Survival and Early Seedling Growth of Conifers with Different Shade Tolerance in a Sitka Spruce Spacing Trial and Relationship to Understorey Light Climate

William L. Mason, Colin Edwards and Sophie E. Hale

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Alternative silvicultural systems to clearfelling are being adopted in Great Britain as a means of increasing the species and structural diversity of conifer plantation forests. One area where knowledge is lacking is the critical level of below-canopy light for survival and growth of young seedlings. This was investigated by planting seedlings of European larch *Larix decidua* (Mill.), Scots pine *Pinus sylvestris* L., Sitka spruce *Picea sitchensis* (Bong.(Carr.)), Douglas fir *Pseudotsuga menziesii* (Mirb.(Franco.)), and western hemlock *Tsuga heterophylla* (Raf. (Sarg.)) in a Sitka spruce plantation thinned to 3 different spacings. The incident light intensity beneath the canopy ranged from about 2 to over 60 per cent of full light. Planting in an adjoining open area provided an indication of growth under full light. Growth and survival of these seedlings were followed for 4 growing seasons. The highest seedling survival was found under the widest spacing and declined with closer spacing and lower light intensity. Only Douglas fir and western hemlock seedlings survived at the closest spacing, and in low percentages. The tallest seedlings of each species were found in the open grown conditions but survival was variable due to increased weed competition. Species-specific growth responses showed little difference under high light conditions but performance at low light was generally consistent with shade tolerance rankings in the literature except that Sitka spruce shade tolerance was slightly lower than expected. Minimum light requirements for these species increased from 10 to 30 per cent of full light with decreasing shade tolerance. Other studies of incident light in Sitka spruce plantations indicated that target basal areas in the range 25–30 m^2 ha^{-1} are required if these light conditions are to be met, which suggests an irregular shelterwood system with frequent interventions should be favoured.

Keywords seedling growth, light regime, stand density, irregular silviculture
Authors´ address Forest Research, Northern Research Station, Roslin, Midlothian, Scotland, UK, EH25 9SY
E-mail bill.mason@forestry.gsi.gov.uk
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1 Introduction

There is increasing interest in many parts of the world in the use of stand management regimes that will increase the structural and species diversity of forests and so achieve the objectives of multipurpose forest management (O'Hara 1998, Pretzsch 1998, Lähde et al. 2001, Schutz 2002). In Great Britain, these regimes are often termed 'Continuous Cover Forestry' (CCF) and are characterized by a number of features including the favouring of natural regeneration, creation of varied stands with a number of tree species, working with site limitations, managing the ecosystem rather than the trees, and a presumption against clearfelling (Mason et al. 1999). Recent forestry strategies for Scotland (Forests for Scotland … 2000) and for Wales (Woodlands for Wales … 2001) both include specific commitments to increase the forest area managed by CCF regimes; in Wales the aim is to transform at least 50 per cent of the forest area to this type of management by 2020. Appreciable levels of public funds will also be involved since grant schemes for private forestry will provide support for measures taken to increase the use of CCF (e.g. Scottish Forestry Grant … 2003). These strategic targets present a major challenge to British forest managers, not least because the area currently under CCF management is probably considerably less than 100 000 ha, i.e. less than five per cent of the British forest area (W.L. Mason, unpublished data).

The small area of British forests managed under CCF means that there is very limited experience of the appropriate silvicultural regimes to use, unlike the situation in Central Europe where there is a long tradition of irregular forest management (e.g. Schutz 1997). The two main areas of uncertainty are firstly the interaction between silvicultural system, stand stability and thinning regime (Mason 2002, Hale et al. 2004), and secondly the interaction between thinning, understorey microclimate (primarily incident light) and the occurrence and development of natural regeneration. Malcolm et al. (2001) attempted to relate seedling growth of a range of native and introduced conifers found in British forests to gap size on the basis of reported species shade tolerance. They developed these relationships to propose that an appropriate gap size for satisfactory natural regeneration and seedling growth of the major British conifers (Sitka spruce (*Picea sitchensis* (Bong.) Carr.); Scots pine (*Pinus sylvestris* L.); and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco)) should be at least 0.1 ha with a gap diameter: top height (d/h) ratio of 1.5–2.0. An irregular shelterwood system was recommended as the preferred method of providing suitable gaps and so implementing CCF in British conifer forests. This was based upon the supposition that these species were intermediate to light demanding in terms of shade tolerance, could not be expected to survive for long periods under the low light conditions characteristic of closed conifer plantations (Hale 2001) and would therefore require a gap large enough to provide at least 50 per cent of ambient light (Coates and Burton 1997) for adequate growth. However, the relationships proposed by Malcolm et al. (op. cit.) were based largely on theory supplemented by scanty experimental data (Brown and Neustein 1972) and personal observation with gap size used as a surrogate for light climate.

The theory of shade tolerance suggests that there are species-specific physiological and growth adaptations which influence their ability to survive and grow at different levels of light. For example, in low light, shade tolerant *Abies* species exhibit reduced height and diameter growth without mortality, but this is not true of light demanding *Pinus* species (Kobe and Coates 1997). Such differences result in interspecific differences in growth-related light responses such that shade tolerant species maintain positive carbon gain under low light, but show lower gain than light demanding species at high light (Bazzaz 1979). While the broad classification of species as 'shade tolerant', 'intermediate', or 'light demanding' appear to be consistent between regions (e.g. Claveau et al. 2002), there are still uncertainties over the details. For instance, field studies have suggested that interspecific trade-offs in shade tolerance are much less evident in whole plant studies than when based upon whole leaf physiological measurements (e.g. Wright et al. 1998, Coates and Burton 1999). Shade tolerance within species has also been shown to be affected by site quality, with decreasing tolerance with increasing soil moisture having been reported for Douglas fir, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red cedar (*Thuja plicata* D. Don.) (Carter and Klinka 1992). A more detailed understanding of species response to different light levels can help develop appropriate silvicultural prescriptions for fostering varied forest structures with a range of species (Coates and Burton 1997) and can be linked to other decision support tools to allow exploration of the impact of different stand management regimes (Hale et al. 2004).

We report here the results of an experiment to test the relationships proposed by Malcolm et al. (2001). This involved growing seedlings of 5 conifer species over 4 years in a Sitka spruce stand thinned to different stocking densities with a consequential range in below-canopy light regime. Sitka spruce is the major commercial species in British forests (~30 per cent of the forest area; S. Smith, Forest Research, pers. comm.) and widespread implementation of CCF in Britain will therefore depend upon foresters' ability to create desirable conditions for seedling regeneration and growth in this particular forest type.

2 Materials and Methods

2.1 Seedling Growth

The five species used in the experiment were European larch (*Larix decidua* Mill.), Scots pine, Sitka spruce, Douglas fir, and western hemlock. They were chosen because of reported differences in shade tolerance (Malcolm et al. 2001) with European larch being considered least tolerant and western hemlock most tolerant.

The experimental site was a 30 year old stand of Sitka spruce located at 370 m asl, in Cloich forest about 20 km south of Edinburgh (55°42'N, 3°16'W). The stand was originally established at 2.0 m spacing (≈2500 trees ha^{-1}) and in 1986 it was respaced to 3 different densities; wide (W) (8 × 8 m spacing ≈ 156 trees ha^{-1}), medium (M) (6 × 6 m ≈ 280 trees ha^{-1}), and narrow (N) (4 × 4 ≈ 625 trees ha^{-1}), plus an untouched control. Plot areas in the W, M and N treatments were 0.84, 1.01, and 0.43 ha, respectively. At the start of this experiment these plots had basal areas of 9.25, 27.3 and 40.8 m^2 ha^{-1} with top heights of 13.1, 14.1 and 15.0 m. An unplanted area immediately to the north of these plots was used to provide open (O) ground conditions equivalent to full ambient light.

The annual rainfall at the site is about 1000 mm and the accumulated day-degrees (>5.6°C) are approximately 1150. The site therefore falls into the 'Cool-Wet' climatic zone of the British Ecological Site Classification (Pyatt et al. 2001). The soils vary from an intergrade upland brown earth to a shallow peaty gley across the site depending upon local topography. The vegetation varied from a dense grass sward dominated by *Deschampsia caespitosa* with some *D. flexuosa*, *Agrostis capillaris* and *Anthoxanthum odoratum* in the open area, to predominant *D. flexuosa* with some *Vaccinium myrtillus* and *Calluna vulgaris* in the W and M treatments, while little or no vegetation was present under the N treatment. The combination of vegetation and soils indicates a site of 'poor' soil nutrient status (Pyatt et al. 2001) where remedial fertiliser applications would not be required in the establishment phase (Smith and McKay 2002).

One-year-old containerised seedlings of commercial provenances of each species were raised at the Northern Research Station in 1998 and outplanted on May 4–5, 1999. Ten replicates of each species were planted in the narrow, medium, and wide spacings as well as in the open area in a randomised block design, with 10 plants per species per replicate. Spacing was 0.5 m within and 0.3 m between rows. No plot in the respaced treatments was sited closer than 2.0 m to an overstorey tree. Plots in the open area were 25–30 metres away from the nearest tree.

The whole site was fenced against deer and sheep. However sheep broke into the enclosures during winter 1999 and caused particularly severe damage to the Scots pine seedlings which were all replanted in spring 2000. Competing vegetation was controlled by annual applications of glyphosate in late spring (Willoughby and Dewar 1995). The nation-wide outbreak of foot-and-mouth disease in 2001 restricted access to the site between March and late June and prevented herbicide application that year, as well as limiting assessments.

Height and root collar diameter were measured on a subsample of 50 seedlings per species before planting (Table 1). Survival, height and root collar diameter were assessed on a permanently marked subsample of 2–3 seedlings per species per plot in 1999 (4 times between June and October); 2000 (4 times between June and October); October 2001 and December 2002. All seedlings surviving at the time of the last assessment were lifted, measured for height and root collar diameter, placed in a coextruded bag and cold stored (+2°C) for up to 10 weeks. During this period, between 20–30 seedlings per species and spacing treatment were randomly chosen for destructive assessment of shoot and root dry weights. If fewer than 20 seedlings of a given treatment had survived, then all survivors were destructively assessed. All soil was removed from roots before assessment, shoots and roots were placed in separate paper bags, and oven dried at 80°C for at least 48 hours.

Light measurements were made using a Sunscan Ceptometer (Delta-T Devices, Cambridge, U.K.) whereby incident radiation at a given point below the canopy is expressed as a percentage of that simultaneously measured in the open. The Sunscan was logged for five minutes at the centre of each replicate plot in a spacing treatment with the ceptometer levelled at a height of 1.3 m, and the average transmittance for the period was calculated. This measurement was repeated each year from 1999 to 2002. These measurements, taken on overcast days, can be used to represent the transmittance throughout the growing season (Messier and Puttonen 1995, Parent and Messier 1996); the data presented here are the averages of measurements made in these conditions (N: two years; M: three years; W: two years). Light intensities recorded expressed as a percentage of the O treatment were W: 60.6 ± 13.4%; M: 15.9 ± 13.6%; N: 2.4 ± 0.5%. The wide variation in the W and M treatments reflected the degree to which the light falling upon a given plot was influenced by adjacency to an overstorey tree.

Data on seedling survival, growth, and dry weights were assessed using normal analysis of variance procedures for a randomised block design. Results for each spacing were analysed separately because of the lack of replication. Survival data were transformed by arcsine before analysis. For each spacing, the hypothesis tested with the ANOVA was that there would be no difference in species mean response for the growth trait under consideration.

Table 1. Height (cm) and root collar diameter (mm) of seedlings of 5 conifer species before planting into 4 different levels of canopy cover (+/– one S.D.)

Species	Height	RCD
European larch	25.3 (4.4)	3.4 (1.0)
Scots pine	29.1 (4.5)	2.9 (0.5)
Sitka spruce	20.2 (2.7)	2.4 (0.4)
Douglas fir	25.3 (3.8)	2.9 (0.6)
Western hemlock	16.3 (4.1)	4.0 (5.0)

The relationships between measures of seedling growth and incident light were explored using a Michaelis-Menten function where:

$$Y = \left\{ (aL) / \left[(a/s) + L \right] \right\} + \varepsilon$$

where Y is the chosen growth measure, a and s are estimated growth parameters, L is the percentage of full light measured by the Sunscan for each replicate and ε is a normally distributed error term. The parameter value a is the asymptote at high light levels whereas the value of s measures the slope of the growth function at low light. Thus species with high a values can be considered to be light demanding and those with comparatively high s values as more shade tolerant (Coates and Burton 1999). We used this approach because it formed the basis of the asymptotic relationship between growth and light proposed by Malcolm et al. (2001) and adapted from Coates (2000). Wright et al. (1998) found the Michaelis-Menten function to provide the most consistent and biologically meaningful results out of 3 non-linear models linking light and seedling growth.

In applying the Michaelis-Menten function, a trial replicate mean for the growth measure (Y) was determined and, for each species, model parameters (i.e. a and s) were estimated using a modified Gauss-Newton method with the FITNONLINEAR routine in GenStat version 4.2 (GenStat 2000). Data were logarithmically transformed to stabilise the variance anticipated as a result of variation in light intensity within a spacing treatment. Standard errors (SE) and proportion of variation explained (R^2) were also calculated.

3 Results

3.1 Seedling Experiment – Survival

At the end of the first growing season (October 1999) there was over 95 per cent survival in all treatments other than for the European larch and Scots pine in the N treatment (32 and 58 per cent respectively). However, differences between species within spacing treatments and between treatments increased progressively thereafter. In general, the greatest changes in survival occurred between the end of the second and the third growing seasons. Note that the trends in Scots pine were slightly delayed compared to the other 4 species because of the replacement of damaged seedlings in the spring of 2000. After 4 years, the highest overall survival (95 per cent) was found in the W treatment, compared with 55–60 per cent in the O and M treatments, and a low of 5 per cent in the N treatment. There were significant differences after four years between species in all spacing treatments but the trends varied with treatment (Table 2). Thus in the O plots, Douglas fir and western hemlock had much poorer survival than the other species; in the W treatment Scots pine showed higher survival than all the others; in the M, Scots pine and European larch had lower

Table 2. Survival (%), seedling height (cm), root collar diameter (RCD; mm), total, shoot and root dry weights (g), and shoot: root ratios of seedlings of 5 conifer species after 4 years growing under 4 different levels of canopy cover (spacing treatments).

Treatment	Species	Survival Trans.	Survival Actual	Height	RCD	Total dry weight	Shoot dry weight	Root dry weight	Shoot: root ratio
O	EL	62.6	78.8	72.7	15.0	86.0	74.6	11.4	6.2
	SP	86.3	99.6	42.5	7.9	10.1	8.5	1.6	6.4
	SS	46.5	52.5	34.2	7.1	8.5	7.0	1.4	5.2
	DF	17.7	9.2	32.3	7.3	11.7	9.8	2.0	4.6
	WH	30.9	26.4	21,7	7.3	17.2	13.5	3.7	3.6
	Signif.	***	–	***	***	***	***	**	**
	5% LSD	14.9	–	12.3	3.0	34.9	29.8	5.3	1.5
W	EL	78.1	95.8	31.7	8.3	8.1	5.9	2.2	2.9
	SP	90.0	100.0	40.2	5.3	4.4	3.7	0.8	5.5
	SS	78.3	95.9	22.3	6.0	6.5	4.8	1.7	2.9
	DF	70.3	88.6	20.4	4.9	4.7	3.2	1.5	2.1
	WH	79.2	96.5	37.6	6.7	12.1	9.3	2.8	3.6
	Signif.	**	–	***	***	***	***	***	***
	5% LSD	10.1	–	4.2	0.8	3.3	2.5	0.9	0.9
M	EL	39.9	41.2	38.7	5.6	2.9	2.2	0.7	3.7
	SP	34.2	31.6	39.0	4.1	2.0	1.6	0.4	4.6
	SS	53.7	65.0	30.5	4.4	2.4	1.9	0.6	4.8
	DF	68.5	86.6	22.4	4.4	1.9	1.3	0.7	3.2
	WH	60.9	76.3	28.2	4.5	3.8	2.8	1.1	3.3
	Signif.	*	–	**	**	*	n.s.	*	n.s.
	5% LSD	21.7	–	8.8	0.7	1.4	1.1	0.4	2.2
N	EL	0.0	0.0	–	–	–	–	–	–
	SP	0.0	0.0	–	–	–	–	–	–
	SS	0.0	0.0	–	–	–	–	–	–
	DF	11.9	4.2	21.2	3.9	1.0	0.7	0.3	5.8
	WH	25.6	18.7	19.6	3.4	1.2	0.8	0.4	2.2
	Signif.	**	–	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	5% LSD	9.9	–	6.5	0.5	0.7	0.4	0.3	3.8

Species codes are: EL – *Larix decidua*; SP – *Pinus sylvestris*; SS – *Picea sitchensis*; DF – *Pseudotsuga menziesii*; WH – *Tsuga heterophylla*.
*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; n.s. = non-significant.
Shoot: root ratios may not equate to shoot dry weight/root dry weight because of rounding errors.
'Trans.' are percentage values after arcsine transformation.

Table 3. Parameter estimates for fourth-year total dry matter (g) and root collar diameter (mm) using the equation Y = (aL) / [(a/s) + L] where L is the growing season transmittance measured with a Sunscan Ceptometer. Estimates for total dry matter used logarithmic transformation – see text for further details.

Species	*a* parameter		*s* parameter		R^2	n
	Estimate	S.E.	Estimate	S.E.		
Total dry matter						
Scots pine	2.4	0.5	0.07	0.02	66.1	28
Sitka spruce	2.5	0.2	0.14	0.05	62.1	28
Douglas fir	2.2	0.2	0.20	0.08	47.4	31
Western hemlock	2.4	0.2	0.42	0.13	57.6	36
Root collar diameter						
European larch	96.0	200.0	0.17	0.06	46.3	28
Scots pine	8.9	1.4	0.36	0.15	26.7	28
Sitka spruce	6.5	0.3	1.68	0.48	46.4	28
Douglas fir	6.0	0.4	2.97	1.19	23.4	31
Western hemlock	7.1	0.4	1.95	0.55	46.2	36

survival than Douglas fir; while in the N only western hemlock and Douglas fir seedlings had survived, albeit at low levels.

3.2 Seedling Experiment – Growth

The tallest, sturdiest and heaviest plants of each species were found in the open grown O treatment. There were significant differences between species for all parameters in the O and W spacings, but they were less frequent in the M, and there were none in the N. In the O treatment, the European larch seedlings were significantly bigger and heavier than those of other species. The results in the W treatment were more complex with Sitka spruce and Douglas fir seedlings being significantly shorter than others, while the European larch was significantly sturdier. However, western hemlock seedlings showed higher total dry weights in this spacing treatment, primarily due to higher shoot dry weights. In the M treatment, European larch seedlings were again significantly taller and sturdier than others (except Scots pine for height), but western hemlock seedlings had higher total dry weights and the highest root dry weight. The few Douglas fir and western hemlock that had survived in the N treatment appeared to have made very little growth since planting. Shoot: root ratios were significantly different between species in both the O and W treatments: in the former these were highest in European larch and Scots pine and least in western hemlock, whereas in the latter the highest was in Scots pine and the least in Douglas fir.

3.3 Seedling Growth – Light Regime

Incident light appeared a poor predictor of tree height after 4 years, but was found to be a better indicator of tree dry weight and root collar diameter under field conditions (Table 3). It proved almost impossible to get equation 1 to fit to the height growth data; the only exception was for European larch, but the goodness-of-fit was only 6.5%. By contrast, after logarithmic transformation of the total dry weight data, there was a successful fit (R^2 of 47.4 to 66.1 per cent) for all species except European larch (Table 3 and Fig. 1). The fits for root collar diameter data were successful with all species, but there was more variation than for total dry weight (R^2 of 23.4 to 43.6 per cent) (Table 3 and Fig. 2). Difficulties in obtaining a reasonable fit were largely due to the wide variation in growth of trees of all species in the open grown treatments (see Figs. 1 and 2).

Where fits were successful, inspection of the *a* and *s* parameters showed relatively little difference in the high light asymptote for total dry matter (parameter *a*), but values of *s* increased from Scots pine to western hemlock (Table 3). Similar examination of the root collar diameter results showed highest values of *a* in European

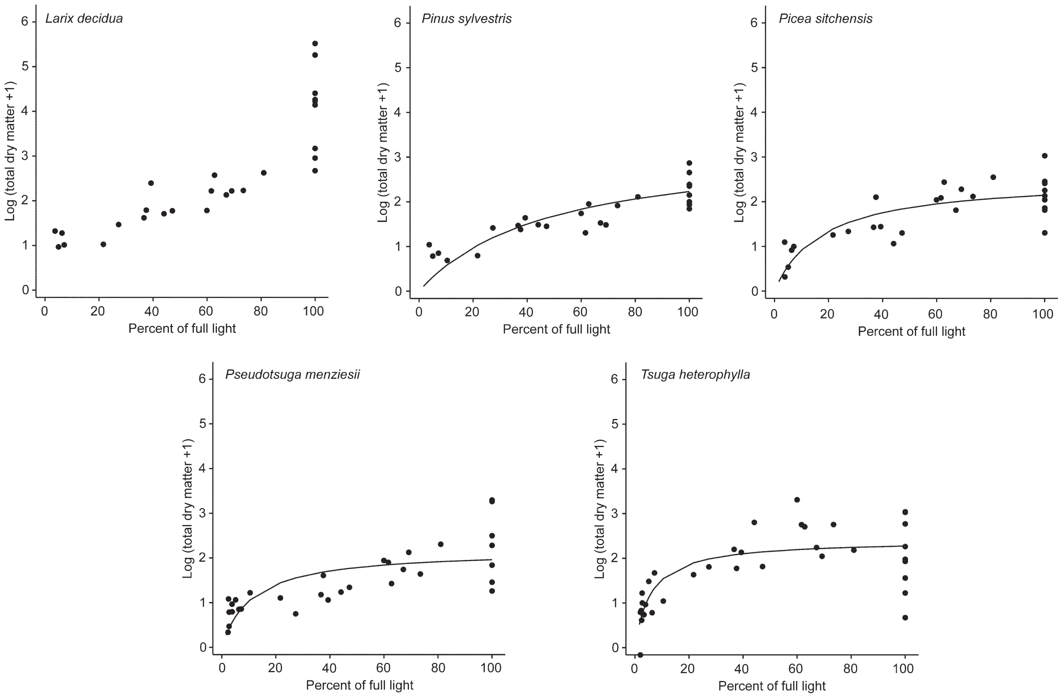

Fig. 1. Observed values and fitted regression lines for log total dry matter (g) against per cent of full light for 5 conifer species 4 years after planting using parameter values from Table 3. *Larix decidua* – European larch; *Pinus sylvestris* – Scots pine; *Picea sitchensis* – Sitka spruce; *Pseudotsuga menziesii* – Douglas fir; *Tsuga heterophylla* – western hemlock. No fit was possible for the European larch data – see text for details.

larch, albeit with a high degree of variation in the estimate, but lowest values of *s* in the same species. Higher values of *s* were found in Douglas fir and western hemlock.

4 Discussion

There was a clear trend in all species for the seedlings with the greatest dry weight to be found in the open conditions and for growth and survival to decline progressively from the wide spacing towards the narrow spacing (i.e. from higher to lower light levels). Similar trends are reported in other underplanting studies (e.g. Chen 1997, Chen and Klinka 1998). The between species growth differences were more apparent under high light conditions (treatments O and W) as a result of European larch and Scots pine showing greater response to these conditions, a characteristic of shade intolerant species (Coates and Burton 1999). By contrast, survival differences between species occurred in all treatments partly reflecting more difficult establishment conditions in the open (see below) as well as changes in light environment. European larch and Scots pine had notably lower survival at the M spacing with an average light intensity of around 16 per cent of full light whereas the three other species still had acceptable survival at these light levels. The high mortality of all species, with the partial exception of western hemlock, at the N spacing is not surprising since at less than five per cent full light most seedlings would have been growing at below their light compensation point (Grossnickle 2000).

Examination of differential species survival from the W to the N treatments suggests a ranking in terms of increasing shade tolerance as Euro-

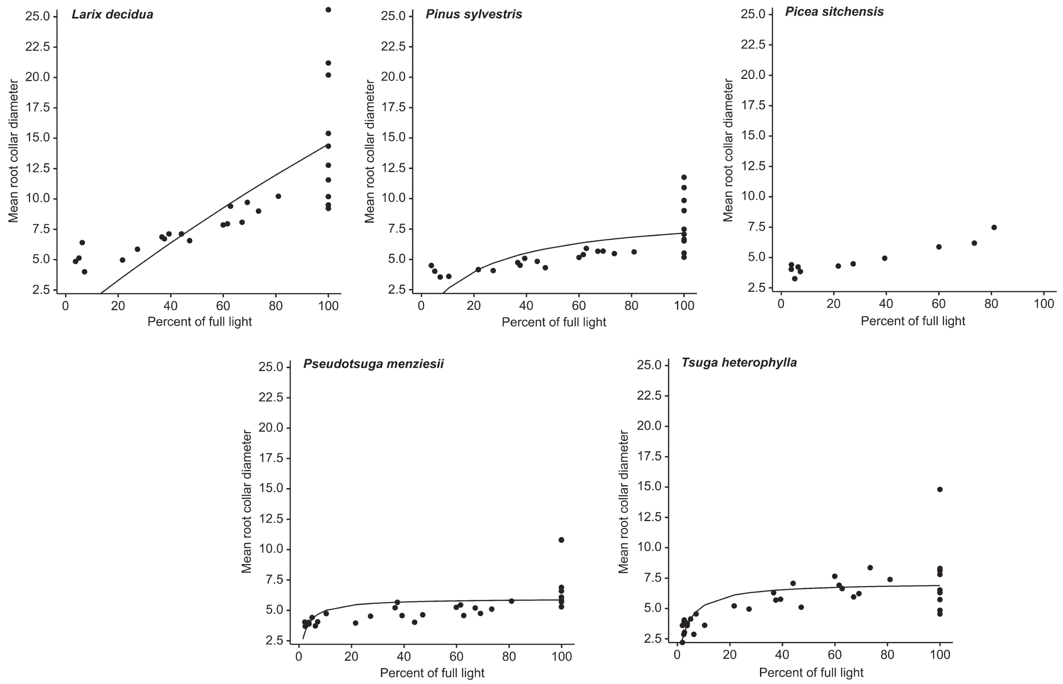

Fig. 2. Observed values and fitted regression lines for root collar diameter (mm) against per cent of full light for 5 conifer species 4 years after planting using parameter values from Table 3. *Larix decidua* – European larch; *Pinus sylvestris* – Scots pine; *Picea sitchensis* – Sitka spruce; *Pseudotsuga menziesii* – Douglas fir; *Tsuga heterophylla* – western hemlock.

pean larch = Scots pine < Sitka spruce = Douglas fir < western hemlock. We have not found any other underplanting studies in the literature that have compared these five species on the same site over a number of years so only partial comparisons with this tentative ranking can be made. Coates (2000) found lower mortality in western hemlock compared to intermediate hybrid spruce (*Picea glauca* (Moench) Voss. × *Picea sitchensis* (Bong.) Carr.) with highest mortality in shade intolerant lodgepole pine (*Pinus contorta* var *latifolia* Engelm.) in a forest understorey (around 10 per cent of full light) in British Columbia. Hybrid spruce is considered to be similar in tolerance to Sitka spruce (Wright et al. 2000). Lodgepole pine proved very similar to Scots pine in tolerance of shade in a two-year nursery shading study in Britain (Brown and Neustein 1972). There was generally higher survival of western hemlock than Douglas fir after seedlings of both species were underplanted into a 50 year old Douglas fir stand thinned to four different densities, although no difference was found at the highest density (Brandeis et al. 2001). In the shade intolerant western larch (*Larix occidentalis* Nutt.), survival declined with decreasing light from around 50 per cent full light; at two of the three planting sites no survival occurred below 20 per cent of full light (Chen and Klinka 1998). Our provisional ranking agrees with that outlined by Malcolm et al. (2001), with the exception of an apparent difference in survival between Sitka spruce and Douglas fir at lower light levels suggesting that these two species might not be as similar in shade tolerance as previously proposed.

Further information on the relative shade tolerance of these five species can be provided by the growth parameters estimated by fitting the Michaelis-Menten equation. A shade tolerant species would show the greatest growth response to an increase in light levels but a relatively low asymptote at high light (i.e. high *s* and low *a* values). Shade intolerant species would show the inverse response (Wright et al. 1998). There was relatively little difference between species in terms of the asymptote at high light (parameter *a*) with the exception of predicted root collar diameter in European larch (Table 3). However, the estimate of the latter was subject to considerable variation because of the vigorous growth of some seedlings in full light. Thus it was not possible to discriminate between species in terms of their growth at full light, probably because the effects of weed competition and possible frost damage were damping the observed response. However, there were appreciable differences in the slope of the relationship at low light levels (parameter *s*) where the lowest values were observed in Scots pine or European larch (i.e. least shade tolerant) and the highest in western hemlock (i.e. most shade tolerant) with Douglas fir and Sitka spruce intermediate. When comparing average radial growth of saplings within the same climatic zone in British Columbia, Wright et al. (1998) found western hemlock to have higher *s* values than hybrid spruce which in turn was higher than lodgepole pine. Drever and Lertzman (2001) reported *s* values 3–4 times larger for saplings of shade tolerant western red cedar (*Thuja plicata* Donn ex D. Don) than for more light demanding Douglas fir. The estimated *s* values for these four species conform with measurements of shoot photosynthesis under low light where the light compensation point of Scots pine was twice as high as for western hemlock (Leverenz 1996). He also found the light compensation point for Douglas fir and Sitka spruce lies between that of the pine and hemlock, with spruce having a slightly lower value than Douglas fir.

The proportion of variation in growth that was explained using the Michaelis-Menten function varied appreciably according to the parameter under consideration. The poor prediction of height growth appears to be due to an inconsistent species response to declining light intensity. In particular, the tendency was for European larch, Scots pine, Sitka spruce and Douglas fir seedlings to be either taller or of similar height at the lower light intensity M treatment to those at the higher light W treatment. A tendency for height growth of shade intolerant pine species to be less responsive to changes in light regime has been reported elsewhere (Messier et al. 1999). By contrast, acceptable fits were obtained with respect to root collar diameter after 4 years for all species and for total dry matter of all species except European larch. The failure in the last instance is thought to be due to the very vigorous growth of the larch seedlings in the open area compared to the treatments planted under the canopy. Diameter growth had been found to be more responsive to light climate than height in an earlier shading study including all these species except European larch (Fairbairn and Neustein 1970). Kobe and Coates (1997) showed that levels of radial increment were linked to sapling life expectancy and that this varied with shade tolerance. Thus, in light demanding lodgepole pine an increment of 0.6 mm yr^{-1} gave a life span of about 10 years while the equivalent increment needed for western hemlock was 0.2 mm yr^{-1}. The proportion of variation explained by the function tended to be lower (R^2 of 23 to 66 per cent) than in similar studies carried out in British Columbia where R^2 values of 55 to 89 per cent were reported for 5 year height and diameter of *Abies lasiocarpa*, western hemlock, western red cedar, and hybrid spruce (Coates and Burton 1999). This may either reflect the greater sample size used in the Canadian work or the more conservative R^2 values used in this study which are based on a model with a corrected sum of squares. Comparison of the observed values in Coates and Burton 1999 (their Figs. 1 and 2) with those in our Figs. 1 and 2 do not suggest greater scatter in our data.

An assumption made when fitting the function is that light is the prime factor influencing seedling survival and growth, and that other aspects such as competition from weeds or overstorey trees are of lesser importance. In this experiment, careful weed control plus not planting seedlings close to overstorey trees would have reduced competition for nutrients and soil moisture compared to that found in operational conditions (e.g. Coates 2000). Furthermore, in the oceanic climate of upland Scotland, such factors may still not be major influences on seedling growth under a forest canopy since studies of soil moisture regime in fully stocked even-aged plantations in the same region suggest that soil moisture deficits were rarely sufficient to limit growth (Pyatt and Craven 1979). One would also expect such deficits to be less severe under a partial canopy because of reduced interception and evapotranspiration (Malcolm et al. 2001, Grossnickle 2000). Ricard et al. (2003) also concluded that light availability was the main factor influencing understorey sapling growth on sites where neither nutrients nor precipitation were limiting. The influence of factors other than light was more serious in the plots in the open area since the access restrictions in 2001 meant that weed control was less than adequate in these grass dominated plots, resulting in greater competition for the planted trees. This period coincided with the greatest change in seedling survival. Measurements of air temperature within the experiment during 2002 showed appreciably lower night temperatures within the open area (Helen Sellars, Forest Research, unpublished data). Thus trees in this treatment are likely to have been subjected to a higher incidence of damaging frosts, as has been found in a number of studies evaluating frost incidence on clearcuts and under partial canopies (Grossnickle 2000, Langvall and Ottosson Lofvenius 2002). For these reasons, survival and growth in the open area were reduced and more variable than expected and may not provide a complete indication of potential growth response when light is not limiting. Nevertheless, the relative difference between species in their response to changes in light level is unlikely to have been affected so that the shade tolerance rankings for the various species should be reliable.

After 4 years, seedling growth in this experiment was less than that reported in other similar studies. For instance, Coates and Burton (1999; their figure 1) indicated 5 year tree heights of c.1 m for seedlings of *Abies lasiocarpa* (Hook.) Nutt., nearly 2 m for seedlings of western hemlock, and about 2.5 m for those of lodgepole pine, all growing in full light in northwestern British Columbia. Similarly, Chen (1997) reported heights of 50–120 cm for 3 year old seedlings of *Pinus ponderosa* (Douglas ex Lawson and Lawson), Douglas fir, and *Picea engelmanii* (Parry ex Engelm.) planted in full light in interior British Columbia. In both cases, the seedlings were of similar size at planting to those in our study. We think the lesser growth in full light in our study was due to

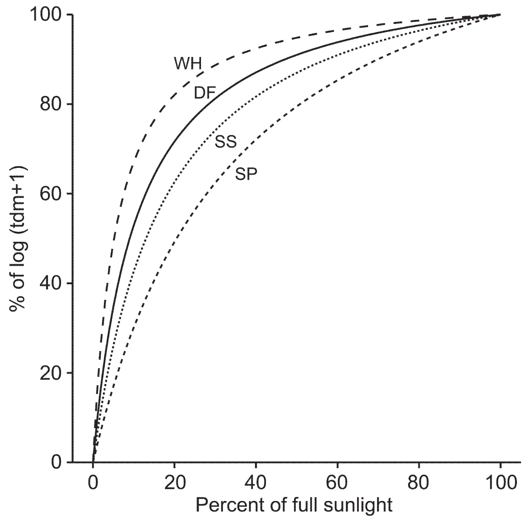

Fig. 3. Fitted regression lines for log total dry matter against percentage of full light from Fig. 1 for western hemlock (WH); Douglas fir (DF); Sitka spruce (SS) and Scots pine (SP) expressed as a proportion of the highest values.

weed competition and other microclimate factors discussed above.

Other studies have suggested (Messier et al. 1999) that more shade tolerant species will have a proportionately greater allocation to roots than light demanding ones. In this experiment, all species showed a decline in shoot: root ratio from open ground to the medium spacing (i.e. from full light to around 16 per cent light). However, this decline was proportionately greater for European larch and Scots pine (40–30 per cent) than for Sitka spruce and western hemlock (around 10 per cent), supporting the classification of the first two species as light demanding. We have ignored Douglas fir when discussing this aspect because of the low survival in the open ground conditions.

In Fig. 3, we present the fitted regression lines for total dry matter against percentage of full light for Scots pine, Sitka spruce, Douglas fir, and western hemlock on a percentage scale to aid comparison of growth responses between species. The more shade tolerant western hemlock responds faster to increases in light at low levels than the more light demanding Scots pine. This figure is in broad agreement with the qualitative species rankings proposed by Malcolm et al. (2001). However, the regressions suggest a slightly greater shade tolerance in Douglas fir than in Sitka spruce which may also be evident in the marginally different survival of these species at the M and N spacings (Table 2). Brown and Neustein (1972) also found Douglas fir seedling dry weight to be proportionately greater than that of Sitka spruce with decreasing light levels. This contradicts traditional thinking in Great Britain and north America where the two species have either been classed together as having intermediate shade tolerance (e.g. Mason et al. 1999) or Sitka spruce has been considered more tolerant than Douglas fir (Minore 1979). Resolving this discrepancy may require further research given the importance of Sitka spruce in British forestry.

Implications for Uneven-aged Management

The practical application of this study requires determining critical below-canopy light levels for satisfactory seedling survival and growth and linking these to observations of light regime in the field. Hale et al. (2004) used a seedling growth model to show that, for one-year old Sitka spruce seedlings, mortality occurred at less than five per cent incident radiation and growth increased non-linearly at more than 5–10 per cent transmittance. They predicted that for a spruce seedling to survive beneath a canopy it would require some 20 per cent transmittance which would be equivalent to about half the growth achieved in full light. This percentage transmittance is similar to critical light levels reported for white spruce (*Picea glauca* Moench. Voss.) (Grossnickle 2000). For Sitka spruce, the regression line in Fig. 3 gives comparable results to those predicted by Hale et al. (2004) in that 20 per cent full light is equivalent to about 60 per cent of growth in full light. Assuming that 60 per cent of growth in full light can be used as a general indicator across all species, then the minimum light for satisfactory growth of the other species in this study would be about 30 per cent of full light for Scots pine, for Douglas fir about 15 per cent and western hemlock 10 per cent. Given that the regressions are based on small trees less than one metre in height (Table 2), these critical light levels will need to be increased to allow for the increased demands of taller seedlings and saplings (Messier et al. 1999).

Studies of below-canopy light levels in a number of Sitka spruce stands in Britain and Ireland (ages 35–65) have found canopy openness values of 0.05–0.15 to be normal except where basal areas were < 30 m^2 ha^{-1} where values of 0.2–0.5 occurred (Hale 2001, 2003, and unpublished data). Given that canopy openness is closely related to per cent full light (Whitmore et al. 1993), we can combine these values with the results of this study to propose critical ranges of stand density which will favour seedling regeneration and growth. Current management recommendations for Sitka spruce stands in Britain are to maintain stocking densities above 35 m^2 ha^{-1} from about 30 years of age (Edwards and Christie 1981). Our results indicate that such stands will not provide sufficient light for survival and adequate seedling growth of most of the important conifer species. The implication is that the density of mature Sitka spruce stands should be reduced to around 25–30 m^2 ha^{-1} to facilitate the growth of regeneration of a range of species of differing shade tolerance as part of the process of transformation to CCF regimes. Page et al. (2001) also found that regeneration success in British Sitka spruce stands was improved when basal areas were < 30 m^2 ha^{-1} while Schutz (2002) reported a limiting basal area of 27–33 m^2 ha^{-1} for recruitment in central European forests of Norway spruce (*Picea abies* (L.) Karst.) and European silver fir (*Abies alba* (Mill.)). Thus the need to develop and maintain a more open stand structure than found in even-aged management may be a prerequisite for transformation to uneven-aged silviculture. However, there may be detrimental implications for stand stability if stands are opened up too quickly towards these target basal areas in that the risk of windthrow is substantially increased (Hale et al. 2004). The comparatively low light levels in existing spruce stands also explain why there is a tendency for any small gaps or openings to be preferentially colonised by less commercially desirable but more shade tolerant species such as western hemlock.

In their attempt to outline desirable forms of transformation silviculture for British conifer forests, Malcolm et al. (2001) proposed an irregular shelterwood system as the preferred option for stands of larch, Scots pine, Sitka spruce and Douglas fir, with only western hemlock being suitable for group or single stem selection. The findings of this seedling study agree with their proposal, but also highlight the need for comparatively low retained basal areas to provide adequate light for satisfactory seedling growth of the range of intermediate to shade intolerant species that dominate these forests. A fairly rapid transformation period with frequent interventions that also involves the creation of gaps 1–2 tree heights in diameter may be necessary if spruce or other more light demanding species are not to be out-competed by less desirable and shade tolerant species (Nyland 2003). Kenk and Guhne (2001) describe a similar situation in Germany where light demanding Scots pine was disadvantaged by less frequent interventions and a longer transformation period in favour of more shade tolerant European silver fir.

In conclusion, the results of this study of the morphological responses of five different species to variations in below-canopy light climate support the general ranking of shade tolerance of British conifers proposed by Malcolm et al. (2001). Such qualitative rankings can be linked to quantitative studies of regeneration success and analysis of the seedling/sapling growth environment to provide better understanding of the success or failure of measures taken to foster natural regeneration. However, to further our understanding of these processes, there is a need for the development of robust ecophysiological tools for examination of seedling and sapling growth with the data used to inform growth models. Modelling would permit identification of critical microclimatic and physiological parameters for survival and growth of the chosen species in the understorey of a given forest stand. After validation, such parameters would be used to provide improved guidance for managers who are confronted with the demanding task of diversifying the species and structural composition of even-aged plantation forests.

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