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Free or Lammas Growth and Progeny Performance in Picea sitchensis

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Summary

Free growth is an efficient mode of leader growth expressed most by young trees of southerly provenances of *Picea sitchensis*, and to varying degrees by different open-pollinated progenies. With free growth, the stem units (needle internodes) are elongated sooner, become longer, and fewer are used to produce bud scales. Progenies which produced large amounts of free growth at a favourable site in Britain tended to improve their height rankings during the first six years after planting. These were progenies of plus trees selected within particular plantations in Britain, which were considered to be of southerly provenance. Some of these progenies performed outstandingly at the favourable site and selection for such 'responsive' progenies could be improved by selecting for an ability to produce free growth. At two less favourable sites, free growth production had little influence on progeny height rankings. However, progenies which were better-adapted to the poorest site were among those that were least able to produce free growth. These were progenies of plus trees in other particular plantations in Britain which were considered to be of more northerly provenance.

Thus, free growth was considered a useful criterion to select (or reject) progenies which contributed to genotype × site interactions. But it was not a reliable criterion to select for good general performance at a range of sites. Free growth was not necessarily associated with greater leader growth or stem unit production.

Key words: Free growth, genotype × environment interaction, physiological-genetics, progeny evaluation.

Zusammenfassung

Freies Wachstum oder Johannistriebbildung und die Wüchsigkeit von Nachkommenschaften von *Picea sitchensis*.

„Freies Wachstum" ist eine effiziente Weise des Haupttriebswachstums, welches überwiegend bei jungen Bäumen südlicher Herkünfte von *Picea sitchensis*, aber auch in unterschiedlichem Maße bei verschiedenen Nachkommenschaften, beobachtet wurde. Beim freien Wachstum strecken sich die Stammeinheiten (Nadel-Internodien) bereits eine Wachstumsperiode früher. Diese werden insgesamt länger und es werden weniger verbraucht, um Knospenschuppen zu bilden. Nachkommenschaften, die an einem günstigen Standort an der schottischen Westküste größere Anteile freien Wachstums produziert hatten, zeigten die Tendenz, ihren Rang hinsichtlich des Höhenwachstums im Laufe der

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sechs Jahre nach der Pflanzung zu verbessern. Es handelte sich dabei um Absaaten von Plusbäumen, die in bestimmten Beständen Großbritanniens ausgewählt wurden und von denen man annimmt, daß sie mit Saatgut südlicher Herkünfte begründet worden waren. Einige dieser Nachkommenschaften waren unter den genannten günstigen Standortsbedingungen überaus wüchsig. Die Auslese solcher „ansprechenden" Nachkommenschaften könnte verbessert werden, indem man auf die „Eignung freies Wachstum zu produzieren" selektierte. Auf zwei weniger günstigen Standorten hatte das freie Wachstum nur wenig Einfluß auf die Rangfolge des Höhenwachstums. Aber unter den Nachkommschaften, die an die Bedingungen des schlechtesten Standorts am besten angepaßt waren, befanden sich diejenigen, die am wenigsten in der Lage waren, freies Wachstum auszubilden. Es waren dies Nachkommenschaften von Plusbaum-Auslesen in anderen britischen Beständen, von denen man annimmt, daß sie nördlichen Ursprungs seien. Infolgedessen wurde freies Wachstum als brauchbares Kriterium betrachtet, um Nachkommenschaften auszuwählen (oder auszuscheiden), die zur Genotyp-Umwelt-Interaktion beitragen. Aber es war kein geeignetes Merkmal, um für allgemein gute Wüchsigkeit auf einer Reihe von Standorten zu selektieren. Freies Wachstum war nicht notwendigerweise mit einem größeren Wachstum des Haupttriebes oder der Bildung von Stammeinheiten verbunden.

Introduction

Height is a major criterion used to evaluate progenies of *Picea sitchensis* (Bong.) Carr. during their first 10 years from seed. In those years the trees increase in height by extending (a) overwintered buds with preformed needles, producing the early summer flush of 'predetermined' or 'fixed' growth (Pollard and Logan 1974, Lanner 1976), and (b) additional needles and stem units[1]) formed during the current season and extended during July — September as 'free' or 'lammas' growth (Jablanczy 1971, Pollard and Logan 1974). Jablanczy (1971) defined 'free' growth as occurring after 'fixed' growth without interruption, whereas

[1]) A stem unit in *Picea* is a needle or scale plus its associated internode *(sensu stricto)*, that is, the lenght of stem per needle or scale.

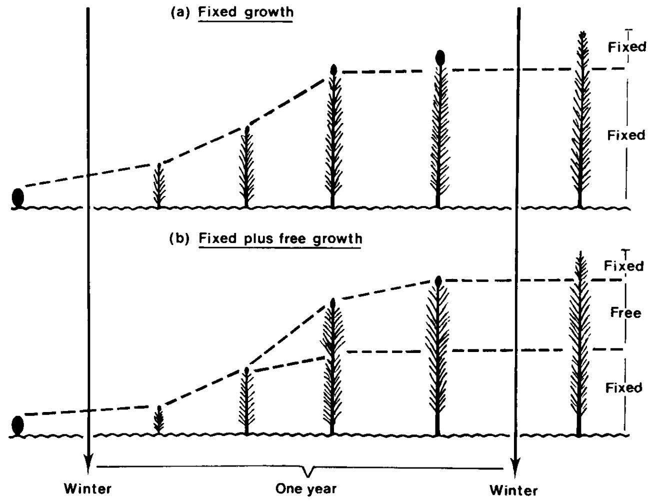

Figure 1. — Diagram of shoot morphogenesis in *Picea sitchensis* without (a) and with (b) free growth.

'lammas' growth is normally considered to be a late-summer flush occurring after scale formation and a temporary halt in shoot extension. In this paper we shall, for simplicity, call both these modes of growth 'free' growth, defined as (b) above.

It is well known that provenances of many conifers which are adapted to prolonged, mild growing seasons are capable of producing more free growth than provenances adapted to shorter growing seasons. Observations on *P. sitchensis* suggest that the tendency to produce free growth also differs greatly among young progenies selected within provenances. What influence does this have on their performances on different sites? Pollard and Logan (1974) and Pollard *et al.* (1975) thought of free growth as a supplement to fixed growth which enabled southerly provenances of *Picea mariana* (Mill.) B.S.P. and *P. sitchensis* to produce more stem units and grow more in height each year than northerly provenances. But do progenies which produce free growth necessarily grow more in height than progenies which do not?

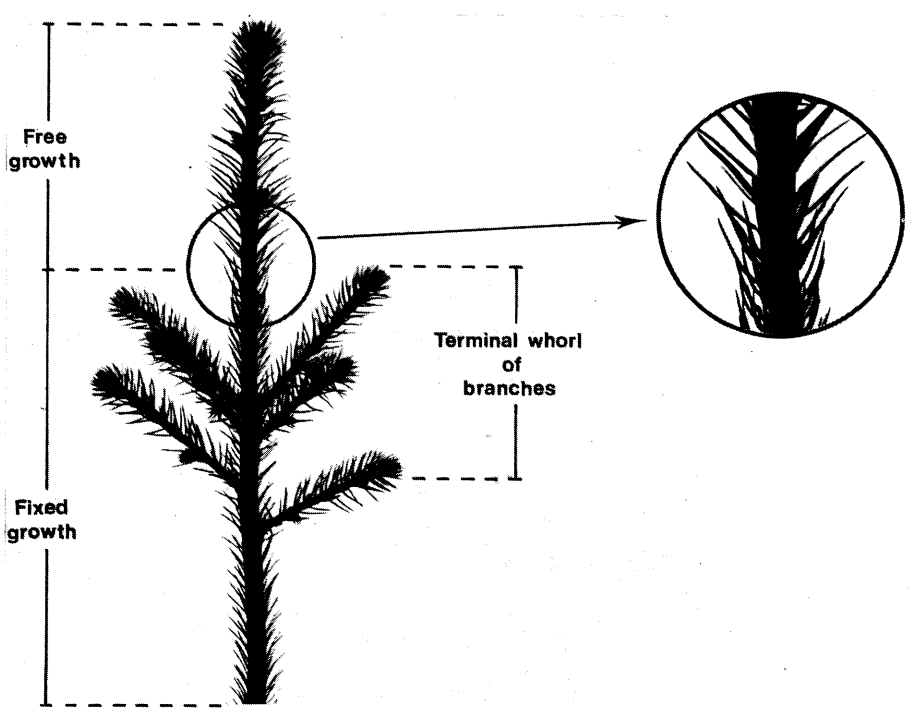

Figure 2. — Leader of *Picea sitchensis* showing a difference in needle size, angle and needle internode length between free growth and fixed growth.

This paper describes the characteristics of free growth on nursery-grown 5-year-old (from seed) *P. sitchensis,* and examines relationships between the 6-year heights (since planting as 2 year olds) of progenies at three forest sites and the amount of free growth they were still producing in their sixth year.

Characteristics of free growth on P. sitchensis

Initiation and extension

Two shoot meristems are involved in height growth: (a) apical meristems which generate new stem units, and (b) sub-apical meristems (cortical and rib) which are concerned with the elongation of stem units. Both contribute to differences in leader length among *P. sitchensis* progenies; that is, there are inherent differences in both numbers of stem units and mean lengths per stem unit (Cannell *et al.* 1976).

In north temperate climates, stem units are produced at the shoot apices of *P. sitchensis* from April to October (Cannell and Willett 1975, Owens and Molder 1976). When growth is entirely fixed, all the stem units are used to build buds which overwinter and elongate the following year as one 'fixed' growth flush *(Fig. 1 a).* When there is free growth there are two flushes of growth, the first from overwintered stem units formed during the latter part of the previous season (the fixed growth flush) and the second from stem units formed early in the current season (the free growth flush) *(Fig. 1 b).*

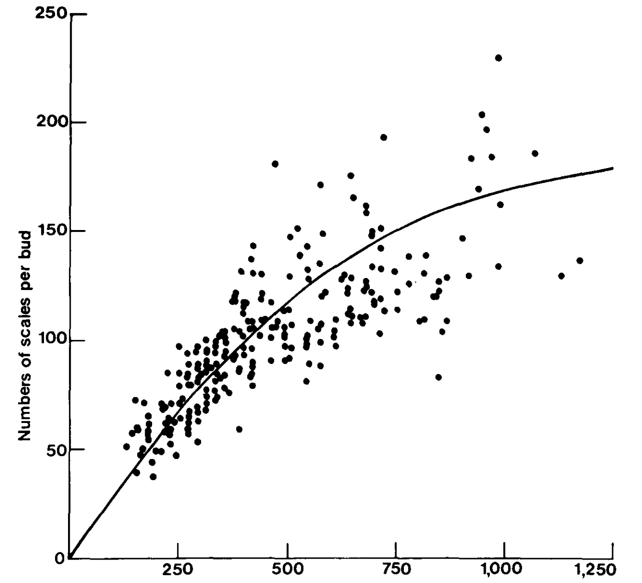

Figure 4. — Relationship, for winter buds of *Picea sitchensis,* between numbers of protective scales and numbers of overwintering needle primordia within the buds. The data were collected from 20 leaders of 15-year-old trees and their one-year-old first-order branches.

Boundary between fixed and free growth

On seedlings there is little interruption between the elongation of fixed and free growth, and the boundary between them can only be determined by (a) estimating numbers of needles on the fixed growth at bud-break, before free growth has begun, or (b) preventing some seedlings from producing free growth by growing them in short photoperiods (Pollard and Logan 1974).

However, on saplings and young trees, free growth occurs as a more distinct second flush, and there is often a region of poorly extended stem units, or even scales, at the boundary between fixed and free growth *(Fig. 2).* This region was estabilshed as the boundary using technique (a) on 34 replicate 5-year old trees of *P. sitchensis.* The boundary region of short stem units was always distal to the terminal whorl of branches on the fixed growth *(Fig. 3),* and where the region was indistinct it could be taken, with acceptable accuracy, to be 6 cm above the lowest branch of the terminal whorl *(Fig. 3 f).*

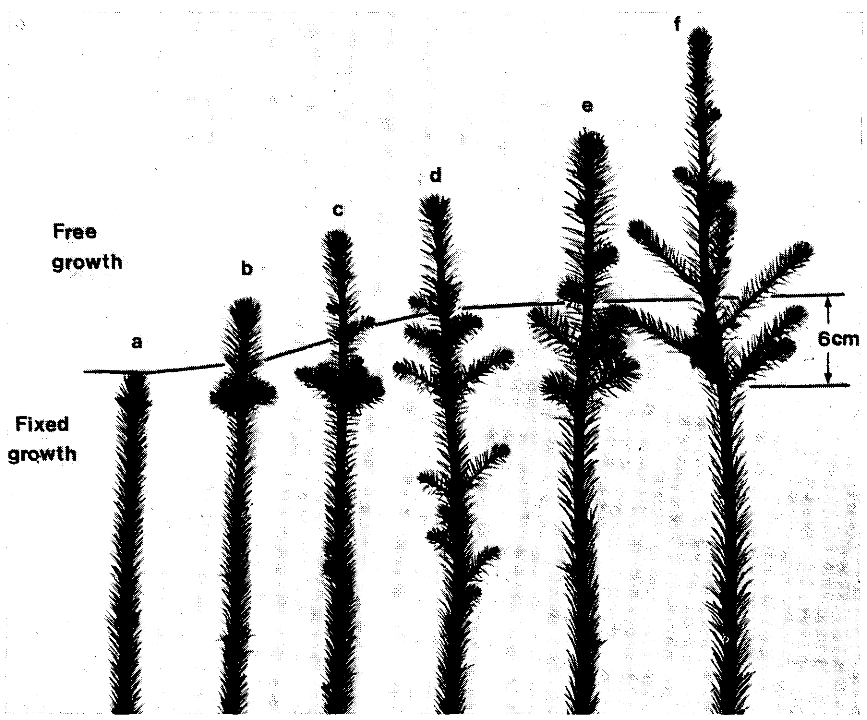

Figure 3. — Leaders of *Picea sitchensis* with different proportions of fixed and free growth. (a) No free growth. (b) Free growth clearly defined by a change in needle characteristics. (c) Free growth less clearly defined by a change in needle characteristics. (d), (e) and (f) Free growth estimated to begin 6 cm above the base of the terminal whorl of long proleptic branches.

Desirable characteristics of free growth

There are four reasons to suppose that trees which produce a lot of free growth when they are young may grow more rapidly in height during those early years than trees which produce little free growth.

1. Needles are displayed up to 9 months sooner if they are developed on free growth rather than held overwinter as primordia within buds. Therefore, trees with free growth begin each year being taller and having more photosynthetic tissue. They may, consequently, progress more rapidly through the early years of exponential growth in height and crown size.

2. Southerly provenances of *P. mariana* and *P. sitchensis,* which produce more free growth than northerly provenances, also produce more stem units per year (Pollard and Logan 1974, Pollard *et al.* 1975). When making these provenance comparisons the free growth habit appears to be linked with faster or more prolonged stem unit initiation. However, this may not always by the case, when comparing progenies for instance (see below), because it is known that primordia (new stem units) can be produced equally as rapidly within developing buds (forming fixed growth) as on elongating shoots (during free growth) (Cannell 1978).

3. The needle internodes on free growth of *P. sitchensis* are up to twice as long as those on fixed growth and the needles themselves are larger *(Fig. 2).* Thus, trees with free growth will tend to produce longer leaders, and more photosynthetic tissue, each year than trees without free growth even when they produce the same numbers of stem units per year.

4. When there is only fixed growth the total annual complement of needles is stored within buds which are protected overwinter by bud scales. The more needle primordia the buds contain, the more bud scales they have *(Fig. 4).* Those bud scales contribute little to photosynthesis and almost nothing to height growth. Stem units elongated as free growth are not stored within winter buds, so those buds are often smaller, and by definition contain less than 100% of the annual complement of needles. Consequently fewer, or smaller proportions, of the total annual complements of stem units are devoted to bud scales. A study of the leaders of 5-year old trees of *P. sitchensis* showed that 6 replicate trees with an average of 266 free growth needles produced winter buds containing 699 needle primordia protected by 91 bud scales, which therefore comprised 8.6% of the total stem units, $(91 \times 100/(266 + 699 + 91))$, whereas 6 replicates without free growth produced winter buds containing an average of 769 needle primordia protected by 121 bud scales, which therefore comprised 13.8% of the total annual complement. Teleologically speaking, the trees with free growth 'wasted' fewer stem units on bud scales.

Relationships between free growth and height growth among progenies of P. sitchensis

Johnstone and Samuel (1978) reported the early results of British trials testing open-pollinated candidate plus tree progenies of *P. sitchensis.* They were planted as 2-year-olds in 1970 and 1971 at eight forest sites in Britain, and measured in height in 1975 and 1976, at the end of their sixth growing season in the field. The plus trees had been chosen from within 13 different stands in Britain (Farigaig, Beauly, Cairn Edward etc., see *Table 2)* which had themselves been planted from seed imported from unknown

Table 1. — Details of three sites with progeny trials of *P. sitchensis* in Britain.

Site name	Location	Mean max. and min. temperature (°C) and total rainfall in 1975*	Randomized block lay-out
Aultmore	Invernesshire lat. 57° 35' N alt. 250 m.	11.9 / 3.7 756 mm	6 blocks of 6 tree lines
Kershope	Northumberland lat. 55° 05' N alt. 168 m.	12.1 / 3.8 797 mm	2 blocks of 16 tree plots
Tighnabruaich	Argyllshire lat. 55° 55' N alt. 65 m.	12.6 / 6.7 1199 mm	4 blocks of 8 tree lines

* Meteorological data are from Keith (57° 33' N, 105 m); Wauchope (55° 23' N, 155 m) and Rothesay (55° 50' N, 43 m), near to Aultmore, Kershope and Tighnabruaich, respectively.

Table 2. — Numbers of progenies of *P. sitchensis* with different free growth characteristics listed according to the names of the stands where the parent plus trees were located in Britain.

	Location of parent plus tree*	Over 18%† free growth at all 3 sites (see Table 1)	Over 18% free growth only at Kershope and Tighnabruaich	Less than 18% free growth at Kershope and Tighnabruaich	Less than 12% free growth at all sites
A	Farigaig	6	5	3	0
A	Inverary and Dean	2	0	0	0
A	Beauly	0	7	11	0
B	Cairn Edward	1	0	1	2
B	Laggan	0	0	1	4
B	Newcastleton	0	0	2	3
B	Kershope	0	0	2	1
B	5 other locations	0	0	5	1

* These are locations of stands planted in Britain with seed imported from unknown areas within the natural range of *P. sitchensis* along the western seaboard of N. America. It is, however, suggested that group A were of southerly origin (especially Farigaig) whereas group B were of more northerly origin.

† $\frac{\text{Length of free growth on 6th year leader}}{\text{Total length of 6th year leader}} \times 100$

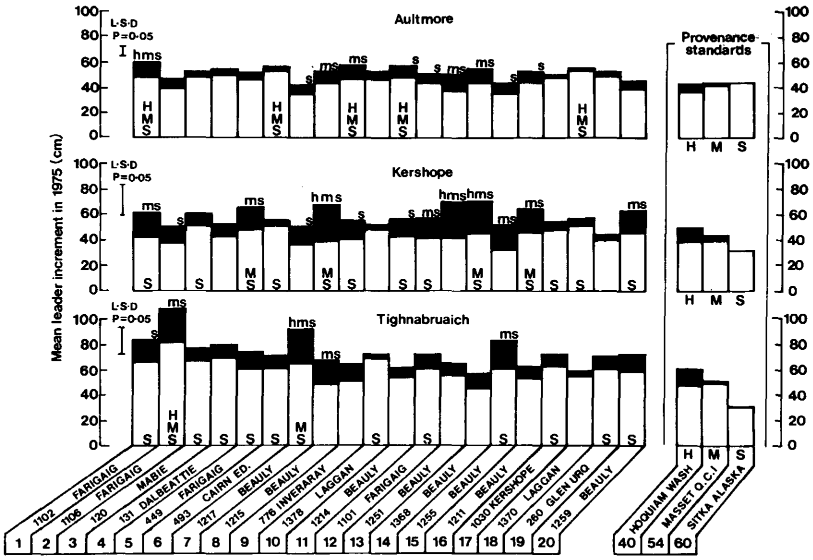

Figure 5. — Lengths of leaders produced by progenies of *Picea sitchensis* at 3 sites, in their 6th year after planting, divided into fixed and free growth (unshaded and shaded). Twenty progenies (out of 57) are shown which had the longest mean leader lengths over all sites, plus 3 provenance standards. H, M and S = significantly longer leaders (fixed plus free growth) at P = 0.05, than Hoquiam, Masset and Sitka, respectively, using Dunnett's test. h, m and s = significantly longer free growth than Hoquiam, Masset and Sitka, respectively.

locations within the natural range of *P. sitchensis* along the western seaboard of North America.

At the end of 1975 estimates were made of the lengths of fixed and free growth on the leaders of 57 progenies which had been planted in spring 1970 at three of the eight sites. These were, namely, Tighnabruaich on the mild, wet west Scottish coast, where the progenies had grown tallest; Kershope, an intermediate site in the cooler drier Scottish southern uplands; and Aultmore on the relatively cold, dry northeast coast of Scotland where the progenies had grown least (see *Table 1*). Measurements were also taken on three North American provenances, adopted as standards in these trials, namely Hoquiam (Washington State), Masset (Queen Charlotte Is., B.C.) and Sitka (Alaska). Half the trees were measured in each trial (layouts are given in *Table 1*). The heights of the trees had been measured before

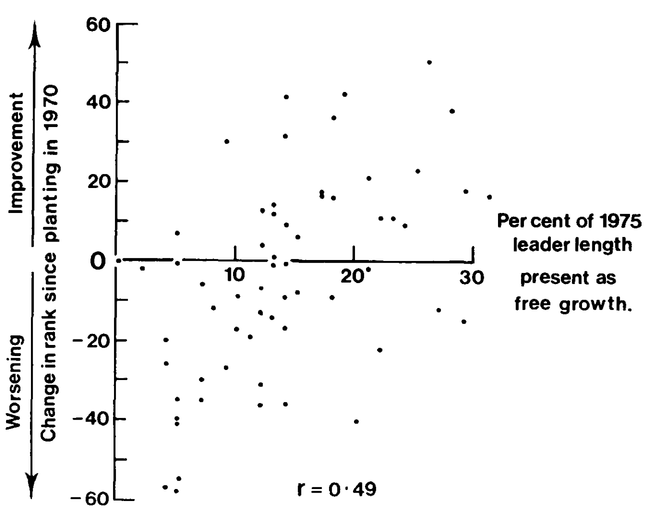

Figure 6. — Relaionship between (a) the mean percentage, free growth on the leaders of 57 progenies (plus 3 provenance standards) of *Picea sitchensis*, 6 years after planting, and (b) the number of places moved up or down in height rank since planting. Data are for Tighnabruaich (see *Table 1*).

planting as well as at the end of 1975. Analyses of variance were done for each site separately. Progeny-site interactions, reported by Johnstone and Samuel (1978), are discussed here with reference to histograms of progeny means rather than regressions on only three site means.

General differences among progenies and sites

The trees grew, on average, about 64% taller at the mild wet Tighnabruaich site (mean 2.82 m) than at the cold, dry Aultmore site (1.72 m), and progeny differences were greatest at Tighnabruaich (see *Fig. 7* and Johnstone and Samuel 1978). There were significant ($P < 0.01$) differences among progenies at all three sites in heights, 1975 leader lengths and lengths of free growth. Some progenies produced little free growth at any site, whereas others produced up to 25 cm at Tighnabruaich and Kershope.

Progenies were ranked according to their mean 1975 leader lengths across all sites. Means of the 20 top-ranking progenies in *Fig. 5* illustrate a portion of the variation observed. Sitka provenance was ranked last except at Aultmore. Masset and Hoquiam were ranked 46th and 45th at Aultmore, 52nd and 41st at Kershope, and 49th and 31st at Tighnabruaich.

Relationships were sought between the amounts of free growth on the 1975 leaders of the 57 progenies and (a) changes in their height ranks during the 6 years since planting, (b) progeny heights at the end of 1975, (c) differences in their heights at the three sites, and (d) their origins, as plus trees, within the 13 British stands of unkown North American provenance.

(a) *Free growth and changes in height rank*

Considerable rank changes occurred during the six years since planting, and were still occurring in the sixth year, that is, some progenies which were small at the end of 1974 (1975 heights minus 1975 leader lengths) produced relatively long leaders in 1975 and so improved their height ranks. Progenies which had improved their height ranks since planting tended to be those which produced most free

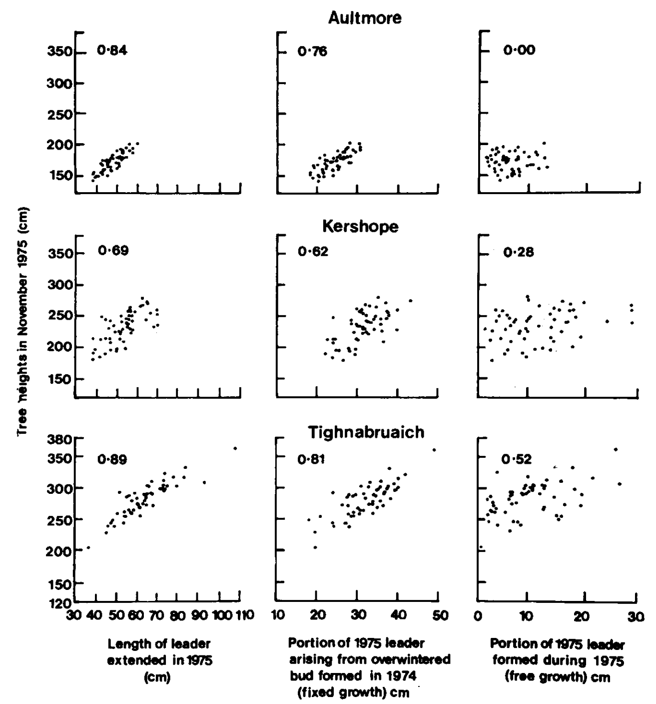

Figure 7. — Relationships between the heights of 57 progenies of *Picea sitchensis* at 3 sites, 6 years after planting, and: (left), lengths of the leaders elongated in the 6th year: (middle), lengths of fixed growth on those leaders, and: (right), lengths of free growth on those leaders. The values (0.84, 0.76 etc.) in each scattergram are correlation coefficients (r).

growth in 1975. This relationship was significant at Tighnabruaich *(Fig. 6)* accounting for almost 25% of the variation in rank change, but it was not significant at Kershope or Aultmore.

(b) *Free growth and progeny heights at age 6*

Whereas progeny heights were closely correlated with the lengths of fixed growth produced in 1975 at all sites *(Fig. 7,* centre), they were not significantly correlated with lengths of free growth except at Tighnabruaich *(Fig. 7,* right). That is, fixed growth was always an important determinant of height growth, whereas free growth was important only at the most favourable site. Even there, it was possible to find tall progenies with less free growth than shorter ones, and the amount of free growth produced on the 1975 leaders varied independently of the amount of fixed growth (correlations between free and fixed growth based on progeny means were not significant at any site; see also *Fig. 5).*

Thus, as noted above, the only important role of free growth seems to have been to hasten the growth rate of some progenies before age 6 at the most favourable site. At other sites, an ability to produce free growth had apparently had little effect on progeny performance.

(c) *Free growth and progeny-site interactions*

Johnstone and Samuel (1978) reported significant progeny-site interactions in these trials across eight sites. They attributed these partly to the large climatic differences between sites like Aultmore and Tighnabruaich, and partly to the wide, but unknown, range of provenances represented by the parent plus trees.

On the one hand, there were progenies which were better adapted to favourable sites like Tighnabruaich. From our data on 6th year leader lengths these would include 1106 Farigaig and 1217 Beauly *(Fig. 5).* The southerly provenance, Hoquiam, was also of this type. The feature distinguishing Hoquiam and these 'responsive' progenies was that they were all among those which produced at least 18% of their growth as free growth at Tighnabruaich and Kershope, and often at Aultmore as well.

On the other hand, there were progenies which ranked higher at less favourable sites, like Aultmore, than at Tighnabruaich. From our data, these would include 493 Cairn Edward and 1370 Laggan, and the northerly Sitka provenance *(Fig. 5).* All of these types included in this study produced less than 18% free growth in 1976 at all sites.

The remaining progenies which were not specifically adapted to any particular site, varied greatly in free growth production. Some were like the progenies mentioned above, producing either a lot or little free growth at all sites. Others produced a large proportion of free growth only at Tighnabruaich or Kershope *(Fig. 5).*

(d) *Free growth and origin of the plus trees*

Progenies of plus trees chosen within British stands at Farigaig, Inverary, Dean and to a lesser extent, Beauly, had the greatest tendency to produce free growth, particularly in response to favourable site conditions at Tighnabruaich and Kershope *(Table 2* group A). All of the 'responsive' progenies in this study came from those stands, which, it is suggested, were grown from seed imported from the southerly part of the natural range of *P. sitchensis*, perhaps from areas with climates at least as mild as that at Hoquiam, Washington State.

By contrast (with only one exception) the progenies from British stands at Cairn Edward, Laggan, Newcastleton, Kershope and five other locations, produced less than 18% free growth even at Tighnabruaich and often less than 12% at all sites. They behaved more like Masset provenance from the Queen Charlotte Islands, B.C. *(Table 2* group B).

Discussion

Implications for tree improvement

These studies showed that free growth was an efficient habit of growth, enabling young trees to make maximum height growth from given annual complements of stem units. The stem units were elongated sooner, became longer, and fewer were used to produce bud scales. But these advantages significantly influenced 6-year progeny height rankings only at a favourable, mild site in Britain (Tighnabruaich), and probably even then only because many of the progenies were apparently of southerly seed origin in N. America and so were genetically capable of producing large amounts of free growth at climatically favourable sites (Pollard *et al.* 1975).

The main effect of selecting progenies which produced large amounts of free growth would have been to favour progenies of southerly provenance type with maximum potential on favourable sites. Johnstone and Samuel (1978) listed nine such progenies within the trials sampled in this study; five from British stands at Farigaig, two from Beauly, and two from stands not represented in our sample. This study provided circumstantial evidence that stands at Farigaig, and to a lesser extent Beauly, were of southerly provenance type because they yielded progenies which, like Hoquiam provenance, tended to produce a lot of free growth at favourable sites *(Table 2).*

The main effect of selecting progenies which produced little free growth would have been to favour progenies of more northerly provenance type, better adapted to less favourable sites in Britain. JOHNSTONE and SAMUEL (1978) listed seven such progenies, three from Newcastleton, three from Laggan and one from Cairn Edward — all British stands which appeared from their meagre production of free growth to be of more northerly provenance type *(Table 2)*.

In short, if breeders want to select *P. sitchensis* progenies with maximum potential at climatically favourable or unfavourable sites in Britain there would be some advantage in selecting for or against free growth, respectively — preferably within known suitable-adapted provenances. KLEINSCHMIT and SAUER (1976) found that the tallest clones within provenances of *Picea abies* growing at a favourable nursery site tended to be those which produced most free growth.

But if breeders want to select for good general performance at a range of sites then free growth does not appear to be a useful selection criterion. Thus, in this study, both the tallest and smallest 20 progenies, ranked on mean heights or 6th-year leader lengths, included types with varying proportions of free growth, from plus trees in various British stands and probably different provenance origins. JOHNSTONE and SAMUEL's (1978) list of 13 progenies with good performances at eight sites included ones from Beauly, Inverary and Dean (southerly-provenance type) as well as from Newcastleton and Cairn Edward (northerly-provenance type). There were, however, none in their list from Farigaig, where the most 'responsive' southerly-type genotypes were found.

There are, however, risks in including genotypes in a breeding programme which owe their superiority to free growth production. They may be prone to damage during the free growth flush in early autumn. And they may not grow so well when they are past their juvenile stage (perhaps after age 10, LOGAN and POLLARD 1975) when they will no longer produce so much free growth and so no longer benefit from its advantages.

Implications for shoot growth physiology

Within latitudinal clines, or among ecotypes, southerly provenances tend to produce most free growth and also most stem units, (POLLARD and LOGAN 1974). Then, the activities of the sub-apical and apical meristems appear to be linked; the southerly provenances having not only active sub-apical meristems in mid-summer (producing free growth), but also generating stem units either faster of for longer in the season than northerly provenances. Consequently, the occurrence of free growth is correlated with total leader growth and it would appear that selection for free growth is desirable. This is not surprising when comparing latitudinal provenances. It is well-known for *P. sitchensis* that seedlings of southerly provenances both increase in height (by sub-apical meristematic activity) and generate stem units in the buds for more prolonged seasonal periods than northerly provenances (POLLARD *et al.* 1975, CANNELL and WILLETT 1975).

However, when comparing individual tree progenies within provenances, as done here for trees within particular British stands, there was strong evidence that the activities of the apical and sub-apical meristems varied independently. Consequently, selection for free growth at the progeny level did not appear to be universally desirable. The proportion of stem units that elongated as free growth almost certainly varied irrespective of the total number of stem units produced each year by the different progenies. Consequently, it may be misleading to regard free growth as a supplement to fixed growth, implying that it represents an 'extra' complement of stem units. Free growth is the precocious extension of current-year stem units. When the trees are young, on favourable sites, or adapted to climates with prolonged, mild growing seasons, it is a more efficient strategy of stem unit display than fixed growth. But it may have little direct bearing on the number of stem units produced per year.

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