

Long-term development of nursing mixtures of Sitka spruce and larch species in an experiment in northern Scotland

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Abstract

Aim of the study: An experiment was established in 1966 to compare the growth and development of 50: 50 mixtures of Sitka spruce (*Picea sitchensis*) with either Japanese larch (*Larix kaempferi*) or tamarack (*L. laricina*) with that found in pure plots of Sitka spruce. The site was one of moderate nitrogen availability where the presence of heather (*Calluna vulgaris*) could be expected to limit the growth of Sitka spruce.

Area of the study: North-east Scotland.

Material and methods: There were different patterns of spruce growth in the pure plots and in the mixtures, with faster spruce growth in mixture in the years approaching and immediately following canopy closure (*i.e.* ages 15-25). Foliage analysis suggested that this was linked with improved nitrogen status of spruce trees in the mixed compared to the pure plots.

Main results: At years 20 and 25 there were significant differences in height, diameter, and basal area between treatments, with the largest basal area being found in the Japanese larch/Sitka spruce mixtures, indicative of overyielding in the mixed plots. However, when the experiment was clearfelled at 41 years of age, all treatments had self-thinned to produce spruce dominated stands of similar height with only an occasional larch tree surviving in plots that were originally 50:50 mixtures.

Research highlights: There were no differences between treatments in basal area, harvested volume or sawlog outturn after 41 years. These results can be interpreted as showing facilitation between the larch and the spruce during the establishment phase followed by competition for light once canopy closure had occurred.

Key words: Mixed stand dynamics; facilitation; nitrogen status; product outturn.

Introduction

Successful establishment and subsequent management of mixed species forests depends on an understanding of the growth 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). Everything else being equal, one would expect higher growth from a mixed-species stand where the niches occupied by the component species are different so that the species can be said to have complementary characteristics (Kelty, 2006). 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). The extent of overyielding can vary over time depending upon the relative growth rates and life spans of the various species (Pretzsch, 2009). Positive mixing effects can also occur where the growth of a valuable species is favoured by mixture with another, usually through improvement of the nutrient availability to the former, a process often termed facilitation (Kelty, 2006). Paquette & 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

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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 pose a particular challenge in determining the potential role of mixtures since they are mostly characterised by single species plantations of fast growing non-native conifers grown on relatively short rotations (Mason, 2007; Mason & Perks, 2011). Thus the last major review of mixed species stands in British forestry (Kerr *et al.*, 1992) found that only around 26 per cent of the public forest estate was made up of mixed species stands. More recent data (Forestry Commission, 2003) suggested that the total area of mixed-species stands was only around 200,000 ha or about 8 per cent of the forest area of Great Britain. However, 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, pp 174–175). For example, the UK Forestry Standard, which sets out the national basis for sustainable forest management, encourages forestry practices which promote species diversity, such as mixed stands (UKFS 2011, p 96). These aspirations are also included in separate policy guidance in Wales and Scotland which seek to increase the diversity of planted forests through a number of silvicultural practices including wider use of a range of 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.

In recent decades, the only aspect of the silviculture of planted conifer forests in the British Isles which involved the use of mixtures was in the afforestation of nutrient poor soils in the uplands (Carey *et al.*, 1988). Observational experience and experimental work in the early decades of the last century had shown the importance of site cultivation and drainage combined with remedial phosphate fertilisation for the establishment of tree species on these difficult sites (Zehetmayr, 1960). While this proved sufficient to establish less demanding species such as Scots pine

(*Pinus sylvestris* L.), lodgepole pine (*Pinus contorta* Dougl.), and Japanese larch [*Larix kaempferi* (Lamb.) Carr.], growth of more productive species such as Sitka spruce [*Picea sitchensis* (Bong.) Carr.] rapidly stagnated ('checked') particularly in the presence of ericaceous vegetation such as heather [*Calluna vulgaris* (L.) Hull] (Morgan *et al.*, 1992). This checked growth was caused by an antagonistic effect of heather upon spruce mycorrhiza resulting in nitrogen deficiency in the spruce (Robinson, 1972). As a result, depending upon the lithology, a combination of herbicide control of the heather and one or more applications of nitrogen could be required to achieve canopy closure in pure spruce stands (McIntosh, 1983; Taylor, 1991). This comparatively expensive establishment regime meant that managers of such sites were often forced to plant less productive species such as pines and larches.

However, from the 1930s onwards, researchers had observed that where Sitka spruce was growing in close proximity to either Scots pine or Japanese larch, the growth of the spruce improved after an initial period of check and that the trees eventually closed canopy (Macdonald, 1936; Macdonald & Macdonald, 1952). This 'nursing' effect (Weatherell, 1957) was also associated with improved nitrogen status of the spruce (O'Carroll, 1978) which was linked to higher nitrogen concentrations in soils in the mixed stands (Carlyle & Malcolm, 1986). Subsequent investigations indicated these effects were due to mycorrhizal fungi associated with the nurse species enhancing nitrogen availability to the spruce (Ryan & Alexander, 1992). Provided that the nurse species was not too vigorous (Garforth, 1979), once canopy closure had occurred the mixed stands were expected to progressively self-thin towards a spruce dominated stand (Carey *et al.*, 1988). As a result, the use of 'nursing' mixtures where Sitka spruce was planted in combination with either pine or larch became a recommended practice for afforestation and reforestation regimes on the most nutrient poor soils in upland regions of the British Isles (Carey *et al.*, 1988; Taylor, 1991; Smith & McKay, 2002). The nursing benefit provided by pines and larches has more recently been reported to occur when these species were grown with a number of broadleaved species (Gabriel *et al.*, 2005) and has also been reported from more fertile sites where nitrogen deficiency would not have been anticipated (Mason & Connolly, 2014).

Despite the adoption of nursing mixtures on nutrient poor sites in British plantation forests, there have been

few published reports of the long-term effects of these mixtures upon stand growth and productivity, with most studies being concentrated in stands 15-25 years of age (Carey *et al.*, 1988; Morgan *et al.*, 1992). A pair of studies examined the impacts of these mixtures upon the growth and wood properties of Sitka spruce in trees 25-30 years of age (Watson & Cameron, 1995; Cameron & Watson, 1999). They found that, of all the nurse species compared, Japanese larch had the greatest positive influence upon the diameter and volume increment of the adjacent spruce, but that this resulted in spruce with wider annual rings, larger branch area and more detrimental knot characteristics. They concluded that this would make larch an inadvisable species for use as a nurse for Sitka spruce because of the negative impact of these features on timber quality, particularly if sawlog production was envisaged (Cameron & Watson, 1999).

The presumption generally made about the long-term performance of nursing mixtures is that, once canopy closure has been achieved, the stand will self-thin towards spruce dominance provided that the nurse species is no more than 2 m taller than the nursed trees (Carey *et al.*, 1988; Mason & Quine, 1995). It is assumed that productivity will be sustained because of efficient nutrient cycling within closed canopy stands (Miller, 1981). These assumptions can now begin to be verified by examining some of the older nursing mixtures experiments which are now over 40 years of age and so close to the normal felling age in plantation forests in Britain of 40-60 years (Mason, 2007). The objective of this paper is to report on the long-term growth and productivity observed in one experiment involving nursing mixtures of Sitka spruce and two different larch species. The development of the component species in the mixed plots is examined over time and is contrasted with that of adjoining plots of pure Sitka spruce. The impact of the mixtures on sawlog outturn was also investigated and the implications for the wider use of such mixtures on nutrient-poor sites are considered.

Material and methods

The experiment described in this paper was planted in 1966 as part of an afforestation scheme in Clashindarroch forest near Huntly in North-East Scotland (57°22'N and 2°49'W). Before afforestation, the area had been managed for sheep grazing and for sport

shooting of red grouse (*Lagopus lagopus scotica*). The experiment site receives around 900 mm rainfall per year, is located at 275-280 m asl with an accumulated growing season temperature (>5.6°C) of 922 degree days, and is comparatively sheltered (a DAMS score of 12 – Quine, 2000). The soil is an ironpan (Kennedy, 2002) with some gleying overlying a lithology of Dalradian slates, considered to have moderate nitrogen availability (Taylor, 1991). The site is estimated to lie on the transition between a 'poor' and a 'very poor' Soil Nutrient Regime and a 'moist' to 'fresh' Soil Moisture regime using the Ecological Site Classification (ESC) (Pyatt *et al.*, 2001).

Before planting, the vegetation was dominated by heather, but the whole site was burnt in 1965 so that at time of planting the dominant vegetation were soft grasses, principally *Deschampsia flexuosa*, but also *D. caespitosa* and *Festuca ovina*. After burning, the site was ploughed in summer 1965 using a single furrow tine plough and the experiment was planted in March 1966 with the trees planted into the side of the plough furrow at a spacing of 1.5 to 1.6 m along and between the furrows.

The initial intention was to establish two immediately adjoining experiments on the site. One compared the performance of pure plots of Sitka spruce with that of Sitka spruce of Queen Charlotte Islands (QCI) provenance in 50:50 mixtures with different larch species, either Japanese larch or tamarack (*Larix laricina* (Du Roi) K. Koch). This was originally designed to have two replicates of each of the mixtures plus one control plot of Sitka spruce of the same QCI provenance. The other experiment was intended to examine the performance of unreplicated pure plots of a range of Sitka spruce provenances or of hybrids between Sitka spruce and white spruce (*Picea glauca* (Moench.) Voss.). However, within a few years of the two experiments being established, it was recognised that the main interest at this site lay in the comparison of pure plots of Sitka spruce with the performance of the mixtures, and therefore the pure plot of Sitka spruce from the second experiment (of the same QCI provenance) was integrated into the first experiment, providing a design with two replicates of the three treatments. Plot size was 0.1 ha in the mixture plots and 0.05 ha in the pure plots. The pattern of mixture consisted of alternating groups of three plants of the two different species, planted along the row. This layout was staggered along the adjacent rows so that a group of one species was surrounded by groups of the other species.

Table 1. Height (m) and mean dbh (cm) of Sitka spruce (SS) growing pure or in mixture with either Japanese larch (JL) and tamarack over 41 years at Clashindarroch forest

Treatment	Height at different years of age							DBH at different years of age		
	3	6	10	15	20	25	41	20	25	41
SS pure	0.47 ^a	1.35	2.58	4.24	9.24 ^{bc}	11.20 ^b	23.89	12.1 ^b	14.4 ^c	21.5
SS/(JL)	0.56 ^{ab}	1.36	2.43	5.39	10.58 ^c	12.65 ^b	24.19	13.3 ^b	16.2 ^c	22.9
(SS)/JL	0.70 ^c	1.50	3.17	5.12	8.50 ^{ab}	10.65 ^b	Nd	10.8 ^b	11.3 ^b	Nd
SS/(tamarack)	0.61 ^{bc}	1.44	2.27	4.71	9.83 ^{bc}	11.68 ^b	24.19	12.8 ^b	16.2 ^c	23.8
(SS)/tamarack	0.67 ^{bc}	1.29	1.82	Nd	6.65 ^a	7.78 ^a	Nd	5.9 ^a	7.1 ^a	Nd
Significance (p value)	0.03	0.77	0.06	0.08	0.03	0.01	0.79	0.007	0.0005	0.40
SED	0.05	0.17	0.32	0.33	0.79	0.82	0.49	1.2	0.9	1.4
5% LSD	0.13	0.44	0.83	0.90	2.02	2.12	1.55	3.0	2.2	4.6

Notes:

1. In the mixtures, the values are presented for the species that is not in parentheses.
2. SED is standard error of a difference.
3. Nd indicates no data were recorded for that species at that assessment age.
4. Note that height up to and including year 15 is mean height and thereafter is top height (see text for details).
5. In columns with significant differences, different letters indicate where treatment means are significantly different at $p < 0.05$.

Following planting, the plants were treated with phosphate fertiliser in summer 1966 and again in 1973 at rates of 25 and 50 kg P ha⁻¹ respectively. In the first 2-3 years after planting, limited hand weeding was used as necessary to control competing vegetation. The pure Sitka spruce plots were sprayed with 2,4-D ester (8 litres product ha⁻¹) in August 1974 to control heather regrowth. There was considerable deer browsing in the early years of the experiment which particularly affected the growth of the tamarack, but also to a lesser extent that of the Japanese larch. No thinning took place during the life of the experiment. After canopy closure, there was occasional defoliation of spruce trees by the green spruce aphid (*Elatobium abietinum*) which appeared to be more serious in the western part of the site and caused greater mortality in one of the replicates. The experiment was clear felled in 2007 at 41 years of age as part of standard forest management in the local forest district.

Height of all trees in the plots was assessed at 3, 6, 10, and 15 years after planting. Subsequently, top height (based on the four largest diameter trees per species per plot), mean diameter at breast height (1.3 m; dbh), and basal area were measured at 20, 25 and 41 years after planting using internal assessment plots (*i.e.* external rows excluded to avoid edge effects) of 0.01 ha in the mixed plots and either 0.036 ha or 0.005 ha in the pure plots (Blocks 1 and 2 respectively). Limited foliage analysis of macronutrient status in the different treatments was carried out at 15, 20 and 25

years after planting. When the experiment was clear-felled, the opportunity was taken to obtain a measure of the felled outturn including the product breakdown (*i.e.* sawlogs, pulp etc.) by using the output from each whole plot (*i.e.* including the buffer rows) via the on-board computer mounted in the cab of the Timberjack 1470 harvester using for the felling operation. Data analysis followed standard analysis of variance procedures for a randomised block design. When comparing individual tree measures (height, dbh), the performance of an individual species in a mixed plot was treated as an independent plot value. However, where whole plot parameters (basal area, log outturn) were compared, values for both species in a mixture were combined.

Results

The experiment showed differential patterns of spruce growth in the pure plots and in the mixtures, particularly in the years approaching and immediately following canopy closure (*i.e.* ages 15-25). However, by the time the trees were felled at 41 years of age, the plots had self-thinned to produce spruce stands of similar height with only an occasional larch surviving in plots that were originally 50:50 mixtures. Top height of all three treatments (Table 1) indicated the productivity for Sitka spruce was about 18 m³ ha⁻¹ yr⁻¹ (Edwards & Christie, 1981).

Table 2. Basal area ($\text{m}^2 \text{ha}^{-1}$), mixture ratio, volume outturn ($\text{m}^3 \text{ha}^{-1}$) and green sawlog proportion (%) of Sitka spruce (SS) growing pure or in mixture with either Japanese larch (JL) and tamarack at 20, 25 and 41 years in Clashindarroch forest

Treatment	20 years		25 years		41 years		41 years	
	Basal area	Mixture ratio	Basal area	Mixture ratio	Basal area	Mixture ratio	Volume	Green sawlog
SS pure	38.5 ^a	—	61.4 ^b	—	78.9	—	755	35.5
SS/JL	51.2 ^b	6:4	69.2 ^c	7:3	77.6	9:1	721	39.2
SS/tamarack	34.2 ^a	8:2	52.9 ^a	9:1	84.8	10:0	799	44.9
Significance (p value)	0.007	—	0.009	—	0.89	—	0.88	0.63
SED	2.0	—	2.1	—	15.9	—	159	9.1
5% LSD	6.2	—	6.6	—	50.6	—	506	29.1

Notes:

1. Mixture ratio is based on the proportion of the basal area occupied by the two species.
2. In columns with significant differences, different letters indicate where treatment means are significantly different at $p < 0.05$.

There were significant differences ($p < 0.05$) in height at three years after planting and again at 20 and 25 years (Table 1). The first instance mainly reflected poorer growth of the Sitka spruce in the pure plots and in mixture with Japanese larch compared to the taller Japanese larch and tamarack. At 20 years the tamarack trees were significantly smaller than all other treatments except the Japanese larch. The tallest trees were found in the spruce growing in mixture with Japanese larch but there were no significant differences between this and the other two spruce treatments. By 25 years, all other treatments were significantly taller than the tamarack with no differences between them. A similar trend was evident for diameter at 20 years with the tamarack being significantly smaller than the other treatments. By 25 years the Sitka spruce in the mixed plots had significantly larger dbhs than the nurse larch species, while these dbh values were also larger than those found in the pure spruce plots but these differences were not significant. Nevertheless, differences in height and dbh at 41 years were non-significant.

Highly significant differences in basal area ($p < 0.01$) were also apparent at 20 and 25 years, but not at 41 years (Table 2). These reflected superior growth in the mixtures of Sitka spruce and Japanese larch compared to the other two treatments. The mixture of Sitka spruce and tamarack was less productive than the pure Sitka spruce, particularly at 25 years after planting. The proportion of larch in the mixtures declined from 20 years until 41 years, with the incidence of tamarack decreasing faster than that of Japanese larch. When the experiment was felled, all the tamarack had died out while only a few Japanese larch trees remained.

There were no overall differences in volume production harvested from the plots at 41 years (Table 2) although there was considerable variation between treatments in different replicates resulting in high standard errors. The amount of top quality green sawlogs of Sitka spruce produced ranged from 36 in the pure spruce plots to 45 per cent in the mixtures with tamarack, but with no difference between treatments. There were also no differences in the proportions of lower quality sawlogs or pulpwood harvested (data not shown).

Foliar analysis results (Table 3) suggested that Sitka spruce trees in the pure plots had an N status at 15 years after planting that was borderline between marginal and deficient whereas those in the mixture with tamarack showed an optimal nutrient status. All treatments had a similar marginal N status at 20 years and an optimal status 25 years after planting. P and K nutrient status was optimal in all treatments at all ages of sampling.

Discussion

The value of the results reported here is restricted by the limited replication used in the design of this experiment. However, at Clashindarroch the pattern of growth up to 25 years conforms to the general trends found in other studies of nursing mixtures at a range of sites in Britain and Ireland (O'Carroll, 1978; Carey *et al.*, 1988; Morgan *et al.*, 1992). This involves a period in the late stand initiation phase usually between years 10-15 where the spruce in mixture shows faster growth and a more favourable nitrogen status than

Table 3. Macronutrient status (dry matter %) of foliage of Sitka spruce (SS) growing pure or in mixture with either Japanese larch (JL) and tamarack at 15, 20 and 25 years in Clashindarroch forest

Treatment	15 years			20 years			25 years		
	N	P	K	N	P	K	N	P	K
SS pure	1.23 ^m	0.3	1.34	1.46 ^m	0.25	1.23	1.50	0.31	1.1
SS/JL	nd	nd	nd	1.49 ^m	0.27	1.04	1.55	0.27	1.01
SS/tamarack	1.61	0.32	1.51	1.41 ^m	0.24	1.25	1.79	0.27	1.21

Notes:

1. Suffix m indicates a marginal status for a given nutrient according to Taylor (1991 - Table 2). Critical values for N are: *optimal* > 1.5; *deficient* < 1.2; with values in between classed as *marginal*.

spruce grown in pure stands (O'Carroll, 1978; Morgan *et al.*, 1992). Since these trends are also apparent in this experiment (Tables 1, 3), this suggests that the findings reported here can be relied on to give a reasonable indication of the development of a nursing mixture over a full rotation.

Although the mixtures of Sitka spruce and Japanese larch had significantly higher basal areas than pure Sitka spruce at years 20 and 25, by the end of rotation there was no difference between these treatments in terms of basal area or of the volume harvested (Table 2). Also the proportion of larch in the mixtures had progressively declined following canopy closure as a result of mortality caused by inter-species competition in these unthinned stands (Table 2). Given that the onset of canopy closure is normally at around 5-6 m in planted conifer forests in upland Britain, this would have occurred at around 15 years of age in this experiment (Table 1) when the difference in height between the two species of the Japanese larch/Sitka spruce mixture was less than 50 cm (Table 1). Thus the subsequent self-thinning of the mixture towards the Sitka spruce conforms to the predictions of Carey *et al.* (1988) that such mixtures would progress towards a pure spruce stand provided that the height of the nurse did not exceed that of the nursed species by more than 2 m at time of canopy closure.

The lack of difference in productivity after 41 years between the pure spruce plots and the mixed ones would conform to predictions based on understanding of the site fertility. The underlying Dalradian lithology at Clashindarroch is considered to have moderate nitrogen availability (Taylor, 1991) so that the site would be classed as one where heather competition was the main cause of nitrogen deficiency in Sitka spruce (category B of Taylor & Tabbush, 1990). On such sites a combination of herbicide control of the

heather plus adequate phosphate status could be anticipated to provide satisfactory growth of pure spruce stands (Taylor, 1991) as shown by the pure Sitka spruce plots in this experiment. The comparatively high productivity achieved at this site (18 m³ ha⁻¹ yr⁻¹) from both the pure and the mixed stands is an indication of how apparently nutrient poor vegetation types can arise as a result of unsustainable land management practices (*e.g.* burning, litter removal) and that such vegetation can mask inherent site fertility (Dimbelby, 1962).

Previous studies of the impacts of mixtures upon spruce timber properties had suggested that Japanese larch, or indeed any larch species, would have a negative effect upon spruce timber quality, and especially sawlog quality (Watson & Cameron, 1995; Cameron & Watson, 1999). However, after 41 years in this experiment there was no evidence in the green sawlog or other product outturn from the different treatments (Table 2) to suggest a negative impact of the larch mixtures upon the quality and volume of spruce sawlog produced. Although the output recorded from the harvester would have been based upon the operator's assessment of log quality and would not have allowed for internal characteristics such as ring width or knot size, stem straightness is the main criterion used in grading green sawlogs and poor straightness is the main reason causing the downgrade of Sitka spruce sawlogs (Macdonald *et al.*, 2009). Given that there were also no significant differences between treatments in timber volume harvested (Table 2), the implication would be that, on this site, the mixed stands would have provided a similar final crop timber revenue to the grower as a pure stand and without as much expenditure on establishment (*i.e.* lower herbicide input).

It is useful to examine the Clashindarroch results from the nursing mixtures in the context of wider discussions about the processes underpinning the deve-

lopment of mixed stands (Pretzsch, 2009; Forrester *et al.*, 2011; Forrester 2014). This is a site where the existing ground vegetation was antagonistic to the growth of Sitka spruce because it limited nitrogen availability to the tree species. During the latter part of the establishment phase, Japanese larch, which is unaffected by heather provided it has received adequate phosphate (O'Carroll, 1978), facilitated the growth of the Sitka spruce, presumably because the mycorrhizal species on the larch roots increasing nitrogen availability to the spruce (Ryan & Alexander, 1992). While at this stage the Japanese larch/Sitka spruce mixture had enhanced growth compared to the spruce (Table 2), it is difficult to quantify the extent of any overyielding (Pretzsch, 2009) for at least two reasons. The first is the absence of a pure Japanese larch control plot and the second is that the growth of the pure spruce plot was improved due to the herbicide control of the heather. However, given that the recorded productivity of Japanese larch stands in Britain ranges from 4-14 m³ ha⁻¹ yr⁻¹ (Edwards & Christie, 1981), the basal area of a pure Japanese larch stand at this site would have ranged between 13 and 25 m² ha⁻¹ at age 20 and 20 and 33 m² ha⁻¹ at year 25. Since these values are appreciably less than those recorded for either the mixture or the pure spruce treatments at these ages it seems safe to infer that overyielding did occur in the mixtures at this stage of stand development.

The positive interaction between the two species allowed the spruce to enter the closed canopy stem exclusion phase at either a comparable height to the Japanese larch or at a height advantage over the tamarack, at which point the interaction between the two tree species switches from facilitation to competition for light. During this latter phase, the evergreen habit of Sitka spruce, its faster height growth, and somewhat greater shade tolerance (Mason *et al.*, 2004) enable it to dominate the larch species so that the mixtures eventually self-thin towards a pure spruce stand. These results underline how the dynamics of mixed species stands can change over time and that interactions at one phase of stand development do not necessarily apply at another, particularly if the action of the mixture has served to alleviate a site factor limiting the growth of one of the component species. Such findings indicate that there is much work yet to be done to improve our understanding of the growth and silviculture of mixed species forests, if the aspirations of forestry policies seeking to encourage the use of mixtures are to be implemented successfully and sustainably.

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