CHAPTER 4

Exploration of the relationship between relative growth rates in woody species and irradiance

4.1 Introduction

There is a well-established view that in plants there is a trade-off between tolerance of shade and growth rate in high irradiance. Recently empirical evidence for this viewpoint has been published for trees in both tropical rain forest (Hubbell & Foster, 1992) and the northern temperate deciduous forests (Pacala *et al.*, 1994; Kobe *et al.*, 1995; Grubb *et al.*, 1996). A possible basis for this has been published by Grime (1966). Shade tolerant plants grown in deep shade have low maximum rates of photosynthesis; if they cannot raise these rates very appreciably in high irradiance, they must grow relatively slowly there. Likewise, light demanding plants grown at high irradiance have high rates of respiration and if they cannot reduce these rates greatly in deep shade, they will grow very slowly or die there. Furthermore mass based net photosynthetic rates of the leaves of shade plants have been found to exceed those of sun plants, with the reverse occurring at high irradiance, (Bjorkman & Holmgren, 1963; Boardman, 1977; Givnish, 1988).

The above findings have been assumed to scale up to a level of whole-plant relative growth rate (RGR) (Shugart, 1984). However, there is a contrary view that if a plant grows faster than another at high irradiance, it will also do so in the shade (Kitajima, 1994; Poorter, 1999). According to this later view, light plays a role in maintaining the mixture of forest species only through the well-established trade-off between survival rate in deep shade and growth in high light. Certainly, in the literature, this trade-off is more convincing when shade tolerance is measured by survival in the shade (Hubbell & Foster, 1992; Kobe *et al.*, 1995; Grubb *et al.*, 1996). Growth in the shade as a measure of shade tolerance tends to produce more conflicting results. Some studies show negative trends between growth in high light and growth in deep shade (Grubb *et al.*, 1996; Agyeman *et al.*, 1999). Others show no pattern at all (Popma & Bongers, 1988; Walters & Reich, 1996) but most show over-all positive correlations which vary in strength (Kitajima, 1994; Osunkoya *et al.*, 1994; Poorter, 1999).

In a recent review, Sack & Grubb (2001) argue that positive relationships between growth in high light and growth in deep shade are reflective of short term studies and the influence of the seed reserve. They assume that if a species has a higher RGR than other species in deep shade, it will have a lower RGR at high irradiance (Spurr & Barnes, 1998; Thomas & Bazzaz, 1999). As a consequence, species change rank (crossover) between low and high irradiance. In the initial establishment stages, the additional energy stored in the seed reserve will enable species that grow fast in high light (typically small-seeded pioneer species) to also grow fast in deep shade. As their grow rates are similar to shade tolerants in the shade, cross-overs in RGR between species are limited (otherwise known as rank retentions).

In physiological terms, a small-seeded seedling (pioneer) will have an initial burst of relative growth consistent with its initially very high specific leaf area (lamina area/lamina dry mass SLA) which gives it a relatively high leaf area ratio (lamina area /plant dry mass) (in Sack & Grubb, 2001). As a result, it will have the superior RGR at both gap and understorey irradiances. However as the seedlings grow larger, differences among SLAs diminish, lose their correlation with seed size and cease to be the chief determinant of RGR. The large seeded shade tolerator may outrank the small-seeded light demander at understorey irradiance, although not at higher irradiance. Thus, as the seed reserve becomes exhausted in a longer term study, the number of rank reversals in RGR between species increase. The potential effect leads to a negative correlation between growth rate in high light (RGRgap) and growth rate in the shade (RGRunderstorey).

Sack & Grubb (2001) developed an approach to support the above theory. The approach involves the concept of the cross-over point irradiance (CPI); an estimate of the irradiance at which the crossover of RGR functions occur for any two species (explained in methods). The RGR function of a species is its relative growth response to irradiance. The next step involves calculation of the percentage of cross-over points (CP%) for species pairs that occur between understorey (2% daylight) and gap irradiance (10-25% daylight). A comparison of studies, showed that longer term studies had relatively high CP%, whilst short term studies had lower CP% where the presence of rank retentions is inferred.

The aim of this study was to investigate and explore reasons for the positive response that occurs between growth in deep shade and responsiveness to light amongst 15 Scottish native species. The possibility of rank retentions and influence of the seed reserve was explored by applying Sack & Grubb's approach. This application also has the potential to provide estimates of the specific irradiance levels at which cross-overs occur for particular species pairs: information which is particularly interesting and useful in terms of woodland succession and prediction.

4.2 Methods

The relative growth rate (RGR) of one-year-old seedlings of 15 temperate species grown under 2.5%, 14%, 33% and 100% PAR (full daylight) for a growth period of 18 weeks (April-August 2000) was calculated and means for each species obtained (Chapter 3). RGR was calculated from the mean natural logarithm of plant weights (Hoffmann & Poorter, 2002) (Chapter 3). To investigate the relationship between responsiveness to light and shade tolerance, plots of RGRgap vs RGRunderstorey were produced. This involved plotting RGR in higher light (14%, 33% and 100% PAR) against RGR in deep shade (2.5% PAR).

Methodology from Sack & Grubb (2001) was followed to apply the Crossover Point Irradiance Approach. In brief, a line representing dry mass relative growth (in g g^{-1} $week^{-1}$) as a logarithmic function of irradiance (% daylight) was fitted using ordinary linear regression (Equation 4.1).

$$RGR = R \times \ln(\text{irradiance} + 1) + L \qquad \text{Equation 4.1}$$

where *R*, the slope of the line, represents responsiveness to irradiance, and *L*, the intercept, represents the theoretical dark loss rate, the negative RGR in complete darkness. A constant of one was added to irradiance so that the ‘0’ on the ln-transformed x-axis would represent 0% daylight.

An estimate of the irradiance at which the crossover of any two species’ RGR functions occurs, the “crossover point irradiance” (CPI) was calculated using equation 4.2.

$$CPI = e^{-(\mathrm{Lspecies}_A - \mathrm{Lspecies}_B)/\mathrm{Rspecies}_A - \mathrm{Rspecies}_B)} - 1 \qquad \text{Equation 4.2}$$

Equation 4.2 emphasises that just as any two non-parallel lines must cross, any two non-identical species RGR functions must cross over. If the two species *R* values differ, they must switch rank at a particular irradiance. The CPI for each species pair allows prediction of which of the pair grows more quickly at any irradiance. Next the percentage of cross-over points (CPs) occurring between 2.5% PAR and 10% PAR and between 2.5% PAR and 25% PAR were calculated. Tests for differences in species slopes and intercepts were carried out to acquire a level of confidence in the CPI that occurred between species pairs and thus the CP%. Furthermore an effort to place confidence intervals around each CPI was made for each species pair.

The possible effect of seed reserve on RGR and thus on the CP% was investigated by correlating seed mass (mg) with total plant mass at initial harvest and with SLA, LAR and RGR at final harvest. Actual seeds for the one year old seedlings could not be obtained so the literature was searched resulting in seed mass values for 11 out of the 15 species (Peterken & Lloyd, 1967; Carlisle & Brown; 1968; Grime *et al*., 1981; Atkinson, 1992; Grubb *et al*., 1996; Reich *et al*., 1998a) (Table 4.3). Correlations between seed mass and original Ellenberg light indicator values (Ellenberg, 1988) and new Ogilvy shade tolerance ranks for one year old seedlings (Chapter 3) were also carried out. These relationships were explored because a relationship between seed mass and shade tolerance is assumed for seed size to be a major factor influencing rank retention (Sack & Grubb, 2001).

4.2.1 Statistical analysis

Linear regression was used to investigate the trade-off between responsiveness to light and growth in deep shade. Spearman's rank correlation was used to investigate relationships between seed mass and other variables due to non-normality in the data (Minitab 13). Simple linear regression with groups was carried out to test for differences between all species intercepts and slopes simultaneously (Regression function, Genstat, Edition 6). Confidence intervals on CPIs were established by plotting the linear responses with 95% confidence intervals for each species of the pair. The upper and lower confidence limits can be obtained from two of the confidence interval cross over points: one being the point at which the upper confidence limit of the first species crosses the lower of the second (Figure 4.1). The other being the point at which the upper confidence limit of the second species crossed the lower of the first. A special program was written in Pascal (courtsey of Colin Legg, 2002) to apply equation 4.2 to 105 species pairs easing calculation of the CPI.

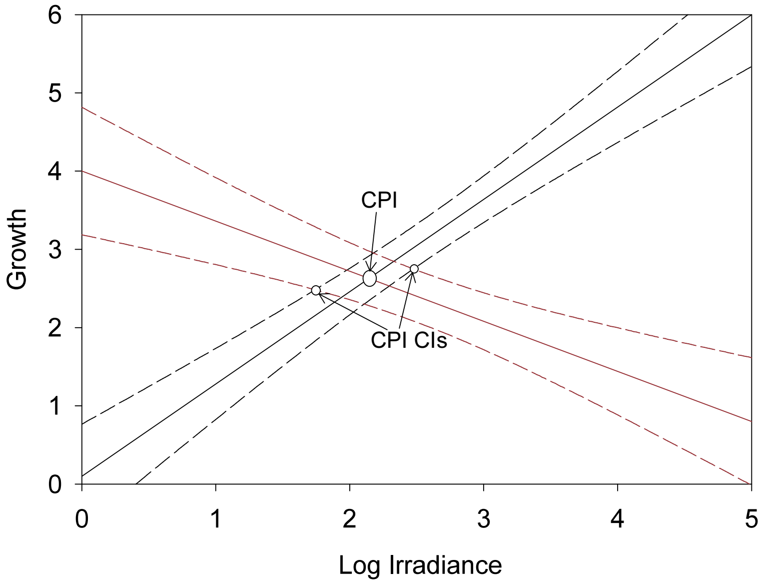

Figure 4.1 An example of the Cross Over Point Irradiance (CPI) and the calculation of upper and lower confidence limits (CI). Dashed lines are the 95% CI for the two regression lines.

4.3 Results

4.3.1 Plots of RGR gap Vs RGR understorey

Plots of RGR gap Vs RGR understorey produced significant positive regressions for all gap irradiance levels (Figures 4.2). The strength of the relationship decreased with increasing light with the strongest relationship found at the lower gap irradiance of 14% PAR. Results from correlations have also been included here for study comparisons: 14% PAR: $r = 0.83$, $P < 0.001$; 31% PAR: $r = 0.76$, $P < 0.001$; 100% PAR: $r = 0.61$, $P < 0.05$.

4.3.2 Cross Over Point Irradiance Approach

Results of linear regressions of mean relative growth rate against irradiance for individual species are shown in Table 4.1. Most species growth responses fitted the linear relationship ($p < 0.05$) with the exception of *Ulmus glabra*, *Betula pubescens*, *Corylus avellana* and *Sorbus aucuparia*. The latter three, however, have a significant fit at the 0.1 probability level.

Eight percent of species pairs had CPIs between 2% and 10% light; 8 of a possible 105 pairs show rank reversals between understorey and gap irradiance (Table 4.2).

The median CPI was 0.58% PAR. Thirteen percent of species pairs had CPIs between 2% and 25%. The median CPI was 0.56% PAR.

Differences in intercepts were found between all species light response curves indicating differences between species (ANOVA: F = 22.4; d.f. = 14,30[1]; P < 0.01). However, no significant differences in slopes were found (ANOVA: F = 0.56; d.f. = 14, 30; P = 0.876). The calculation of confidence intervals around the CPIs was impossible due to the absence of the specific cross over points between the 95% confident intervals of the two lines (Figure 4.1 & 4.3).

---

[1] The treatment degree of freedom is stated first followed by the residual degree of freedom in all ANOVA statements henceforth.

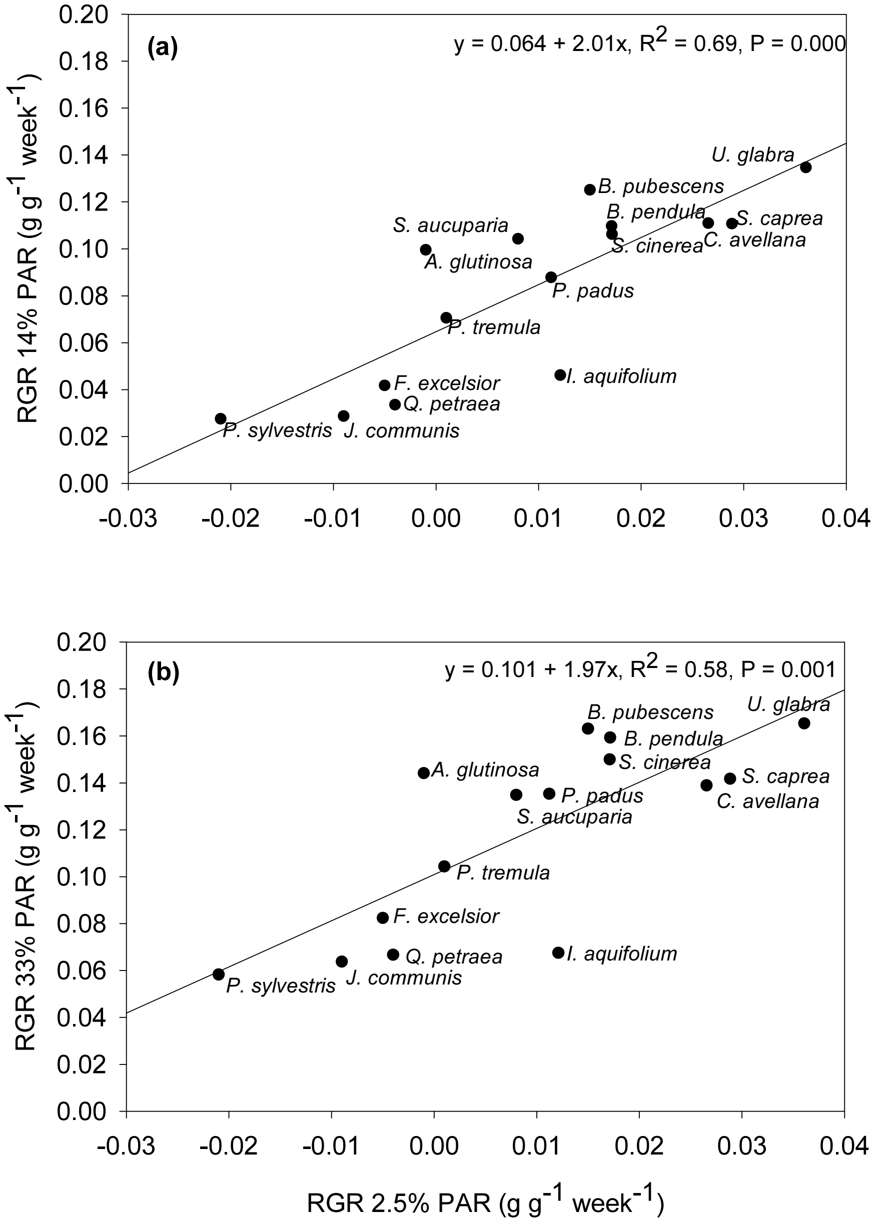

Figure 4.2 Relationships between responsiveness to higher light (a) RGR at 14% PAR (b) RGR at 33% PAR (c) RGR at 100% PAR and shade tolerance (RGR in deep shade at 2.5% PAR). Species names have been attached to points.

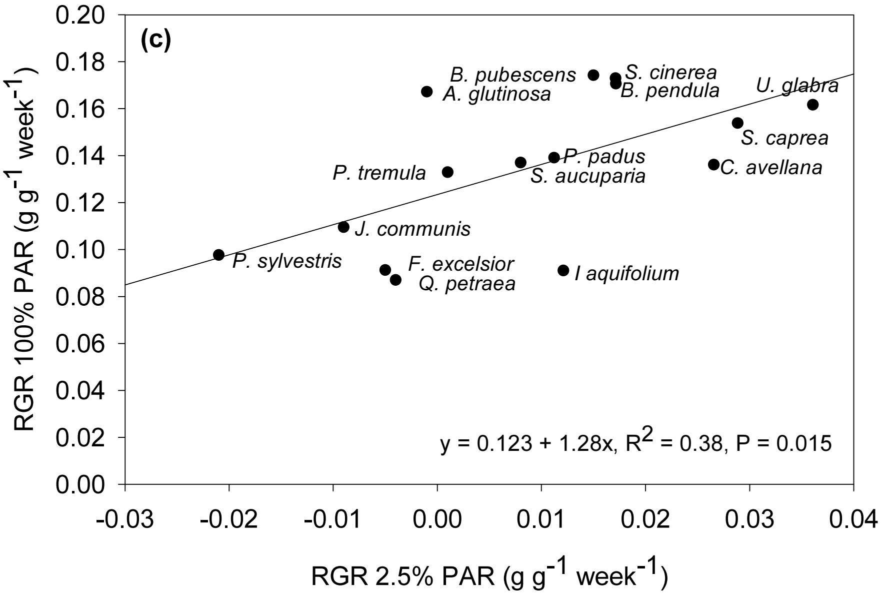

Table 4.1 Linear regression results of mean RGR against irradiance (ln(light +1)) for individual species; R^2, ns = not significant, * < 0.1, ** < 0.05, *** < 0.01.

Species	Linear Model
A. glutinosa	93.9**
F. excelsior	93.4**
P. tremula	97.6**
B. pubescens	88.4*
B. pendula	91.9**
P. padus	89.5**
U. glabra	80.8ns
C. avellana	81.7*
I. aquifolium	99.7***
J. communis	98.5***
Q. petraea	97.0**
P. sylvestris	99.9***
S. aucuparia	84.3*
S. caprea	90.7**
S. cinerea	94.3**

Species 1	R^2%	Intercept (CL 95%)	Slope (CL 95%)	Species 2	R^2%	Intercept (CI 95%)	Slope (CI 95%)	CPI
A. glutinosa	93.9**	-0.053 (-0.164, 0.108)	0.052 (0.012, 0091)	*P. padus*	89.5*	-0.028 (-0.164, 0.108)	0.040 (-0.002, 0.082)	8.0 NA
A. glutinosa	93.9**	-0.053 (-0.164, 0.108)	0.052 (0.012, 0091)	*I. aquifolium*	99.7***	-0.018 (-0.031, 0.006)	0.024 (0.020, 0.028)	2.5 NA
A. glutinosa	93.9**	-0.053 (-0.164, 0.108)	0.052 (0.012, 0091)	*S. aucuparia*	84.3*	-0.023 (-0.194, 0.146)	0.040 (-0.012, 0.092)	10.9 NA
F. excelsior	93.4**	-0.040 (-0.118, 0.040)	0.030 (0.006, 0.055)	*I. aquifolium*	99.7***	-0.018 (-0.031, 0.006)	0.024 (0.020, 0.028)	24.4 NA
P. tremula	97.6**	-0.044 (-0.106, 0.018)	0.040 (0.021, 0.059)	*I. aquifolium*	99.7***	-0.018 (-0.031, 0.006)	0.024 (0.020, 0.028)	3.9 NA
B. pubescens	88.4*	-0.029 (-0.204, 0.147)	0.049 (-0.005, 0.103)	*C. avellana*	81.7*	0.001 (-0.159, 0.160)	0.034 (-0.015, 0.083)	5.9 NA
B. pubescens	88.4*	-0.029 (-0.204, 0.147)	0.049 (-0.005, 0.103)	*S. caprea*	90.7**	-0.007 (-0.128, 0.114)	0.038 (0.001, 0.076)	6.6 NA
B. pendula	91.9**	-0.031 (-0.173, 0.110)	0.048 (0.005, 0.091)	*C. avellana*	81.7*	0.001 (-0.159, 0.160)	0.034 (-0.015, 0.083)	8.8 NA
B. pendula	91.9**	-0.031 (-0.173, 0.110)	0.048 (0.005, 0.091)	*S. caprea*	90.7**	-0.007 (-0.128, 0.114)	0.038 (0.001, 0.076)	11.7 NA
C. avellana	81.7*	0.001 (-0.159, 0.160)	0.034 (-0.015, 0.083)	*S. caprea*	90.7**	-0.007 (-0.128, 0.114)	0.038 (0.001, 0.076)	4.5 NA
C. avellana	81.7*	0.001 (-0.159, 0.160)	0.034 (-0.015, 0.083)	*S. cinerea*	94.3**	-0.032 (-0.148, 0.084)	0.048 (0.012, 0.083)	9.4 NA
J. communis	98.5***	-0.060 (-0.103, -0.017)	0.036 (0.023, 0.049)	*Q. petraea*	97.0**	-0.039 (-0.080, 0.001)	0.028 (0.016, 0.041)	14.1 NA
S. cinerea	94.3**	-0.032 (-0.148, 0.084)	0.048 (0.012, 0.083)	*S. caprea*	90.7**	-0.007 (-0.128, 0.114)	0.038 (0.001, 0.076)	13.1 NA

Table 4.2 Species pairs with Cross Over Point Irradiances (CP1) between 2% and 25% PAR. Regression results for each species include R^2% and probability values (* < 0.10, ** < 0.05, *** < 0.01) intercept (RGR) and slope (g g^{-1} $week^{-1}$) / ln(PAR% +1)) co-efficients and their upper and lower confidence limits at the 95% level, the CPI (%PAR) for each species pair (NA = computation impossible).

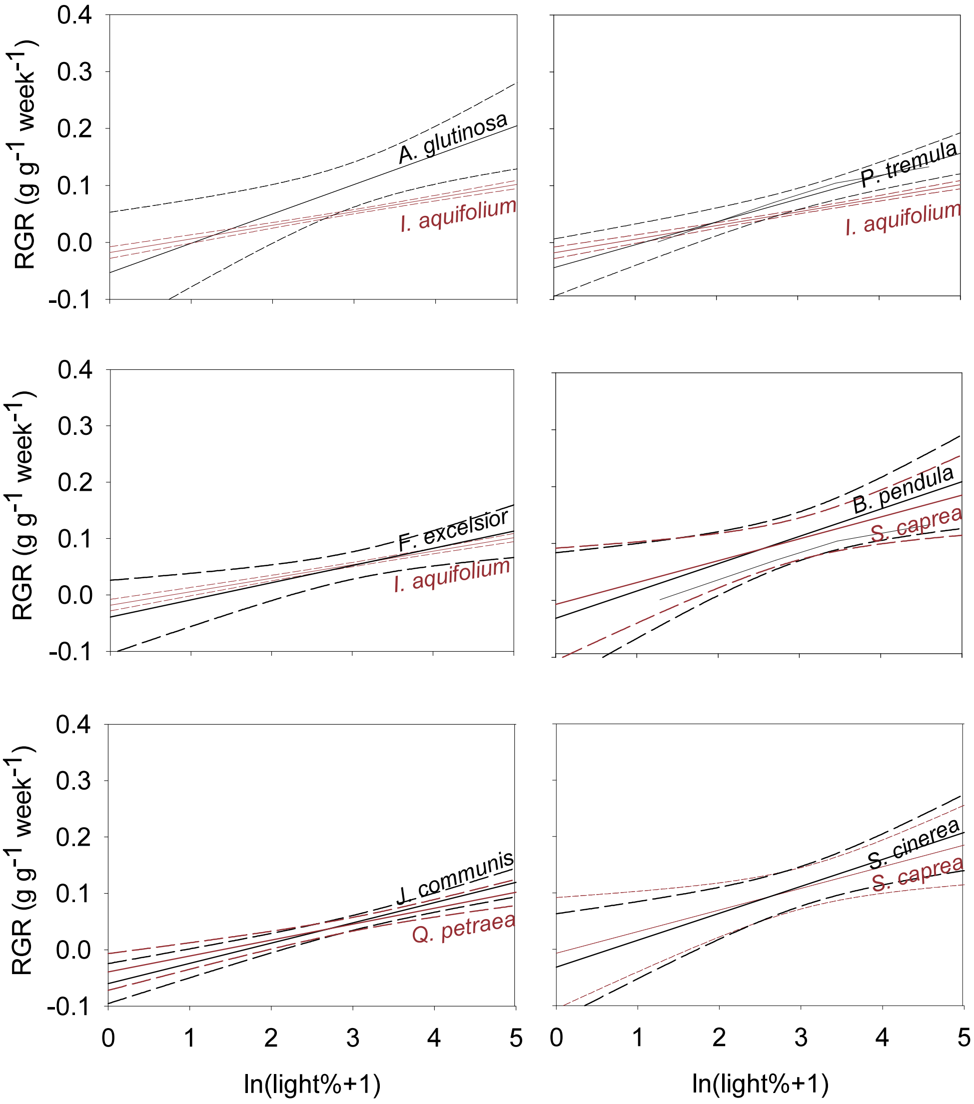

Figure 4.3 Cross-overs in RGR which occur between 2% and 25% PAR for a selection of species pairs.

4.3.3 Relationships between seed mass, shade tolerance and growth

Slightly different degrees of shade tolerance of species were represented by Ellenberg's original light indicator values (Ellenberg, 1988) and the new Ogilvy ranks based on physiology for one year old nursery grown seedlings (Chapter 3). No significant correlation was found between seed mass and Ellenberg Ranks for all species or for deciduous species alone (Table 4.3). A negative trend was found between seed mass and Ogilvy ranks for all species ($P < 0.1$). However, when evergreens were excluded, a stronger significant negative correlation was found clearly indicating a reduction in seed mass with an increase in shade intolerance or demand for light.

Further tests to see if there was evidence of the seed reserve having an effect on the growth of seedlings were carried out. A positive trend was found between seed mass and mean plant mass at initial harvest (before bud burst) for all species ($P < 0.1$). When evergreens were excluded, a significant positive correlation was found between seed mass and initial mean plant mass. No significant correlations were found between seed mass and mean SLA, LAR or RGR at final harvest ($P > 0.05$).

Table 4.3 Seed mass (mg) of 11 of the 15 native tree species with their new Ogilvy shade tolerance rank for one year olds, original Ellenberg light indicator values / ranks and initial mean plant mass (logged) before bud burst. An increase in value indicates an increase in light demand or shade intolerance. Spearman's rank correlations between seed mass and ranks and mean plant mass have been included for all species and just deciduous species (r_s = correlation co-efficient, * < 0.1, ** < 0.05, ns = not significant).

Species	Seed mass (mg)	Ogilvy Ranks	Ellenberg Ranks	ln Initial Plant Mass
Q. petraea	744.70 (Grime *et al*., 1981)	4	6	1.775
I. aquifolium	128 (Peterken & Lloyd, 1967)	4-7	4	1.829
F. excelsior	46.19 (Grime *et al*., 1981)	4	4	1.862
U. glabra	9.93 (Grime *et al*., 1981)	4-7	4	0.976
C. communis	5.20 (Grubb *et al*., 1996)	8	8	0.631
P. sylvestris	4.96 (Carlisle & Brown, 1968)	8	7	0.781
S. aucuparia	2.58 (Grime *et al*., 1981)	6	6	1.398
A. glutinosa	1.30 (Grime *et al*., 1981)	6	5	0.596
B. pubescens	0.17 (Atkinson, 1992)	7	7	0.665
B. pendula	0.15 (Atkinson, 1992)	7	7	0.478
P. tremula	0.13 (Reich *et al.,* 1998a)	6	6	0.773
r_s (all species)		-0.59*	-0.45ns	0.54*
r_s (deciduous)		-0.82**	-0.57ns	0.79**

4.4 Discussion

A trade-off between responsiveness to light and growth rate in deep shade was not found. Instead positive relationships were found for all three plots of RGRgap Vs RGRunderstorey (Figure 4.2). The positioning of species did not change across the three plots with light demanders such as *U. glabra*, both *Betula* and *Salix* species growing fast in both high and low light. The slower growers, *Pinus sylvestris* and *Juniperus communis* are as expected, positioned in the bottom left-hand side of the graph, reflecting their separate physiology from deciduous species. The strength of the relationship however did change with light intensity, weakening with each higher level of gap irradiance. The greatest RGR response to irradiance occurred between 2.5% and 14% PAR, reflective of seedlings shooting up as soon as they were exposed to a small increase in light. The response may lessen at higher irradiances due to species reaching their maximum rates of photosynthesis or due to growth restrictions such as water stress or exposure.

The application of Sack & Grubb's approach yielded 8% of species pairs CPs occurring between 2% and 10% daylight with a median CPI of 0.58% PAR. This result is similar to another single season temperate species trial where 11% of species pairs crossed over between 2 and 10% daylight with a median CPI of 0.11% PAR (Grubb *et al.*, 1996; in Sack & Grubb, 2001). 50% of species pairs changed rank between these two irradiances in a longer term temperate species trial run over two growing seasons (Walters & Reich, 1996) with a median CPI of 2.5%. Sack & Grubb (2001) argue that studies that yield lower CP% and median CPIs are generally linked to short-term studies which inevitably involve newly established seedlings where the seed reserve still has a temporary effect on growth. If trials are run over a longer period, the seed reserve becomes exhausted leading to a wide scattering of crossover points with medians occurring between gap and understorey irradiances.

Results conform with other short-term studies with a low CP% and median CPI (in Sack & Grubb, 2001). However the trial did not involve newly established seedlings but nursery grown one-year-old seedlings where a seed reserve effect would not be expected due to exhaustion after the first season. The positive relationships between seed mass and mean plant mass before bud burst at initial harvest suggests that seed size may have driven growth to some extent in the first season. Grime & Jeffrey (1965) found positive correlations between log mean weight of seed reserve and log maximum height attained. However, in the second season, at final harvest, no significant correlations between seed mass and mean SLA, LAR and RGR were found which suggests that the seed reserve had little influence during this period. If the seed reserve had had an influence, a negative correlation between seed mass and RGR may have been expected (Fenner, 1983; Shipley & Peters, 1990; Leishman & Westoby, 1994; Osunkoya *et al*., 1994; Cornelissen *et al*., 1996). Maranon & Grubb (1993) explain this negative relationship in terms of smaller seeds giving rise to a higher SLA which in turn results in a higher LAR whereby plants intercept more light per unit total mass so grow at a faster rate.

Results suggest that the seed reserve had little to do with the production of the low CP% and median CPI in this study. Seed size tends to be a major factor influencing the CP% when dealing with small-seeded light demanders and large-seeded shade tolerators. The species set involved a mixture of evergreen and deciduous species which, grouped together had no significant correlation with either Hill or Ogilvy shade tolerance rankings. It is acknowledged that seed size may correlate strongly with shade tolerance for certain species sets but for others there is no more than a weak correlation as light demand is only one of host of potentially strong evolutionary influences on seed traits (Grubb *et al*., 1996; Grubb & Metcalfe, 1996; Grubb, 1998). Other influences include drought resistance and dispersal. For example, *I. aquifolium* is a long-lived shade tolerant species but has a relatively small seed; associated with wide seed dispersal by birds (Peterken, 1996). Gymnosperms tend not to have an association between shade tolerance and larger seed size (Hewitt, 1998). A possible explanation for this is that conifers tend to be less flexible in their capacity to change seed size in different environments as there is no selection pressure to do so because most inhabit poor, open sites, out-competed by the hardwoods in the nutrient rich shady sites.

Morphological adjustments in the shade which occur independent of the seed reserve is a more feasible explanation for the low CP% and median CPI. In the previous chapter, the basic equation of growth analysis (RGR = LAR x NAR: Evans, 1972), revealed that LAR determined RGR differences in deep shade (2.5% PAR) whilst NAR determined differences at the three higher irradiance levels (conforming to the paradigm asserted by Veneklaas & Poorter, 1998). The one-year-old seedlings were clearly able to make both physiological (NAR) and morphological adjustments in different irradiances. For all species, especially for the most fast growing species, the potentially deleterious effects of shade on growth rate were offset by higher SLA and LAR. This explains fast growth in low light as well as high light for shade intolerant species such as the *Betula* and *Salix* species. If the study were to have been run into a second growing season, there is evidence that woody species in deep shade eventually enter a second stage of development, where NAR becomes the dominant factor in species RGR differences (Popma & Bongers, 1988; Osunkoya *et* *al*., 1994; Agyeman *et al*., 1999). Eventually, 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). In addition, there is ontogeny to consider. Naturally as plants grow bigger, LAR values decline corresponding to an increase in whole-plant light compensation point, and a slowing of RGR, especially in shade and especially for the most fast growing species (Givnish, 1988).

Even if the study had been run into a second season, a relatively low CP% and median CPI would not be surprising due to what is know about the species' ecologies. The majority of the species lie towards the more light-demanding sector of the shade tolerance range. Furthermore differentiation in growth response causing rank reversals perhaps would be expected at a higher gap irradiance than 10% PAR. Results support this idea to some extent with slightly more cross-overs (13% of species pairs) occurring between 2% and 25% PAR. There are other ecological reasons why a set of species may not show many rank reversals in RGR between understorey and gap. Shade tolerance is not necessarily connected with growth potential or biomass conservation. For example, allocation to defence and storage in low light plants may occur as a trade-off with growth.

Up to now, the CP% has been accepted and explanations for its low value explored. During its calculation, however, a very important statistical flaw emerged which questions the whole validity of the approach. Tests for differences in slopes between species growth response lines were insignificant ($p > 0.05$). This suggests that the lines are close to parallel, which means that there was a large amount of error in the estimation of the CPI. It is very possible that individual species' light response curves were not representative of true responses. Plants were grown under four different light regimes, so response lines were only drawn through four points on the graph with only two degrees of freedom calculated in the regression. As a rule of thumb, degrees of freedom in double figures are recommended (Tom Connolly, personal communication).

Sack and Grubb (2001) admitted they “employed methods of less than ideal exactitude” (ie: two data points). They explain that data become scarce when one is only concerned with the range of irradiance over which species show increasing RGRs excluding growth data for photoinhibitory irradiances or limitation, by nitrogen for example. The straight line part of the growth response curve is of most interest aiding the production of significant linear fits ($P < 0.05$) and the calculation of the CPI (Equation 4.2). It was decided for statistical reasons as well as the fact that only two species showed slight declines in RGR to include the open treatment despite possible growth limitations caused by water stress. Studies that apply Sack & Grubb’s approach with few data points should be viewed with caution. This is evident from this study alone.

Future trials would benefit from not just increasing the number of light levels but also increasing the light levels in the region of increasing RGRs. Other benefits to increasing the number of light levels would include the consequential reduction in error which would tighten the confidence intervals around each regression line and perhaps aid the calculation of confident intervals around each CPI (Figure 4.1). The latter proved impossible due to very large confidence intervals around each linear regression. Furthermore a major problem arose from the fact that species pairs have positive responses to light (Figure 4.3). The likelihood of species pairs having contrasting responses is debatable but perhaps is possible in longer term studies with species from extreme ends of the shade tolerance spectrum. As Walters & Reich (1996) revealed in their two year study, temperate shade tolerants eventually outgrow their shade intolerant counterparts in deep shade.

In further development of the approach, a reassessment of appropriate confident intervals is required. It is acknowledged that 95% confident intervals around log linear functions for species pairs, actually give rise to very conservative confident intervals around the CPI (i.e.: 99.75% CI: $0.9975 = 1 - (0.05^2)$ (the probability of two observations outside limits)). If 95% confident intervals around the CPI, are desirable, the confident intervals around each regression would need to be widened (i.e.:78% CI: 0.776 = 1 - squared root of 0.05).

A critique of Sack & Grubb's CPI approach (Kitajima & Bolker, 2003) was published after completion of Chapter 4. Kitajima & Bolker (2003) also express a concern about the statistical viability of the approach especially in relation to the lack of consideration of measurement and structural error. They also stress the need for sufficiently different irradiances to increase confidence in the shape of light response curves of species.

Kitajima & Bolker (2003) briefly mention that the inclusion of confidence intervals around the CPI would be a good idea but do not elaborate. The use of a log linear function to fit species growth responses to light is criticised as typical forms of the RGR reaction norm are believed to show an asymptotic increase often with a drop at the highest irradiances. They show how the CP% (between 2% and 10% full daylight) can be understimated when the response curve is fitted incorrectly with a logarithmic function rather than a Michaelis-Menten curve. Sack & Grubb (2003), in their reply to this paper, agree that fitting different types of line to data sets can produce different cross-over patterns. They suggest that the log-linear function is perhaps more appropriate for data sets that include RGRs below saturation irradiance and the Michaelis-Menten is more appropriate when more data are available including RGRs above saturation irradiance. Other caveats to the approach which can affect cross-overs between species which have been acknowledged include the problems with ontogenetic drift (see Chapter 3) and pot bound seedlings in longer term trials and the effects of pre-treatment light conditions (Sack & Grubb, 2001; Kitajima & Bolker, 2003).

4.5 Summary

An invaluable and unique comparative dataset was acquired from using 15 species, but it had its trade-off in logistics which limited the number of light levels that could be used to study light response curves with accuracy. Even though the data is statistical poor, it still provides clues on specific species responses to irradiance for one-year old-nursery grown seedlings. Species do not generally appear to cross rank in their second year of growth; this can be accounted for by morphological adjustment to shade rather than seed reserve effects. It is very possible that a longer-term study would have yielded more cross-overs in RGR between understorey and gap irradiance as physiological components become more important in driving RGR. To clarify this, the design of future trials must include more light treatments and should be run over at least two growing seasons. If an appropriate level of confidence in estimates of species different growth response curves and CPI can be achieved, Sack and Grubb's approach could be developed to pinpoint specific irradiance levels at which specific pairs change rank.