
CHAPTER 6

Spatial and temporal growth patterns of *Sorbus aucuparia* within old growth *Pinus sylvestris* woodland

6.1 Introduction

The aim of this study was to develop an understanding of natural regeneration of *Sorbus aucuparia* under Caledonian pine in the absence of browsing by large herbivores. Spatial distribution patterns were studied as well as patterns of growth over time. The study also enabled a comparison to be made between the growth of natural regeneration and planted stock in the field (Chapter 7).

A recent review by Raspe *et al.* (2000) summarises current knowledge on the ecology of *S. aucuparia*. It is described as a fast growing deciduous pioneer (Aas & Riedmiller, 1994), native to British woods, scrub and mountain areas, thriving at elevations up to almost 1000 m on sites where few other broadleaved trees will grow (Savill, 1998). In the uplands of Scotland, *S. aucuparia* is associated with the Caledonian pinewoods and occurs elsewhere occasionally in pure stands, particularly in the west, where it may have replaced oak (McVean & Ratcliffe, 1962). In the pinewoods, *S. aucuparia* is found as scattered trees, forming thicker patches where the canopy cover is more open.

It is an undemanding species, doing well on fairly poor, dry acid soils but growing best on moist, humus rich sites (Aas & Riedmiller, 1994). Height of mature trees range from 10-20 m. It tends to have a slender trunk and narrow crown, although multi-stemmed (polycormic) trees are common as a result of browsing and the subsequent growth of new shoots (Hofgaard, 1993). Reproductive age is reached around 10-15 years, although this can be limited by stunting caused by browsing or climatic factors. In harsh environments such as Glen Affric, mast seed production may occur every few years, with little fruit production in between (Raspe *et al.*, 2000). When berries are produced (August-September), each can contain up to 8 seeds but 2-3 seeds are more common. Seed dispersers in the Caledonian pine forest include blackbirds (*Turdus merula*), various other thrushes (*Turdus* species), robins (*Erithacus rubecula*), warblers (*Sylvia* species) (Snow & Snow, 1988), pine martens (*Martes martes*) (Putman, 2000) and, if growing near streams, water (Raspe *et al.*, 2000). There is evidence that *S. aucuparia* is more susceptible to deer browsing than other tree species which leads to continuous suppression in its juvenile stage (Hester *et al.*, 1996a; Linder *et al.*, 1997; Miller & Cummins, 1998). However, when protected from grazing, *S. aucuparia* recovers well from its suppressed stunted form (Gill *et al.*, 1995) and regenerates abundantly within both coniferous and upland

deciduous forests (Hester *et al.*, 1996a; Linder *et al.*, 1997). It is believed to have been much more common in pinewoods before the introduction of domestic stock and the rise in deer populations (Smout & Watson, 1997). It has been suggested that *S. aucuparia* like *Betula* is a good soil-improver (Anderson, 2002). Emmer *et al.* (1998) comment that the growth of *S. aucuparia* counteracts the effects of borealization which involves enhanced soil acidification and litter accumulation, lower biodiversity and retarded nutrient cycling. Steven and Carlisle (1959) suggest that "on open ground the regeneration of birches and rowan may lead to the reoccupation of the ground by pine, as in the past".

Little is known about the shade tolerance ability of *S. aucuparia* or its preference for germination and establishment. Subsequently its role in Caledonian pinewood dynamics is not clear. *S. aucuparia* has been described as shade tolerant particularly during the seedling stage (McVean & Ratcliffe, 1962; Grime *et al.*, 1988; Raspe *et al.*, 2000; Mountford & Peterken, 2001). However others describe it as a pioneer (Evans, 1984; Aas & Reidmiller, 1994; Findlay, 1998) or strong light demander (Savill, 1998) which requires light for flowering and fruiting (Findlay, 1998; Raspe *et al.*, 2000). The abundant establishment of *S. aucuparia* regeneration under the shade of trees or dead trees in boreal woodland (Vanha-Majamaa *et al.*, 1996) may just be a result of trees providing perches for birds to sit and defecate the seeds. Thus, it is not clear if *S. aucuparia* is shade tolerant and if so, then at what development stage more light is required for successful regeneration and growth.

Another important factor which may influence the natural regeneration of *S. aucuparia* within Caledonian pinewoods involves the abundance of particular understorey species: ericaceous shrubs (mainly *Calluna vulgaris*) and feathermoss (mainly *Hylocomium splendens* and *Pleurozium schreberi*) have been implicated as factors that limit tree establishment and subsequent growth (Malcolm, 1957; Handley, 1963). *C. vulgaris* and *Vaccinium myrtillus* can obstruct light from reaching a germinating or growing seedling (deHullu & Gimingham, 1984; French *et al.*, 1997). At the same time, the extensive, woody root system of these shrubs prevents root expansion (Mallik, 1995), chemically inhibits root growth and mycorrhization (Jalal & Read, 1983a 1983b) and competitively reduces the available supply of mineral nutrients (Leake, 1992). *C. vulgaris* as well as other ericaceous shrubs are extremely effective at acquiring mineral and organic nutrients because of their ericoid mycorrhizas which can enhance the competitiveness of ericaceous roots by extracting organic nitrogen from chitin, lignin and protein sources (Stribley & Read, 1980; Bajwa & Read, 1985; Leake, 1992). This explains why tree seedlings

growing in the vicinity of *C. vulgaris* are often subjected to growth stagnation otherwise known as "heather check".

In this study of spatial and temporal patterns of regeneration, emphasis has been placed on the role of shade tolerance at the seedling/sapling stage. This involved investigating the effects of different levels of irradiance and *C. vulgaris* on the growth and abundance of *S. aucuparia* seedlings and saplings.

The following questions were asked:

- i) How is natural regeneration of *S. aucuparia* spatially distributed at the woodland scale?
- ii) Are there differences in abundance, size, age and growth of *S. aucuparia* between gap and shade habitat types? Does the growth of seedlings differ over time and between sites? How can these results be interpreted in terms of shade tolerance?
- iii) What role does *C. vulgaris* play in the establishment of seedlings? Are the growth or number of seedlings negatively affected by the abundance of *C. vulgaris*? Is there any evidence of an interaction between irradiance and *C. vulgaris* treatments?

6.2 Methods

The study was carried out as part of a collaborative project with a geography Honours student (Wilkins, 2002). The project involved two studies with the same broad aims but with slightly different objectives carried out within the same experimental plots. Raw data from the Wilkins study that were complementary to this study have been analysed here and acknowledgement to fieldwork made throughout the text.

6.2.1 Study site

The study was carried out in a 50 ha enclosure on the upper slopes of Coille Ruigh na Cuileige, a ridge above Loch Beinn a Mheadhein in Glen Affric at an elevation of 250-400 m. The enclosure was set up in 1990 to aid forest restoration by the exclusion of deer with funding provided by the Forestry Commission (FC), Scottish Natural Heritage (SNH) and Trees for Life (TFL), an NGO which currently monitors the site. Within the enclosure, there are areas of pine-dominated and birch-dominated woodland with a large area of open ground. This site focuses on the native pine woodland which has reached the over-mature stage with many old trees and canopy gaps created by fallen dead trees. The NVC classification for the site is

W18b *Pinus sylvestris* - *Hylocomium splendens* woodland of sub-community, *Vaccinium myrtillus* - *Vaccinium vitis-idaea* (Rodwell, 1991). Prolific natural regeneration of *Sorbus aucuparia* occurs under the pine woodland, not seen in so much abundance anywhere else in the Glen. *Pinus sylvestris*, *Betula pubescens* and *Ilex aquifolium* regeneration is also present but in much lower abundance.

6.2.2 Experimental design

The design involved six blocks with each block containing two woodland stand treatments: gap (open) and shade (old-growth). Ten replicate seedlings were selected within each treatment (10 reps x 2 treatments x 6 blocks = 120 individuals).

The fence lines of the enclosure were treated as axes on a grid drawn onto an enlarged map of the enclosure. Pairs of random numbers were generated on a calculator and used as co-ordinates to establish a starting point for each block. Criteria for each block included the presence of a gap approximately 10 m in width and a shade habitat around an old-growth *Pinus sylvestris* tree within a 15 m x 25 m area. If these criteria were not met, another set of random numbers were chosen. A 5.6 m radial plot (0.01 ha) was located in a representative site near the centre of each gap and around the trunk of an old-growth *P. sylvestris* tree representing the shade treatment. Within each radial plot, all *S. aucuparia* individuals were counted and given numbered tags. A calculator was used to generate 10 random numbers for each plot, to select seedlings to be used in the trial. Before each randomly selected individual was tagged, its age was estimated by counting winter bud scars on the main stem. Only seedlings/saplings equal to or greater than 10 years old (according to winter bud scars) were tagged for sampling. This was done to ensure an adequate size for ring core analysis and adequate time series for exploration.

The second study involved randomly tagging 10 seedlings of all ages in each of the radial plots (Wilkins, 2002). A comparison of these two data sets enabled the potential bias from choosing older seedling stock for ring core analysis to be analysed.

6.2.3 Spatial distribution patterns

Spatial distribution patterns were analysed by reviewing results from a mapping exercise which was done within three of the six blocks (Wilkins, 2002). Mapping involved dividing up each block into 1 m² grid squares with string and bamboo canes. Within each square, tree seedlings (< 1.3 m) were counted and the total noted down for each species. The co-ordinates of individuals greater than 1.3 m high were

recorded separately as saplings. Crown dimensions of mature trees were obtained by measuring the distance from the centre of each trunk to the edge of the canopy in four directions (N,E,S,W). The maps were re-drawn by the author using a business diagram software program (Visio Standard 5.0c). A habitat preference index (Duncan, 1983; Aspinall, 1994) was used to analyse seedling preferences for gap or shade (crown projection areas) using equation 6.1.

$$P_i = \log_{10}(1 + ((U_i/p) / (H_i/A))) \quad \text{Equation 6.1}$$

P_i = Habitat preference index

U_i / p = Habitat usage

H_i / A = Habitat occurrence

U_i = Number of seedlings (of one species) in habitat (i)

p = Total number of seedlings (of one species)

H_i = Area of habitat class (i) within study area (m²)

A = Total area of study area (m²)

A totally random distribution of target species would yield an expected Preference Index of 0.301, which is used as a minimum threshold for defining preferred habitat.

6.2.4 Site measurements

Slope (steepest section) and aspect measurements were taken at each block facing downhill towards the loch using a clinometer and compass. Light measurements were taken above each seedling using a portable Photosynthetic Active Radiation (PAR) quantum sensor and meter (Skye Instruments Ltd., Wales) between 11:00 and 14:00 hrs on overcast uniform sky days to reduce variability. Each PAR reading was accompanied straight away by a reading in an adjacent open area. This enabled light measurements to be expressed as a percentage of PAR relative to the open (PAR%). A 0.5 m x 0.5 m quadrat was placed over each seedling to estimate the percentage cover of surrounding *C. vulgaris*.

Abundance data was collected in the second study (Wilkins, 2002). This involved recording the total number of *S. aucuparia* seedlings in 1 m x 1 m quadrats placed over all tagged seedlings representative of all ages. The percentage cover of *C. vulgaris* was also estimated in each quadrat.

6.2.5 Seedling measurements

In September 2001, stem height was measured for each tagged individual in the field using a metre rule. Then the seedlings were harvested at the root collar. If the root collar was unclear, the cut was made at the lowest point, segregating stem from root. The length of the leader shoot on the main stem was measured to obtain an estimate of height increment for 2001. A basal diameter measurement was also made for each stem using digital callipers (± 0.01 mm). Seedlings were then air-dried in preparation for counting and measuring widths of annual rings. A microtome and microscope with an eye-piece graticule was used for this process. Samples were taken at the root collar or just above the last adventitious root on the main stem. Before a cross-section of the stem was cut by the microtome, the sample surface was painted with a thin layer of distilled water to ensure a clear thin (< 0.2 mm) even slice. On each cross-section, two measurements of width were taken for each ring, going back at least 10 years in time. The first measurement was taken on the widest side, followed by a second measurement at right-angles to the first. Care was taken to avoid sections with damaged rings or ones subjected to mechanical restriction that can hide or convolute outer rings.

Unfortunately, stems with RCD of less than 5 mm, were too small to distinguish rings so they had to be discarded. Before the two measurements for each ring were averaged, both ring widths were plotted against time to check they matched.

6.2.6 Statistical analysis

Maps of blocks were drawn up in ArcView GIS (version 3.2) for statistical analysis of spatial distribution patterns (Wilkins, 2002). This involved quadrat analysis as described by Lee and Wong (2001) to test if patterns differ significantly from a random Poisson distribution (Kolmogorov-Smirnov test).

ANOVA was used to analyse block and treatment effects (Genstat, version 6.1) taking into account *C. vulgaris* as a co-variant. Arcsine of square roots of proportions were taken, growth parameters were \log_e transformed, and counts were square-rooted for data to comply with test assumptions. The interaction between percentage cover of *C. vulgaris* and light was tested by randomly selecting 16 quadrats in four treatment combinations of low (0-44%) and high (45%-100%) cover of *C. vulgaris* and low light (shade) and high light (gap). This enabled a two way ANOVA to be run on variables.

Analysis of ring cores involved logarithmically transforming ring widths.

Correlation co-efficients were used to compare time series (Schweingruber, 1988).

6.3 Results

6.3.1 Mapping

A visual examination of the spatial distribution of *S. aucuparia* seedlings revealed a clustered pattern with a general trend of greater seedling abundance within crown projection areas (Figure 6.1 - 6.3). Quadrat analysis performed on all three maps showed that patterns were significantly different from a random Poisson distribution (Kolmogorov-Smirnov: $D = 0.31, 0.36, 0.29$ respectively, $D_{crit} = 0.07$).

S. aucuparia natural regeneration dominated the stands with a total of 1195 seedlings including 37 saplings (> 1.3 m) found in the three sites. Only 19 *B. pubescens* and 19 *P. sylvestris* seedlings were found in the same area. Calculation of habitat preference indices for individual species (Equation 6.1), suggest that *S. aucuparia*, *B. pubescens* and *P. sylvestris* seedlings are more abundant in crown projection areas (shade) whilst *S. aucuparia* saplings are more abundant in gaps (Table 6.1).

Table 6.1. Habitat preference index for seedling/saplings for shade and gap habitats. Total habitat area included all three blocks (1125m²). A preference index above 0.301 indicates preference for a specific habitat. A value below 0.301 indicates a random distribution.

Species	Habitat Preference Index	
	Shade	Gap
<i>S. aucuparia</i> seedlings	0.356	0.252
<i>S. aucuparia</i> saplings	0.238	0.346
<i>B. pubescens</i> seedlings	0.425	0.168
<i>P. sylvestris</i> seedlings	0.384	0.221

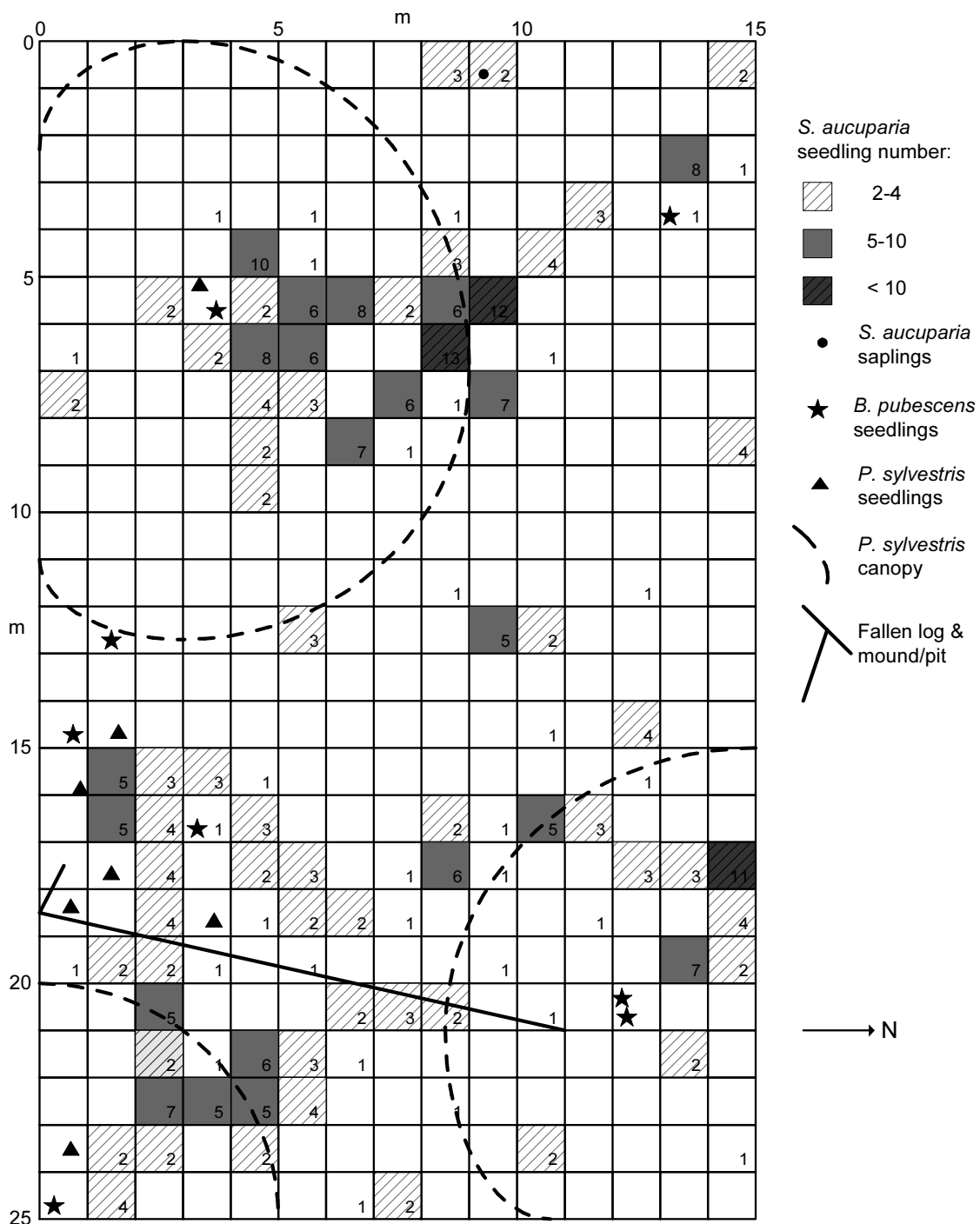


Figure 6.1. Spatial distribution patterns of natural regeneration in Block 1 (15 m x 25 m) of old growth *P.sylvestris* woodland. Raw data provided by Emily Wilkins.

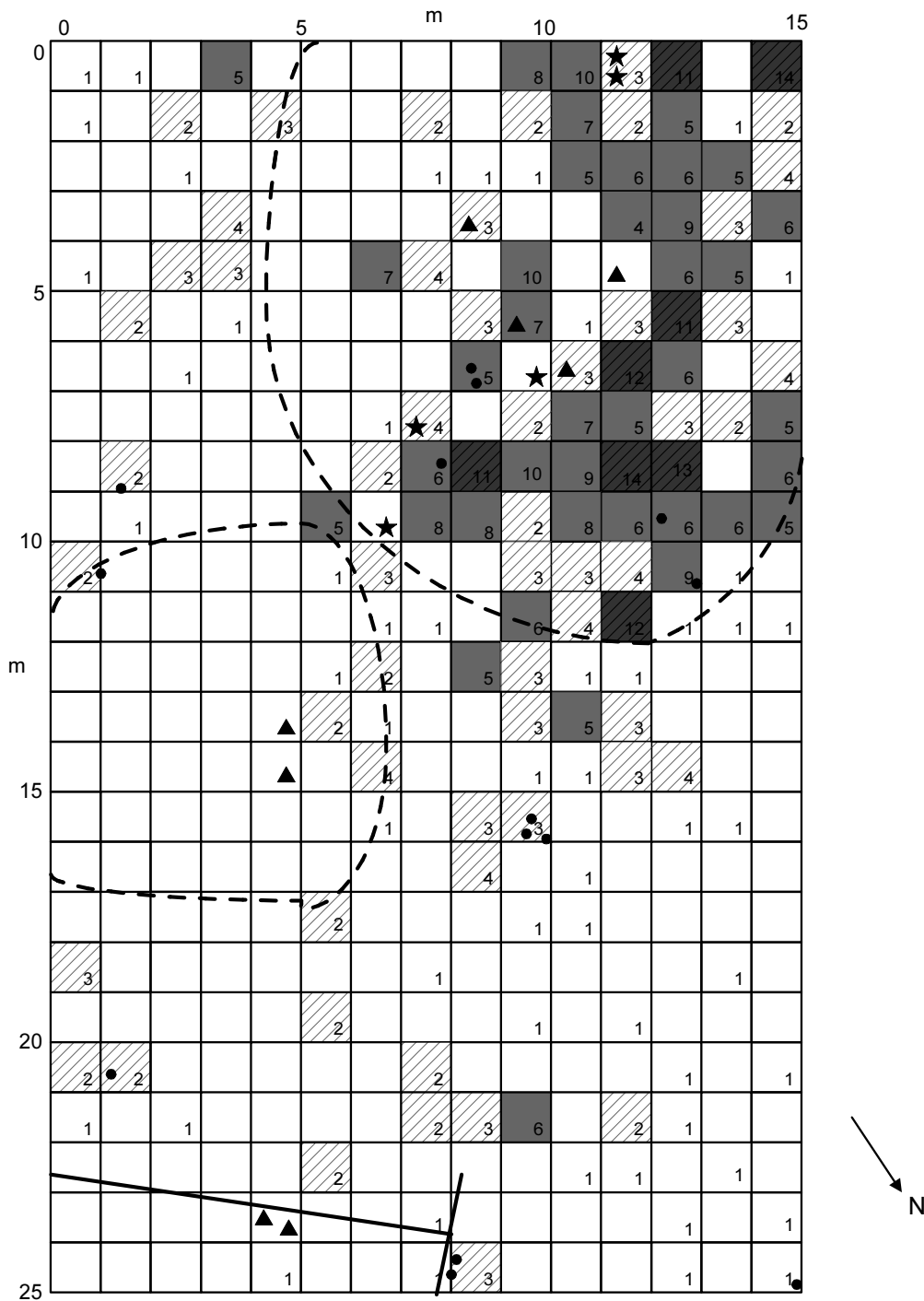


Figure 6.2. Spatial distribution patterns of natural regeneration in Block 4 (15 x 25 m) of old growth *P. sylvestris* woodland. Raw data provided by Emily Wilkins.

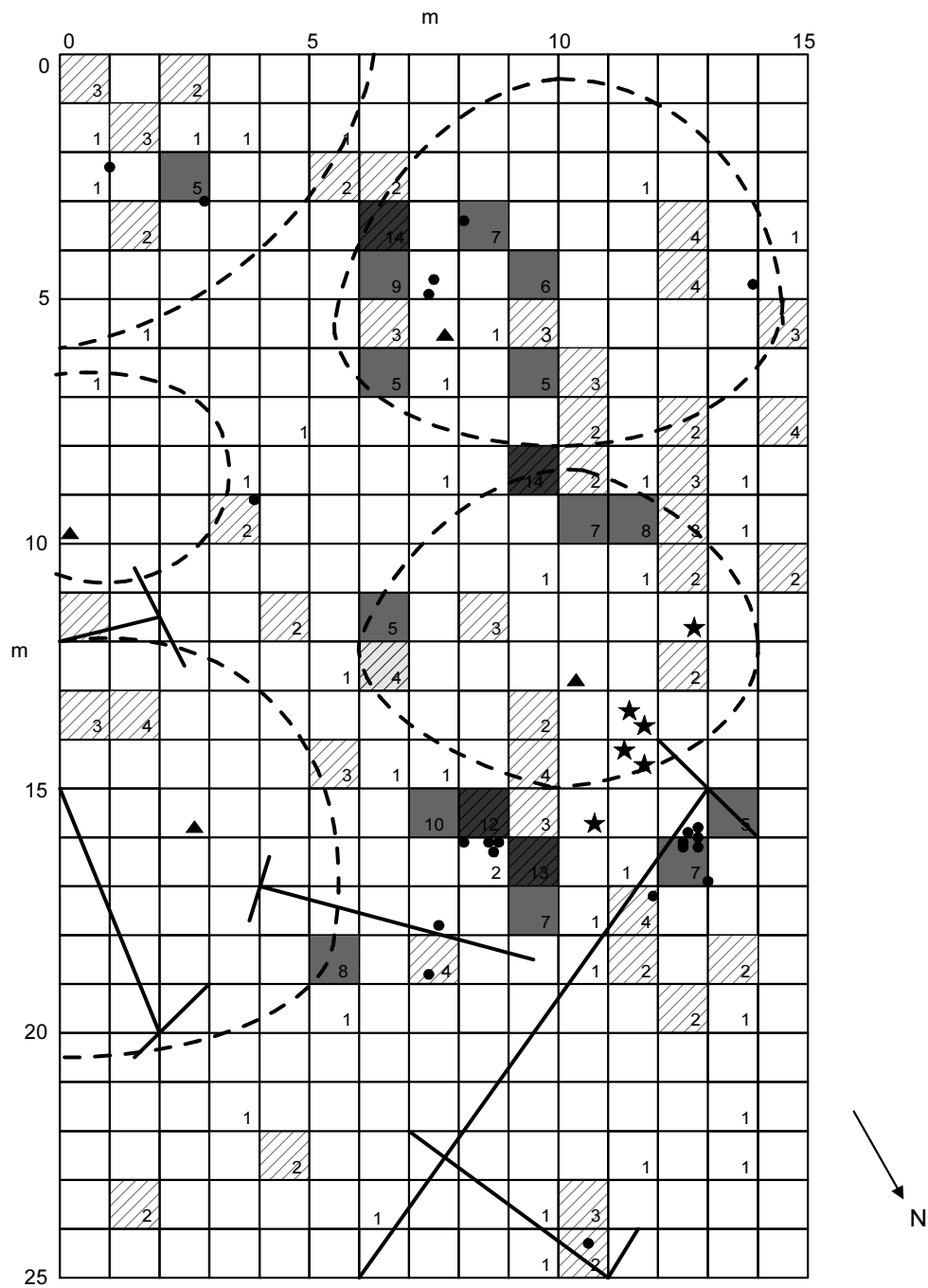


Figure 6.3. Spatial distribution patterns of natural regeneration in Block 5 (15 x 25 m) of old growth *P. sylvestris* woodland. Raw data provided by Emily Wilkins.

6.3.2 Aspect, altitude and slope

Most sites were south to south east facing with slope becoming progressively gentler towards the bottom of the enclosure which is furthest downhill (Table 6.2)

Table 6.2. Altitude, slope and aspect of each block.

Block	Altitude (m)	Slope ^o	Aspect ^o
1	410	24	190 SW
2	350	24	130 SE
3	350	27	150 SE
4	350	15	90 E
5	310	11	160 SE
6	400	19	90 E

6.3.3 Light

ANOVA on transformed proportions of PAR (arcsine square-root) did not reveal a significant block effect ($P > 0.05$) but treatment effects were significant ($F = 228.6$; d.f. = 1, 113; $P < 0.001$). Mean PAR% was lower under the shade (Table 6.3) but minimum and maximum readings revealed an overlap in light regime between the gap and shade treatments.

Table 6.3. Absolute and transformed means of percentage of PAR (taken at the apex of each seedling) and percentage cover of *C. vulgaris* in each quadrat (surrounding each seedling) within in shade and gap treatments with minimum and maximum values (\pm estimated standard errors of means pooled for both treatments). 1. Measurements of seedlings equal to or greater than 10 years. 2. Measurements of seedlings of all ages (raw data provided by Emily Wilkins).

Parameter	Treatment	Arcsine SQRT Mean	Absolute Mean (%)	Min%	Max%
1. PAR%	Shade	0.744 (± 0.024)	45.9	22.2	86.6
	Gap	1.259	86.7	48.9	100.0
1. <i>C. vulgaris</i> %	Shade	0.620 (± 0.050)	40.1	0	100
	Gap	0.725	48.1	0	96
2. <i>C. vulgaris</i> %	Shade	0.441 (± 0.048)	26.6	0	90
	Gap	0.659	41.7	0	90

6.3.4 Understorey vegetation

There was no significant difference in arcsine square-rooted proportions of *C. vulgaris* between gap and shade treatments in this study ($P > 0.05$). However, when quadrats were placed over seedlings of all ages (not just restricted to the seedlings equal to or greater than 10 years used for ring core analysis), there was a significant difference in *C. vulgaris* between treatment (ANOVA: $F = 10.34$; d.f. = 1,

113; $P < 0.01$). Differences between block were nearly significant at the 0.05 level (ANOVA: $F = 2.08$; d.f. = 1, 113; $P = 0.072$).

6.3.5 Seedling abundance

A significant difference in the number of seedlings (square-root transformed) was found between block (ANOVA: $F = 3.15$; d.f. = 5, 113; $P < 0.05$) and treatment (ANOVA: $F = 21.29$; d.f. = 1, 113; $P < 0.001$) with a greater abundance of seedlings in the shade (Table 6.4).

6.3.6 Seedling size and growth measurements

ANOVA tests were initially carried out including percentage cover of *C. vulgaris* as a co-variate. No significant effect of the co-variate was found ($P > 0.05$) for any growth parameters so further tests were run without taking it into consideration.

Significant differences in \log_e stem height were found between block (ANOVA: $F = 10.97$; d.f. = 5, 110(3)¹; $P < 0.001$) and treatment (ANOVA: $F = 6.82$; d.f. = 1, 110(3); $P < 0.05$) with taller seedlings found in the gaps (Table 6.4). No difference in \log_e basal diameter was found between block or treatment ($P > 0.05$). However a significant difference in \log_e transformed diameter:height ratio was found (ANOVA: $F = 10.21$; d.f. = 1, 108(5); $P < 0.01$). These seedlings were not only taller in the gaps but thinner also. Furthermore, stem height increment for 2001 was greater in the gaps than in the shade (ANOVA: $F = 6.84$; d.f. = 1, 110(3); $P < 0.05$). There was no significant block effect for the latter two variables ($P > 0.05$).

It was interesting to note that when stem height of seedlings of all ages was measured a much larger difference was found between treatments (ANOVA: $F = 17.34$; d.f. = 1, 113; $P < 0.001$). A significant block effect was also found (ANOVA: $F = 5.95$; d.f. = 5, 113; $P < 0.001$).

¹ Numbers in brackets refer to missing values

Table 6.4. Number, size and growth increment of seedlings in gap and shade treatments. Absolute and transformed means of stem height (mm), basal diameter (mm), diameter:height ratio, stem increment (2001) of seedlings in gap and shade treatments are shown (\pm estimated standard errors of means pooled for both treatments). 1. Measurements of seedlings equal to or greater than 10 years. 2. Measurements of seedlings of all ages (raw data provided by Wilkins, 2002).

Seedling parameter	Treatment	Transformed mean	Absolute mean
1. Stem height	Shade	6.625 (\pm 0.048)	816
	Gap	6.771	929
1. Basal diameter	Shade	1.904 (\pm 0.030)	7.23
	Gap	1.916	7.27
1. Diameter:height ratio	Shade	-4.701 (\pm 0.032)	0.0092
	Gap	-4.842	0.0081
1. Stem height increment	Shade	1.537 (\pm 0.082)	65.6
	Gap	1.917	85.1
2. Stem height	Shade	6.318 (\pm 0.079)	621
	Gap	6.651	865
2. Number of seedlings	Shade	2.670 (\pm 0.089)	7.8
	Gap	2.092	4.8

6.3.7 Interactions between *C. vulgaris* and light

No interaction effect of light and *C. vulgaris*% (arcsine square-rooted proportional cover of *C. vulgaris*) was found on the squared rooted number of *S. aucuparia* seedlings ($p > 0.05$) (Figure 6.4). However there was a significant main effect of light (ANOVA: $F = 7.55$; 1, 60; $P < 0.01$) with more seedlings found in low light (shade) rather than high light (gap) (Figure 6.4). A greater number of seedlings were found under a low percentage cover of *C. vulgaris* (0-44%) than under high cover but the main effect of *C. vulgaris* was not significant at the 0.05 level ((ANOVA: $F = 2.86$; d.f. = 1, 60; $P = 0.096$).

No interaction effect of light and *C. vulgaris*% was found on the \log_e stem height of *S. aucuparia* seedlings of all ages ($p > 0.05$). There was a significant difference in \log_e stem height between low and high light (ANOVA: $F = 10.13$; d.f. = 1, 60; $P < 0.01$) but no difference between low and high levels of *C. vulgaris* cover ($P > 0.05$). Seedlings were found to be taller in high light than low light (Figure 6.4).

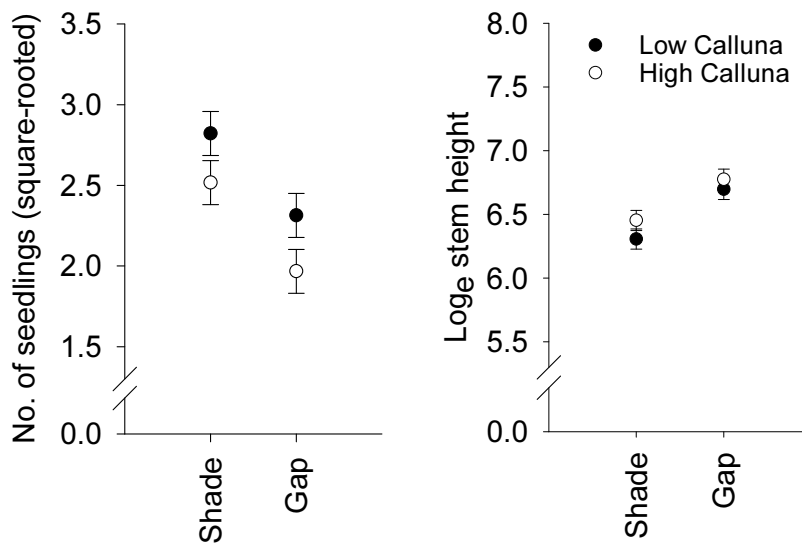


Figure 6.4 Mean number and mean stem height of *S. aucuparia* seedlings of all ages under low (shade) and high (gap) light and low (0-44%) and high (45%-100%) percentage cover of *Calluna vulgaris*. Standard error bars shown (n = 16).

6.3.8 Age of seedlings

Based on winter bud scar counts, the mean age of shade seedlings was estimated to be 9.9 years of age and for gap seedlings, 10.2 years of age. However counting annual rings led to a mean age of 13.6 for the shade seedlings and 14.5 for gap seedlings indicating that most seedlings were present before the fence was erected. The under-estimation of age by counting winter bud scars is probably a result of missing scars due to browsing in the initial years before the enclosure was erected. Despite this, both estimations showed little difference in seedling age between shade and gap habitats. No significant correlations were found between the number of annual rings and light (PAR%) and stem height ($P > 0.05$).

6.3.9 Temporal growth patterns

Plots of both ring width measurements for each individual cross-section over the 10 year period (1991-2001) revealed good matches for half of the samples for each treatment (5 seedlings). An example of a 'good' match is illustrated in Figure 6.5a. 'Acceptable matches between seedlings were achieved when the two ring width measurements were averaged for each year (for just the seedlings with 'good'

matches within each cross-section). An example of an 'acceptable' match is illustrated in Figure 6.5b. Mean logged ring widths with standard errors over time for both treatments in Block 2, 4, 5 and 6 have been illustrated in Figure 6.6. Unfortunately Block 1 could not be analysed, as the diameters of seedlings were too small and ring width matches for Block 3 were poor. Visually, mean temporal growth patterns of gap and shade treatments within blocks look similar (Figure 6.6). Correlations revealed that growth patterns in the two treatments in Block 2 were correlated with each other ($r = 0.52$) but were weakly or negatively correlated with growth patterns in all other Blocks. In Blocks 4, 5 and 6 the correlations between treatments within a block were not noticeably higher than the correlations between blocks.

Mean ring width tends to be greater for seedlings in the gaps compared to shade seedlings but in some years, the opposite occurs. However, the overlap of standard errors between most treatment means for individual years, does not suggest significant differences.

Although relationships between temporal growth patterns and climatic data are weak (Table 6.5), some trends are present (Figure 6.6). All seedlings in the four blocks follow a downward decline in ring width from 1999-2001, which parallels both a decline in temperature and precipitation at the Drumnadrochit weather station.

Table 6.5 Correlation co-efficients (r) between pairs of temporal growth patterns (mean logged ring width) and seasonal mean daily rainfall (mm) and mean maximum temperature ($^{\circ}\text{C}$) at Drumnadrochit. B = Block, S = Shade, G = Gap. Significance of tests not shown due to non-independence of data points.

	B2 S	B4 S	B5 S	B6 S	B2 G	B4 Gap	B5 Gap	B6 Gap	Rainfall
B4 S	0.12	-	-	-	-	-	-	-	-
B5 S	0.09	0.63	-	-	-	-	-	-	-
B6 S	0.10	0.86	0.80	-	-	-	-	-	-
B2 G	0.52	0.79	0.74	0.76	-	-	-	-	-
B4 G	-0.30	0.80	0.80	0.74	0.62	-	-	-	-
B5 G	0.15	0.75	0.64	0.83	0.82	0.68	-	-	-
B6 G	-0.40	0.65	0.21	0.51	0.30	0.68	0.61	-	-
Rainfall	0.68	0.09	0.44	0.20	0.57	-0.01	0.30	-0.52	-
Temp.	0.24	0.26	0.32	0.49	0.34	0.11	0.37	0.17	0.18

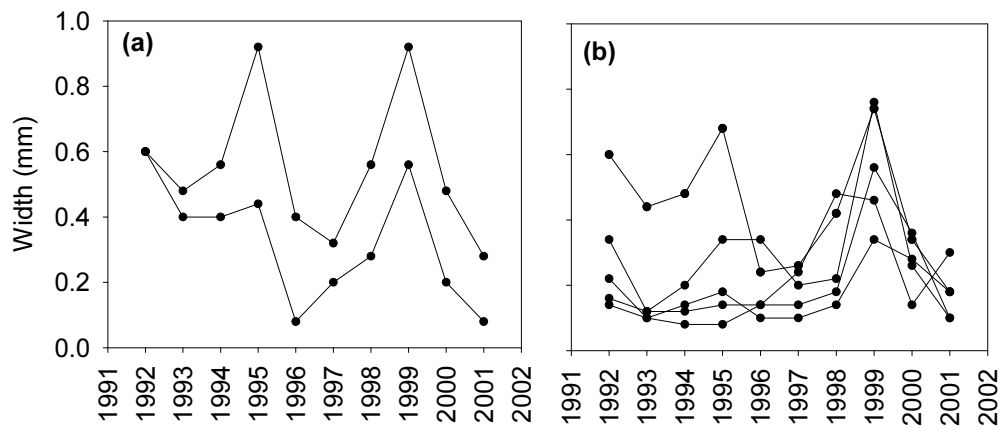


Figure 6.5. Ring widths of *S. aucuparia* seedlings from Block 2 (a) example of the two ring width measurements taken at right angles to each other on one cross-section of one seedling sample; (b) mean ring widths of 5 seedlings from the shade treatment (average of two width measurements for each seedling).

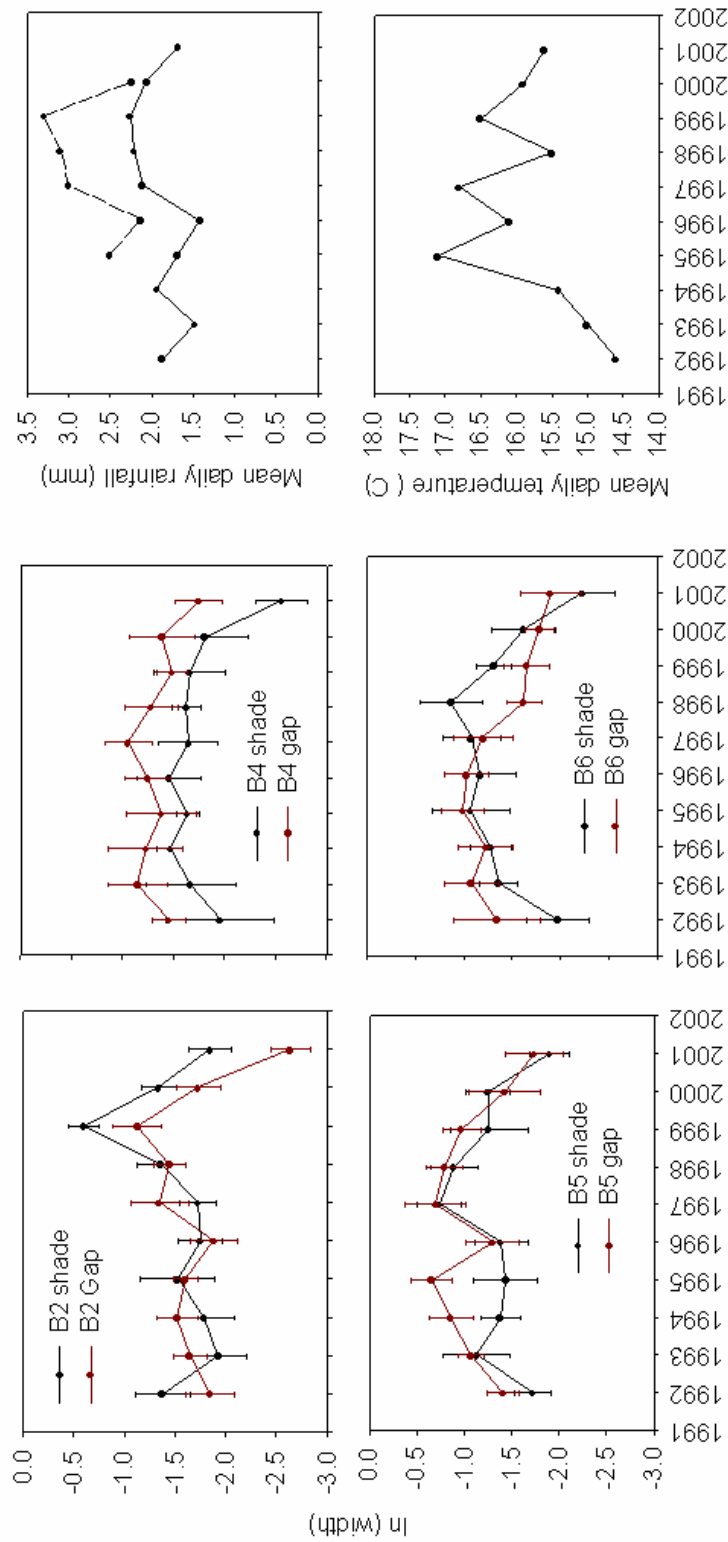


Figure 6.6 Mean ring widths (Log_e) of *S. aucuparia* seedlings over a 10 year period (1992-2001) in both shade and gap treatments in four sites (Block 2, 4, 5, 6). Error bars are standard errors of means (n = 5). Climatic data includes mean daily rainfall and mean daily maximum temperature ($^{\circ}\text{C}$) for the growing season (April - September) for the same 10 year period (— Drumadrochit meteorological station, --- Affric Lodge 2 station, BADC database)

6.4 Discussion

How is natural regeneration of *S. aucuparia* spatially distributed at the woodland scale?

The spatial distribution pattern of *S. aucuparia* seedlings in old growth Caledonian pinewood in Glen Affric was found to be clustered rather than random conforming with results from a former study (Ogilvy, 1999) (see Table 6.6). Clustering patterns may be related to dispersal by birds. On average 2-3 seeds are found in each pome and birds can eat many pomes in one sitting. If these seeds are defecated together, it is reasonable to suggest they may germinate together forming a cluster of seedlings. Some may argue that the clustered pattern may just be a reflection of polycormic growth forms which are particularly prevalent on a site previously subjected to grazing (Hofgaard, 1993) and at higher altitude where viable seeds are seldom produced (Barclay & Crawford, 1984; Kullman, 1986). Multiple stems were not visually obvious for individuals growing in sparse understorey under the mature canopy trees. However in dense understorey sites, a more thorough examination of stem bases hidden deep down in layers of moss and ericaceous shrub would be needed to clarify this.

Table 6.6. Spatial distribution patterns of *S. aucuparia* seedlings and saplings found in random plots (10 m x 10 m) within shade and gap habitats within the enclosure. Spatial distribution can be distinguished as uniform ($R \cong 2.15$), random ($R \cong 1$) and clustered ($R \cong 0$) by using the Nearest Neighbour Index technique (Hammond & McCulleghs, 1979). Statistical significance of deviation from randomness is given by the Z statistic where $P < 0.001$ if $Z \geq 3.5$ (Data from Ogilvy, 1999).

Plot number	Shade			Gap		
	Rowan no.	R	Z	Rowan no.	R	Z
1	34	0.36	7.10*	26	0.30	6.73*
2	27	0.44	5.46*	19	0.26	2.54
3	4	0.03	3.70*	33	0.53	5.18*
4	25	0.33	6.41*	31	0.68	3.44
5	51	0.34	8.98*	7	0.36	3.24
6	26	0.64	3.68*	24	0.34	6.06*
Mean	27.8	0.36	5.88*	23.3	0.41	4.64*

Are there differences in abundance, size, age and growth of *S. aucuparia* between gap and shade habitat types?

The abundance of *S. aucuparia* seedlings and saplings far exceeded any other type of natural regeneration. Visual examination of maps perhaps does not provide satisfactory evidence to conclude that more seedlings are found under tree canopies. However further analysis provided much stronger evidence to support preliminary

observations: i) *S. aucuparia* seedlings had a preference index value indicating “preference” for the shade habitat rather than a random distribution; ii) a significantly greater number of seedlings were found within quadrats in plots around old-growth trees rather than within gaps; and iii) the random selection of quadrats within two levels of light and two levels of percentage cover of *C. vulgaris* revealed a significantly greater abundance of seedlings in low light (i.e. under canopy shade).

The prolific abundance of *S. aucuparia* on Coille Ruigh na Cuileige can be explained by a number of factors specific to its regeneration ecology such as seed dispersal, physiology and browsing tolerance. *S. aucuparia* seeds are mainly distributed by birds which can fly long distances (kilometres) between eating the berries and dropping the seeds. Natural regeneration is not so reliant on the close vicinity of seed-bearing mother trees like *P. sylvestris* and *B. pubescens* whose seed is dispersed by the wind. Its seed is relatively heavy, giving it a better chance of penetrating through ground vegetation and litter for germination (Mountford & Peterken, 2001). Species with lighter seeds such as *P. sylvestris* and *B. pubescens* tend to require bare mineral or humic soils lacking dense vegetation for successful germination and establishment (McNeill, 1955; Kinnaird, 1974; Kuuluvainen & Juutunen, 1998).

S. aucuparia has been classified as a stress-tolerant competitor (Grime *et al.*, 1988). It is an undemanding species with a broader tolerance of different substrates for growth than coniferous species (Hofgaard, 1993). Its ability to grow in exposed conditions and at high altitude can be attributed in part to high tolerance of winter bud desiccation (Barclay & Crawford, 1982) and root desiccation (Dutton & Bradshaw, 1982) with much hardiness to root frost (McEvoy & McKay, 1997). Furthermore, *S. aucuparia* is known to recover rapidly from stunted sapling banks after cessation of repeated grazing whereas *P. sylvestris* seedlings would probably be killed (Miller *et al.*, 1998). Its high tolerance of damage (Miller *et al.*, 1982) can be explained by its ability to form wound periderm quickly, which protects compromised tissues from desiccation and pathogen invasion (Woodward & Pocock, 1996). Seedlings that were aged were found to be older than the exclosure which suggests that a fair proportion of the population (approx. 75%) were a result of recovery from browsing rather than new recruitment.

Other studies have found a greater abundance of *S. aucuparia* under canopy trees than in the open (Kinnaird, 1974; Vanha-Majamaa *et al.*, 1996). It has been argued that this pattern is a result of the trees providing birds with places to sit and defecate the seeds rather than a reflection of shade tolerance. However, if seeds are dispersed

under canopy trees, favourable microsites for germination and initial establishment would still be required as well as a level of shade tolerance for survival (see later).

Results from the growth ring analysis revealed a mean age of 14 years for both shade and gap habitats but it is possible that this result may have been biased by methodology. The more accurate measure of age from ring counts was made for seedlings that were equal to or greater than 10 years of age according to winter bud scar counts. However from the age range of these seedlings (9-22 years), no relationships were found between age and light (PAR%) nor stem height. Pukkala *et al.* (1993) also found that seedlings in their pinewood study were of a similar age throughout the site but mean height was lower in the shade due to suppression. Indeed, seedlings were found to have a greater mean stem height and stem height increment (2001) in gaps with shorter seedlings found in the shade. The above results suggest that *S. aucuparia* as a seedling growing under old growth *P. sylvestris* trees is relatively shade tolerant and can remain so for many main years (+ 14 years) but higher light levels are required for release.

The response of *S. aucuparia* to higher irradiance was expressed predominately in height growth rather than in basal diameter growth leading to long thin stems in the open (lower diameter: height ratio). Seedlings in the shade tended to be more robust in form maintaining steady ring widths over time (Figure 6.6) which were not different from those in the gaps. One would perhaps expect wide rings in the open due to enhanced irradiance levels. It was interesting to note that during years where the mean growing season maximum temperature and daily rainfall was low (ie: 2001, 2002), ring widths for all seedlings declined. Furthermore, the mean ring widths of seedlings in gaps in Block 2 and Block 6 dipped below widths in the shade. It is very possible that the reduction in growth rate is because these seedlings are in much more exposed drier positions in these open sites on the ridge. Linnenbrink *et al.*, (1992) found that plasmatic drought tolerance of leaves of *S. aucuparia* was not exceptionally high leading to the conclusion that they are not well adapted to water-stressed conditions where competitive vigour can be reduced. It was noticed during the growing seasons of 1999 to 2001, that most *S. aucuparia* seedlings and saplings were subjected to a high level of insect damage from leaf miners (*Stigmella*) and secondary fungal attack: associated with weakened form which may be due to exposure to harsher climatic conditions. A comparison in performance in warmer, wetter years would be needed to clarify this point.

It could be argued that the lack of difference between ring widths is a reflection of sampling technique. It was discovered that choosing seedlings that were slightly older (equal to or greater than ten years old according to winter bud counts) for ring

core analysis, had an effect on results. Significant differences between mean stem heights of seedlings and percentage cover of *C. vulgaris* in shade and gap treatments were much greater when sampling seedlings of all ages (Wilkins, 2002) rather than slightly older seedlings. A possible explanation for this is that larger seedlings were (unintentionally) tagged for sampling because it was easier to see and count their winter-buds. These individuals were more likely to have been located closer to the edges of the canopy where irradiance levels are higher along with *C. vulgaris* cover².

The seedlings used for ring core analysis may thus be more representative of a semi-shade environment. A comparison between these seedlings in semi-shade and individuals in the centre of gaps in full daylight is still valuable. Perhaps, the semi-shade environment on the edges of crowns is more suitable for the regeneration of *S. aucuparia* regeneration as height growth is permitted but with a favourable diameter to height ratio producing a more robust form. Furthermore, seedlings are protected from the elements during drier periods unlike their counterparts in the centre of woodland gaps.

Fits between ring widths and climatic data would probably have been better if temperature and precipitation data had been logged on site. Both sets of data were only available from Drumnadrochit, 10 km away from the ridge in a less mountainous environment. The comparison of mean seasonal daily rainfall (mm) between Glen Affric and Drumnadrochit highlights the difference, with Glen Affric receiving more rainfall (Figure 6.6). Normally a good relationship is found between photosynthesis or tree growth and precipitation and temperature as well as other environmental factors (Fritts 1976; in Schweingruber, 1988).

There was much variation between seedling height and number of seedlings between sites indicated by significant block effects in the ANOVA results. This variation is also illustrated in the patterns of growth over time (Figure 6.6). There is variability in the strength of relationships between stand treatments between blocks but also within blocks. It is likely that correlation co-efficients are directly related to site variability at both macro and micro-environmental scales. For example, similarities in temporal growth patterns between gap and shade habitats in Blocks 2 and 4 perhaps indicate that seedlings are growing under similar environmental conditions (apart from irradiance). Larger differences between treatments in Blocks 5 and 6 suggest that environment factors specific to individual sites even within a relatively small area have a very important influence on patterns of growth.

² A greater abundance of *C. vulgaris* is normally found in higher light environments because of its light demanding nature, not tolerating less than 40% light (Gimingham 1960; Ellenberg, 1988).

What role does *C. vulgaris* play in the establishment of seedlings?

Gray & Spies (1997) comment that microsites at the scale of just a few square centimetres can determine the germination and growth of individual plants. The abundance of *C. vulgaris*, as a potentially important microsite factor limiting regeneration, was investigated in this study. The lower percentage cover of *C. vulgaris* did not have a greater effect on the abundance or growth of *S. aucuparia* seedlings in low light (shade) compared with high light (gap) indicated by the insignificant light-*Calluna* interaction (Figure 6.4). However the abundance of *S. aucuparia* seedlings was higher where there was a lower level of *C. vulgaris* cover (0-44%) in both high and low light. It is possible that germination is hindered by the secretion of allelopathetic chemicals (as in *V. myrtillus*, Jaderlund *et al.*, 1996) and so *C. vulgaris* is a less favourable substrate for regeneration. Once established though, seedling growth seems little affected by the abundance of *C. vulgaris* with no significant difference found in seedling stem height between *Calluna* treatments. Other studies have also found tree seedlings frequently associated with *Calluna* dominated slopes (McNeill, 1955; Kinnaird, 1974). There is a theory that it is the drainage conditions associated with *Calluna* that have a more influential effect on seedling establishment. Sub-alpine surveys in the Cairngorms have observed higher densities of *P. sylvestris* seedlings in areas characterised by dry *Calluna* or lichen rich *Calluna* but lower densities on *Trichophorum-Calluna* bog and wet heath (mainly *Calluna-Eriophorum*) (Pears, 1988; French *et al.*, 1997). The old-growth pinewood in this study is classified as NVC type W18b, which is the drier sub-community of W18. The drainage conditions on the ridge may thus account for the more abundant natural regeneration of *S. aucuparia* on *Calluna* dominated slopes.

A more detailed and thorough examination of nutrient deficiency in seedlings and their mycorrhizal associations is required to clarify the impact of allelopathy and other adverse effects of *C. vulgaris* and other ericaceous shrubs on *S. aucuparia* establishment. It is also acknowledged that the separation of treatments into gap and shade is an over-simplification which potentially masks more complex patterns of variation. Further research is thus required to unmask these sources.

6.5 Summary

The spatial distribution pattern of *S. aucuparia* natural regeneration within an old-growth *P. sylvestris* woodland was found to be clustered rather than random. A greater number of seedlings were found under the shade of mature trees. More saplings were found in gaps and seedlings were substantially taller than their shade

counterparts but did not differ in diameter or age. The maintenance of steady radial growth and survival up to 14 years in the shade suggests that *S. aucuparia* seedlings are relatively shade tolerant. It is suggested that a greater abundance of seedlings under tree canopies is a consequence of a combination of enhanced seed rain, less *C. vulgaris* and a tolerance of shade. Higher light levels are required for further height growth and development but results suggest that open exposed conditions can also limit seedling growth. Growth of individuals was very variable within and between sites highlighting the effects of microsite variability on growth.

