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Research paper

Long-term development of experimental mixtures of Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth.) in northern Britain

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Abstract - The Caledonian pinewoods of northern Scotland are a priority conservation habitat in Europe which are dominated by Scots pine (*Pinus sylvestris*), but varying proportions of a number of broadleaved species such as silver birch (*Betula pendula*) can occur in these forests. Better understanding of the dynamics of mixed Scots pine-birch stands would be helpful in informing current initiatives to restore and increase the area of the pinewood ecosystem. Some evidence is provided by two experiments established in the 1960s which compared plots of pure Scots pine and pure birch with two treatments where the two species were mixed in 3:1 and 1:1 ratios. Some fifty years later, Scots pine was the more vigorous of the two species in these experiments, being both taller and significantly larger in diameter. The highest basal area was generally found in the pure Scots pine plots and the values in the mixed plots tended to be intermediate between those of the two component species. Examination of the growth in the mixed plots showed a slight, but non-significant, tendency towards overyielding. This appeared to be due to Scots pine growth being better than predicted, while that of birch was slightly less than predicted. These results suggest that in these mixtures, which are composed of two light demanding species, the main mechanism driving long-term performance is inter species competition and there is little evidence of any complementary interaction. These results suggest that any strategy seeking to increase the long-term representation of broadleaves such as birch in the Caledonian pinewoods will need to create discrete blocks that are large enough to withstand the competitive pressures exerted by the pine.

Keywords - Mixtures, Pinus sylvestris, Betula pendula, competition

Introduction

There has been increasing interest in growing tree species in mixed stands for reasons such as adapting forests to climate change, providing greater biodiversity, and enhancing the visual attractiveness of forests (Quine et al. 2013). However, successful establishment and management of mixed species forests depends on understanding the characteristics of the component species (e.g. growth habit, shade tolerance) and the way in which their mutual interactions change over time (Pretzsch 2009, chapter 9). Paquette and Messier (2011) suggested that beneficial interactions between tree species may be more important in stressful environments such as the boreal forests while reviews of facilitation in wider plant communities have also highlighted the need for taking environmental gradients into account (Brooker et al. 2008). The complexity of these interactions suggests that, despite recent reports of the benefits of mixed stands for the provision of a range of ecosystem services including productivity (Felton et al. 2010, Zhang et al. 2012, Gamfeldt et al. 2013), it may be problematic to extrapolate potential performance of mixtures from one climatic region or site type to another.

Forests of the British Isles and adjoining regions of Atlantic Europe are mostly characterised by single species plantations of fast growing non-native conifers grown on relatively short rotations (Mason 2007, Mason and Perks 2011). Recent data (Forestry Commission 2003) suggest that the total area of mixed-species stands (defined as where no single species occupies more than 80 per cent of the stand) was only around 200,000 ha or about 8 per cent of the forest area of Great Britain. In the last decade there has been increasing recognition of the potential role of growing tree species in mixture as part of a strategy of adapting British forests to projected climate change (Read et al. 2009, p. 174-175). The UK Forestry Standard, which sets out the national basis for sustainable forest management, encourages forestry practices which promote greater species diversity such as fostering of mixed stands (Anon. 2011, p. 96). In addition, recent guidance in Wales and Scotland supports the wider use of a range of

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species mixtures (Anon. 2010, Grant et al. 2012). Nevertheless, the limited experience of the creation and management of mixtures in British forestry makes it difficult to be certain about the regions of the British Isles where mixtures may be most effective, the particular species combinations that should be deployed, and the interactions between management practice and mixture development over time.

One forest type where the role of mixtures has been discussed for several decades is the Caledonian pinewoods of northern Scotland, which are recognised by the European Union Habitats Directive as being of special conservation value (Mason et al. 2004). These forests are dominated by Scots pine (*Pinus sylvestris* L.) at all stages of stand development, but some stands can contain variable amounts of several broadleaved species including birches (*Betula pendula* and *B. pubescens*), aspen (*Populus tremula*) and rowan (*Sorbus aucuparia*) (Edwards and Mason 2006). In broad terms, these pinewoods can be divided into two categories: the remnants of genuinely native pinewoods amounting to about 17,800 ha and a more extensive area of Scots pine dominated plantations amounting to about 101,000 ha (Mason et al. 2004). The remnant pinewoods are managed primarily for biodiversity and landscape while the plantations are managed for a range of ecosystem services including timber production (of sawlogs and small roundwood) on a rotation of 70-100 years. However, the considerable age of many trees in the remnant pinewoods (Edwards and Mason, 2006) plus concerns over regeneration failure in these stands means that sensitive management of the plantations will be important for the long-term continuity of the pinewood ecosystem in northern Scotland. Given earlier studies showing beneficial effects of birch species on soil properties of acid heathland soils (Dimbleby 1952, Gardiner 1968, Miles 1981), it has been proposed that incorporating a proportion of birch into Scots pine plantation stands would improve soil and tree nutrition with consequent benefits for stand productivity, and possibly other ecosystem services. However, there is little published evidence that can be used to examine this proposition.

A study in south-eastern Norway compared productivity of nine paired plots of pure Scots pine with that found in mixtures of Scots pine and birch (Frivold and Frank 2002). Volume growth in the mixtures was less than that in pure stands, although the differences were not significant. Hynynen et al. (2011) investigated performance of mixed Scots pine and silver birch stands of mid rotation age on 14 sites in eastern Finland. Over a 19 year period, they found that volume increment decreased with increasing amounts of birch. However, an earlier report from Finland had suggested 10-14% increases in productivity from Scots pine/birch mixtures over the respective pure stands (Mielikäinen 1980). Models suggested that this increase appeared to diminish between 30 and 70 years of age with an optimum proportion of birch of no more than 20 per cent (Mielikäinen 1996). In an overview of the theory and performance of two species mixtures in Europe, Pretzsch (2005) also suggested that the performance of mixtures of light demanding species such as Scots pine and birch could be strongly affected by site conditions, noting an apparent loss of increment in birch in more oceanic conditions.

The only relevant British study described two experiments with Scots pine-birch mixtures where basal area declined with increasing proportion of birch (Malcolm and Mason 1999). The authors suggested that Scots pine appeared to be benefitting in mixture at the expense of birch. These results were obtained in 30-years-old stands that had only recently closed canopy while the studies by Frivold and Frank (2002) and Hynynen et al. (2011) also involved stands that were mostly under 50 years of age. Given that relative productivity of species can change with age (Pretzsch 2005), it would be dangerous to extrapolate long-term performance of two species mixtures from growth in the early stem exclusion phase (*sensu* Oliver and Larson 1996). In this paper, we report on the further development of Scots pine-silver birch mixtures in the two experiments previously examined by Malcolm and Mason (1999) when the trees were about 50 years of age, which is about two-thirds of normal rotation age for Scots pine in Britain (Mason et al. 2004).

Materials and Methods

The two experiments described in this paper were located at Ceannacroc in north-west Scotland (57° 7' N, 4° 45' W) and at Hambleton in north-east England (54° 15' N, 0° 30' W). The Ceannacroc experiment was planted on a peaty podsol on undulating terrain at 150 m elevation with annual rainfall of 1500 mm while the Hambleton experiment was sited on a podsolic ironpan soil on level ground at an elevation of 210 m with an annual rainfall of 810 mm. Both sites were used for sheep grazing before planting in 1960 (Ceannacroc) and 1961 (Hambleton). At time of planting, both sites were characterised by heathland vegetation with heather (*Calluna vulgaris* L.) being the dominant species. Soil fertility of both experiments would be classed as 'very poor' using the Ecological Site Classification (ESC) (Pyatt et al. 2001), but soil moisture would be classed as 'very moist' at Ceannacroc and 'slightly dry' at Hambleton.

Both sites were cultivated before planting to reduce vegetation competition using a shallow (c. 20 cm deep) single mouldboard plough. The same experimental design was used at both locations with 4 treatments being compared, namely pure Scots pine, pure silver birch, a 1:1 mixture of both species, and a 3:1 mixture of Scots pine and silver birch. These treatments were laid out in a randomised block design with three replications of each treatment using a plot size of 0.2 ha with 900 plants per plot at a spacing of 1.5 m between and within rows. The mixture treatments were achieved by planting alternative 25 plant plots (5 by 5 trees) of each species in a chequer-board pattern. This design would be considered as a 'replacement series' (Sackville Hamilton 1994) since the focus of investigation is on the effect of contrasting species proportions at a constant spacing.

All replicates were located in close proximity to one another at the Hambleton site, but at Ceannacroc one block was located 900 m to the east on a similar site type. At Ceannacroc, all birch trees were fertilised in 1962 at a rate equivalent to 8 kg P ha^{-1}, but no other remedial treatments were undertaken at either site during the establishment phase. At Ceannacroc there was an unauthorised thinning in 2002 which removed a number of Scots pine trees from all plots where this species was present. There has been windblow of isolated trees within this experiment since 2002. The Hambleton experiment was thinned in 1998 and in 2003. These were thinnings from below which removed suppressed and sub-dominant trees, amounting to between 5 and 15 per cent of the basal area in each treatment.

The early assessment history was described by Malcolm and Mason (1999), but essentially involved measurements of height growth at 3, 6 and 10 years after planting, and estimates of basal area and standing volume at around 31-32 years of age. Subsequent assessments at 40, 45 and 55 years (Ceannacroc) and 38, 43 and 48 years (Hambleton) measured dbh of all trees in an internal 0.09 ha assessment plot to calculate basal area plus also providing estimates of top height. The only exception was at Ceannacroc where inspection of the 32 year data revealed very poor growth in one plot of the 3:1 mixture in block two which had been planted on a wet peaty soil: this plot was excluded in the later measurements. The variable thinning history described above with no precise measure of material removed has meant that we have had to use current basal area as a measure of productivity in these experiments.

Analysis of the data followed procedures used recently in examination of results from the long-term mixtures experiment at Gisburn (Mason and Connolly 2014). In brief, this involved comparing species performance pure and in mixture assuming that performance of an individual species in a mixed plot could be treated as an independent value. We then compared the overall performance of the pure species and the two mixed treatments using standard analysis of variance procedures. This was extended to compare the performance of the mixture treatments with what would have been expected from the growth of the species in the pure plots. For this purpose we calculated a *delta* statistic which is derived as (*actual basal area – predicted basal area*) where the *actual* value is the observed performance in mixture while the *predicted* value is based on the species performance in the pure plots. A delta statistic of zero implies that mixed stand performance conforms to the predictions derived from that of the component species in pure stands, a negative value indicates that performance in mixture is less than would be predicted, while a positive value is a sign of enhanced productivity in the mixed stand. We calculated the delta statistic for each mixture combination in each replicate and analysed the results with ANOVA. We also examined the results of the various mixture combinations using methods for presenting results from a replacement series (Kelty 1992).

Positive mixing effects can be shown when the productivity of a mixture is greater than that of pure stands of the individual component species. Such effects are classed either as 'overyielding' where the productivity of the mixture is more than the average of the pure stands or 'transgressive overyielding' where the mixture outyields the most productive of the pure species (Pretzsch 2009).

Results

At both sites, and when averaged over all treatments, there were major difference between the growth of Scots pine and silver birch, with trees of the first species generally being significantly taller and larger at most ages of assessment (Table 1). The only exception was in the first decade after planting when birch trees tended to be taller than the pines. Based upon top height measurements at the last assessment, productivity was similar at both sites being 10 m^3 ha^{-1} yr^{-1} for Scots pine and 4 m^3 ha^{-1} yr^{-1} for birch (Edwards and Christie 1981).

In contrast to the major difference found between the species at most ages, there were relatively few interactions between species and mixture treatments (Table 2). Those that occurred were due to birch trees growing in one or both of the mixture treatments being appreciably taller than those growing in the pure birch plots (e.g. at Hambleton in year 32). At the time of the last assessment, the density of

Table 1 - Comparative growth of Scots pine (SP) and silver birch (BI) planted pure and in varying mixture proportions at different ages of stand development in two separate experiments in Scotland and northern England. Results are averaged over all treatments.

Parameter		**Height (m)**							**Diameter (cm)**			
Age (years)		**3**	**6**	**10**	**32**	**40/38**	**45/43**	**55/48**	**32**	**40/38**	**45/43**	**55/48**
Experiment	Treatment											
Ceannacroc	SP	0.2	1.1	2.6	13.5	-	-	18.9	14.5	17.8	21.4	22.3
	BI	0.3	0.9	1.9	13.5	-	-	17.6	12.9	11.5	15.1	15.4
	Significance	***	**	***	ns	-	-	ns	**	***	***	*
	SED	0.01	0.04	0.1	0.4	-	-	0.8	0.5	1.1	1.0	3.1
	5%LSD	0.02	0.09	0.2	0.9	-	-	1.8	1.2	2.5	2.2	6.9
Hambleton	SP	0.5	1.3	3.1	13.4	15.3	16.1	17.2	13.9	16.7	17.0	19.2
	BI	0.9	1.7	3.0	11.8	14.6	15.6	16.1	8.3	10.5	10.9	12.0
	Significance	***	***	ns	***	*	ns	**	***	***	***	***
	SED	0.02	0.05	0.1	0.2	0.3	0.2	0.2	0.3	0.5	0.7	0.7
	5%LSD	0.04	0.1	0.2	0.4	0.6	0.5	0.5	0.6	1.0	1.6	1.4

Notes:
1. Where two ages are given for an assessment, the first refers to the Ceannacroc experiment and the second to the Hambleton one.
2. Significance is defined as: ***= p<0.001, **= p<0.01, *=p<0.05, ns=non-significant.

Table 2 - Height and diameter growth of Scots pine (SP) and silver birch (BI) planted pure and in varying mixture proportions at different ages of stand development in two separate experiments in Scotland and northern England. Also stand density at the last assessment.

Parameter		**Height (m)**							**Diameter (cm)**				**Density (stems ha^{-1})**
Age (years)		**3**	**6**	**10**	**32**	**40/38**	**45/43**	**55/48**	**32**	**40/38**	**45/43**	**55/48**	**55/48**
Experiment	Treatment												
Ceannacroc	SP pure	0.2	1.0	2.5	13.0	-	-	18.6	13.6	16.4	20.7	24.0	807
	SP3:BI1	0.2	1.1	2.6	13.5	-	-	18.3	14.8	18.1	21.1	25.2	467
	SP1:BI1	0.3	1.1	2.7	14.1	-	-	19.7	15.1	18.5	22.4	26.1	459
	BI pure	0.4	0.9	1.7	12.4	-	-	18.6	12.4	13.0	14.6	16.8	1374
	BI1:SP3	0.3	0.8	1.8	14.2	-	-	16.1	14.4	9.4	16.4	19.1	194
	BI1:SP1	0.3	1.0	2.1	14.0	-	-	18.2	11.9	12.2	14.3	16.8	364
	Significance	**	ns	ns	ns	-	-	ns	ns	ns	ns	ns	-
	SED	0.01	0.1	0.2	0.8	-	-	1.5	1.0	2.2	1.9	5.4	-
	5%LSD	0.03	0.2	0.3	1.7	-	-	3.5	2,3	5.0	4.3	11.9	-
Hambleton	SP pure	0.5	1.3	3.0	13.3	15.4	16.5	17.6	13.3	15.9	16.7	18.6	1585
	SP3:BI1	0.5	1.3	3.0	13.4	15.4	16.0	17.4	13.6	16.4	17.3	19.0	1261
	SP1:BI1	0.4	1.3	3.1	13.4	15.2	15.7	16.7	14.8	17.7	16.8	20.1	922
	BI pure	0.9	1.7	3.0	10.4	13.8	15.0	15.9	7.9	10.4	10.8	11.9	1931
	BI1:SP3	0.9	1.7	3.0	12.1	15.0	16.0	15.9	8.2	10.7	10.7	12.1	305
	BI1:SP1	0.9	1.7	3.1	12.7	15.0	15.8	16.5	8.9	10.5	11.1	12.1	663
	Significance	ns	ns	ns	**	ns	*	*	ns	ns	ns	ns	-
	SED	0.03	0.1	0.1	0.3	0.5	0.4	0.4	0.5	0.8	1.3	1.1	-
	5%LSD	0.07	0.2	0.3	0.6	1.1	0.9	0.9	1.1	1.7	2.8	2.5	-

Notes:
1. In mixed plots, the value shown in a given row is for the first species listed, i.e. in SP3:BI1 the value refers to the Scots pine component of the mixture.
2. Where two ages are given for an assessment, the first refers to the Ceannacroc experiment and the second to the Hambleton one.
3. Height measure is a mean height for years 3-10 and a top height measure thereafter.
4. Significance is defined as: **= p<0.01, *=p<0.05, ns=non-significant.

the pure birch treatment at both sites was appreciably higher than that of the pure pine plots (Table 2). The overall density of the mixture plots was similar to that found in the pure Scots pine, but the pine was the dominant component of the mixture. Thus at the last assessment date, the percentage of Scots pine stems per mixture was 71 per cent (3:1 mixture) and 56 per cent (1:1 mixture) at Ceannacroc: equivalent figures for Hambleton were 81 per cent and 58 per cent (Table 2).

In the Hambleton experiment, basal area production was significantly higher in pure Scots pine than in pure birch at all ages of assessment (Table 3). The values for the two mixtures were intermediate between the two pure plots, but were never significantly different from each other. The 1:1 mixture always had a significantly lower production than the pure Scots pine treatment, but the differences between the latter and the 3:1 treatment were smaller. However, production in the two mixture treatments was always higher than in the pure birch treatment. Results at Ceannacroc were much more variable, reflecting the impact of the unauthorised thinning when the trees were 42-years-old. Until that time, results reflected those from Hambleton with highest values in the pure Scots pine, lowest in the pure birch, and the two mixtures intermediate between the two pure plots. However, at the two later dates, there was little difference between any of the treatments, reflecting the preferential removal of the

Table 3 - Basal area production of Scots pine (SP) and birch (BI) grown pure and in varying proportions in mixture in two different experiments in Scotland and northern England.

Parameter Age (years)		Basal area (m^2 ha^{-1}) 32	 40/38	 45/43	 55/48
Experiment	Treatment				
Ceannacroc	SP pure	41.0	49.7	29.0	34.9
	SP3:BI1	41.9	33.6	32.4	28.8
	SP1:BI1	34.2	42.3	32.1	32.8
	BI pure	19.8	27.5	30.7	33.3
	Significance	**	ns	ns	ns
	SED	2.6	9.5	3.6	7.1
	5%LSD	6.7	22.4	9.1	16.2
Hambleton	SP pure	42.3	42.0	44.9	44.8
	SP3:BI1	36.2	38.3	41.0	41.3
	SP1:BI1	34.2	35.6	30.0	38.5
	BI pure	24.4	23.0	24.7	24.6
	Significance	**	***	*	***
	SED	2.9	1.4	5.6	1.3
	5%LSD	7.1	3.2	13.8	3.1

Notes:
1. Where two ages are given for an assessment, the first refers to the Ceannacroc experiment and the second to the Hambleton one.
2. Significance is defined as: ***= p<0.001, **= p<0.01, *=p<0.05, ns=non-significant.

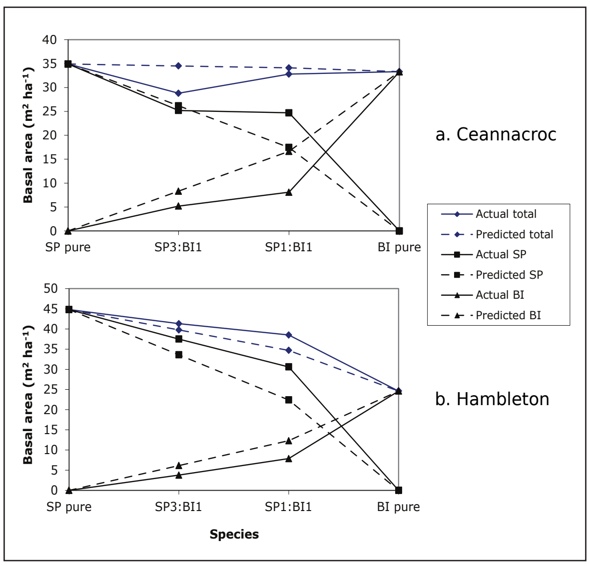

Figure 2 - Graphs of the basal area (m^2 ha^{-1}) at 55 years at Ceannacroc (Fig. 2a) and 48 years (Hambleton) (Fig. 2b) in two Scots pine-birch mixtures compared with the performance in pure plots of these species. Solid lines show the actual productivity in each treatment while the broken lines indicate the expected outturn if intra- and inter-specific interactions were equivalent.

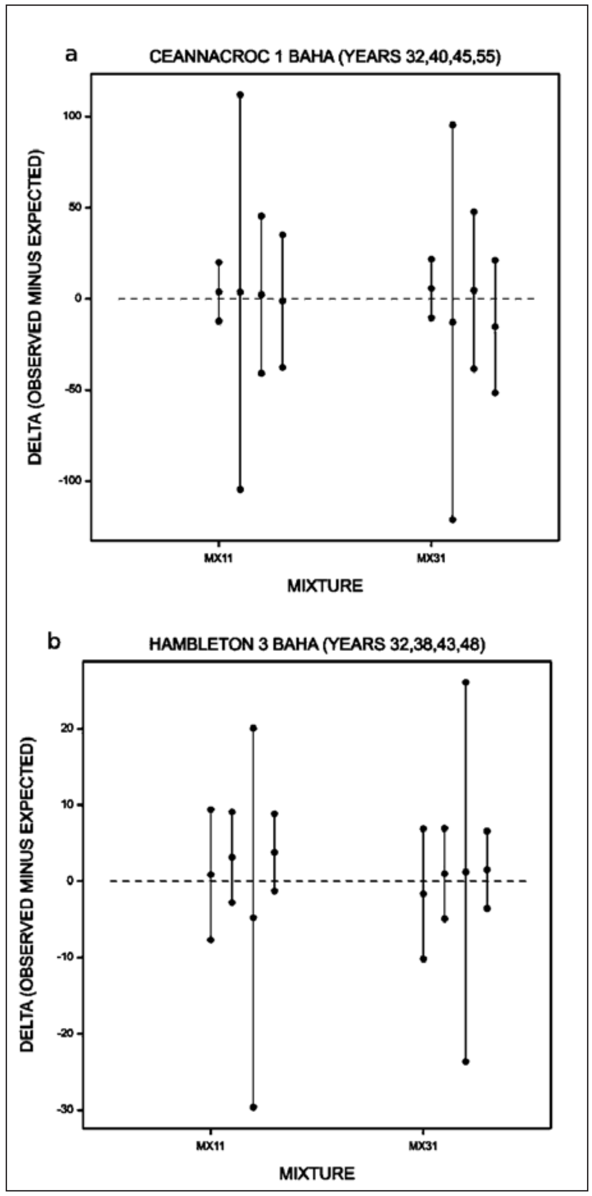

Figure 1 - Graphs showing the values of the delta statistic for differences in basal area (m^2 ha^{-1}) between the two Scots pine-birch mixture treatments and expected values based on the performance of the pure species plots in the experiments at Ceannacroc (Fig 1a) and Hambleton (Fig. 1b). Values are shown for the 1:1 and 3:1 Scots pine: birch mixture combinations in four different years covering tree ages 32-55 (Ceannacroc) and 32-48(Hambleton). At each age of assessment, the mean delta value and the 95 per cent confidence interval is presented.

pine in the thinning. At both sites, Scots pine had the highest proportion of basal area in the mixtures, comprising 83 per cent (3:1 mixture) and 75 per cent (1:1 mixture) at Ceannacroc, compared to 91 per cent and 80 per cent respectively at Hambleton.

Examination of the growth of the mixed plots compared to predictions based on performance of Scots pine and silver birch in the pure plots (Fig. 1a and 1b) revealed a general tendency for performance of the mixed plots to be slightly better than predicted (i.e. delta statistic >0), but these differences were never significant. There was also little evidence of any difference between the two mixture proportions. There were a couple of assessments where there was substantial variation around the predictions, namely year 40 at Ceannacroc and year 43 at Hambleton. The latter almost certainly reflects the thinning carried out in 2003, but the cause of the former is unclear. In both experiments the Scots pine component was more productive in mixture than predicted whereas the reverse applied to the birch (Fig. 2). This differential performance between the species was most apparent in the 1:1 mixture.

Discussion

Although both Scots pine and birches are widely distributed in northern Europe and are often found growing in mixture (Hynynen et al. 2010), there is a surprising lack of long-term experimental evidence to indicate how stands composed of these two light-demanding, pioneer species might interact. These two experiments were planted in parts of Britain which experience different climates, with annual rainfall at Ceannacroc being at least twice that recorded for Hambleton, yet there was relatively little difference in tree growth and productivity between the two sites. This suggests that, despite the variation caused by the unauthorised removal of Scots pine in the Ceannacroc experiment, the pattern of growth in the mixtures would have been quite similar at both locations. For the rest of this discussion, we mainly focus upon the Hambleton experiment to try to understand the processes influencing the patterns of growth and development in these mixtures.

After the initial establishment phase, Scots pine was taller and larger than birch throughout the life of these stands, and so came to dominate the mixed plots (Table 2). There was a period around years 30-40 at Hambleton where birch appeared to grow taller in mixture as also reported from Scandinavian studies (Mielikäinen 1980, Kaitaniemi and Lintunen 2010) but this trend did not persist in the later years. As a result of this differential growth between the species, there was a slight suggestion of overyielding in mixture (Fig. 2 - Hambleton) due to the greater productivity in the Scots pine more than offsetting the lower production in the birch. The poorer performance of birch in mixture is also evident at Ceannacroc (Fig. 2) despite the likelihood that the removal of the pine in thinning would have reduced the amount of inter-specific competition. However, as yet the overall improved performance in mixture has been small and not significantly different from what would have been expected based on the performance of the pure plots (Fig. 1). At Hambleton, there was also evidence that overall basal area production in mixture declined with increasing proportion of birch (Table 3), in line with results recorded in Scandinavia (Frivold and Frank 2002, Hynynen et al. 2011). The slower rate of self-thinning in the pure birch plots (Table 2) will also have influenced the smaller diameters and lower heights recorded for this species compared to Scots pine (Table 1).

Examination of tree species' interactions in mixed stands typically distinguishes three types of response, namely 'competition', 'competitive reduction' and 'facilitation' (Forrester 2014). The first of these responses occurs when one species has a negative impact on the growth or survival of another. The second arises where competition between species is less intense than competition within species, normally because of differential resource use by the component species of the mixture. Facilitation arises when the species interact in such a way that the growth of at least one of the species is positively affected. The second and third response can be difficult to distinguish and therefore the combined response is sometimes referred to as 'complementarity' (Forrester 2014). Although previous reports had shown slight changes in soil properties (e.g. a small increase in pH) with increasing proportions of birch (Malcolm and Mason 1999), the lack of any significant overyielding effect in the mixtures suggests that facilitation is unlikely to have occurred in these experiments.

Therefore, it seems likely that the response observed in the mixtures in these experiments represents a balance between competition between the two species, and competitive reduction in that the Scots pine appears to benefit from reduced intra-species competition due to the presence of birch in the mixtures. A further indication of the latter process is provided by the densities observed in the mixed stands at Hambleton, where there was negligible difference between the combined species density in the pure Scots pine and in the two mixed plots (Table 2) whereas stocking of the pure birch was some 20 per cent higher. The slower rate of self-thinning and lower vigour recorded in the pure silver birch plots would accord with the view that this species performs less well in oceanic Europe (Pretzsch 2005) and reflects the recommendation that dense birch stands should be heavily thinned to maintain vigour and improve timber quality (Cameron 1996). Site quality could also have influenced the outcome if the sites were too nutrient poor for good birch growth, since Scandinavian experience is that typical pine sites are too poor for silver birch (Hynynen et al. 2010). However, evaluation of species potential on these sites using the British ESC system (Pyatt et al. 2001) suggests that growth of both Scots pine and silver birch would be less than optimal (grading of 'suitable' in ESC), with limitations imposed either by lack of soil nutrients or excessive soil moisture.

These mixture experiments are now of an age that is close to two-thirds of that found in a standard rotation for Scots pine in Britain, yet there is no evidence that the magnitude of the limited positive interaction in the mixed plots has altered over time (Fig. 1). This may reflect the fact that the two species are both light demanding and have other similar functional traits which mean that they have limited ecological combining ability (Kelty 2006). The pattern of mixing used in the design may also have influenced the development of the mixtures and the extent of any overyielding since the 'chequerboard' layout will have resulted in small pockets of intense within-species competition alternating with less intense areas of between species competition along the edges of the species groups. Thus, analysis of a similar chequerboard mixture experiment with Norway spruce (*Picea abies* L. (Karst.)) and Scots pine, showed that diameter growth of individual Norway spruce trees was negatively affected by increasing numbers of Scots pine, but there was no effect of increasing numbers of Norway spruce (Yanai, 1992).

Conclusion

As noted earlier, one practical benefit from these experiments is to help improve understanding of the dynamics of the Scots pine-birch mixtures that can develop within the Caledonian pinewoods of northern Scotland, especially in the more oceanic western part of the pinewood zone (Edwards and Mason 2006). The results presented here do not suggest that there is much likelihood of a long-term coexistence of Scots pine and birch in intimate single storeyed mixtures, but rather that the more vigorous growth of the pine will tend to progressively eliminate the admixed broadleaved species. Any plan to enhance the proportion of birch in the Caledonian pinewoods would seemingly need to develop small blocks of birch within a pine matrix that were large enough to withstand the competitive pressure exerted by the pine and which could act as a future seed source.

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References

Anonymous 2010 - *A Guide for Increasing Tree Species Diversity in Wales.* Forestry Commission Wales, Aberystwyth. 41p.

Anonymous 2011 - *The UK Forestry Standard*, 116 p. http://www.forestry.gov.uk/pdf/FCFC001.pdf/$FILE/FCFC001.pdf . Accessed on May 10 2015.

Brooker R.W., Maestre F.T., Callaway R.M., Lortie C.L., Cavieres L.A., Kunstler G., Liancourt, P., Tielborger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B., Michalet, R. 2008 - *Facilitation in plant communities: the past, the present, and the future.* Journal of Ecology 96: 18-34.

Cameron A.D. 1996 – *Managing birch woodlands for the production of quality timber.* Forestry 69: 357-371.

Dimbleby G.W. 1952 - *Soil regeneration on the north-east Yorkshire moors.* Journal of Ecology 40: 331-341.

Edwards C.E., Mason W.L. 2006 - *Stand structure and dynamics of four native Scots pine (Pinus sylvestris L.) woodlands in northern Scotland.* Forestry 79: 261-277.

Edwards P., Christie J.M. 1981 - *Yield models for forest management.* Forestry Commission Booklet 48, HMSO, London, UK.

Felton A., Lindbladh M., Brunet J., Fritz O., 2010 - *Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe.* Forest Ecology and Management 260: 939-947.

Forestry Commission 2003 - *National Inventory of Woodland and Trees: Great Britain*, 68 p. http://www.forestry.gov.uk/pdf/nigreatbritain.pdf/$FILE/nigreatbritain.pdf Accessed on May 15, 2015.

Forrester D.I. 2014 - *The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process.* Forest Ecology and Management 312: 282-292.

Frivold L.H., Frank J. 2002 - *Growth of mixed birch-coniferous stands in relation to pure coniferous stands at similar sites in south-eastern Norway.* Scandinavian Journal of Forest Research 17 (2): 139-149.

Gardiner A.S. 1968 - *The reputation of birch for soil improvement.* Research and Development Paper 67, Forestry Commission, Edinburgh.

Gamfeldt L., Snall T., Bagchi R., Jonsson M., Gustaffson L., Kjellander P., Ruiz-Jaen, M.C., Froberg, M., Stendahl, J., Philipson, C.D., Mikusinski, G., Andersson, E., Westerlund, B., Andren, H., Moberg, F., Moen, J., Bengtsson, J. 2013 - *Higher levels of multiple ecosystem services are found in forests with more tree species.* Nature Communications 4: 1340.

Grant A., Worrell R., Wilson S., McG., Ray D., Mason W.L. 2012 - *Achieving diversity in Scotland's forest landscapes.* Forestry Commission Scotland Practice Guide, Forestry Commission, Edinburgh, 30 p.

Hynynen J., Niemisto P., Vihera-Aarnio A., Brunner A., Hein S., Velling P. 2010 - *Silviculture of birch (Betula pendula Roth and Betula pubescens Ehrh.) in northern Europe.* Forestry 83: 103-119.

Hynynen J., Repola J., Mielikainen K. 2011 - *The effects of species mixture on the growth and yield of mid-rotation mixed stands of Scots pine and silver birch.* Forest Ecology and Management 262: 1174-1183.

Kaitaniemi P., Lintunen A. 2010 - *Neighbour identity and competition influence tree growth in Scots pine, Siberian larch, and silver birch.* Annals of Forest Science 67: 604. DOI: 10.1051/forest/2010017

Kelty M.J. 1992 - *Comparative productivity of monocultures and mixed species stands.* In: "The Ecology and Silviculture of mixed-species forests". Kelty M.J., Larson B.C., Oliver C.D. Eds., Kluwer Academic Publishers: 125-141.

Kelty M.J. 2006 - *The role of species mixtures in plantation forestry.* Forest Ecology and Management 233: 195-204.

Malcolm D.C., Mason, W.L. 1999 - *Experimental mixtures of Scots pine and birch: 30 year effects on production, vegetation and soils.* In: 'Management of mixed-species forest: silviculture and economics'. Olsthoorn A.F.M. et al., Eds. IBN Scientific Contributions 15, IBN-DLO, Wageningen; 79-87.

Mason W.L. 2007 - *Changes in the management of British forests between 1945 and 2000 and possible future trends.* Ibis 149: 41–52.

Mason W.L., Hampson A., Edwards C. 2004 - *Managing the Pinewoods of Scotland.* Forestry Commission, Edinburgh, 234 p.

Mason W.L., Perks M.P. 2011 - *Sitka spruce (Picea sitchensis) forests in Atlantic Europe: changes in forest management and possible consequences for carbon sequestration.* Scandinavian Journal of Forest Research, supplement 11: 72-81.

Mason W.L., Connolly, T. 2014 - *Mixtures with spruce species can be more productive than monocultures: evidence from the Gisburn experiment in Britain.* Forestry 87 (2): 209-217.

Mielikäinen K. 1980 - *Structure and development of mixed pine and birch stands.* Commun. Inst. For. Fenn. 99:1-82 (Finnish with English summary).

Mielikäinen K. 1996 – *Approaches to managing birch-dominated mixed stands in Finland.* In: 'Silviculture of temperate and boreal broadleaf-conifer mixtures'.Comeau, P.G., Thomas, K.D. Eds. Land Management Handbook 36, BC Ministry of Forests, Victoria, British Columbia, Canada, 8-14.

Miles J. 1981 - *Effect of birch on moorlands.* Institute of Terrestrial Ecology, Cambridge. 18 p.

Oliver C.D., Larson B.C. 1996 - *Forest stand dynamics.* McGraw-Hill, New York.

Paquette A., Messier C., 2011 - *The effect of biodiversity on tree productivity: from temperate to boreal forests.* Global Ecology and Biogeography 20: 170-180.

Pretzsch H. 2005 - *Diversity and Productivity in Forests: evidence from long-term experimental plots.* In: 'Forest diversity and function: temperate and boreal forests'. Scherer-Lorentzen M., Korner Ch., Schulze E.D. Eds. Springer-Verlag, Berlin, 41-64.

Pretzsch, H. 2009 - *Forest dynamics, growth and yield.* Springer-Verlag, Berlin, p664.

Pyatt D.G., Ray D., Fletcher J. 2001 - *An ecological site classification for forestry in Great Britain.* Forestry Commission Bulletin 124. Forestry Commission, Edinburgh, UK. 74. p

Quine C.P., Bailey S.A., Watts K. 2013 - *Sustainable forest management in a time of ecosystem services frameworks: common ground and consequences.* Journal of Applied Ecology 50: 863-867.

Read D.J., Freer-Smith P.H., Morison J.I.L., Hanley N., West C.C., Snowdon P. (eds) 2009 - *Combating climate change - A role for UK Forests. An assessment of the potential of the UK's trees and woodlands to mitigate and adapt to climate change.* The Stationery Office, Edinburgh (UK).

Sackville Hamilton, N.R. 1994 - *Replacement and additive designs for plant competition studies.* Journal of Applied Ecology 31: 599-603.

Yanai R.D. 1992 - *Competitive interactions between Norway spruce and Scots pine at Gisburn Forest, NW England.* Forestry 65: 435-451.

Zhang Y., Chen H.Y.H., Reich P.B. 2012 - *Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis.* Journal of Ecology 100: 742-749.