula* and *Salix* species displayed intolerant behaviour with the growth of the two conifers least affected by water-stressed conditions in full daylight. Ellenberg light indicator values were found to be underestimated according to physiological responses to light. One should not expect to transpose directly the results of this study to the field situation where irradiance interacts with many other factors such as nutrients, soil moisture, predators and disease.