Incidence of autumn frost damage and lammas growth in a 4-year-old clonal trial of Sitka spruce (*Picea sitchensis*) in Britain

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Summary
The relationships between lammas growth, frost damage and early height growth in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) were investigated using data from a 4-year-old clonal trial replicated over two sites in southern Scotland. The ability to produce lammas growth is an important component of early height growth in genetically improved Sitka spruce and could account for an average of 22 per cent of early height. Selecting clones exclusively for the ability to produce lammas growth marginally increased potential frost damage compared with unselected material, but there was no evidence to suggest increased frost damage with selection based on absolute height or current increment. It was concluded that selecting clones for total tree height would exploit the potential benefits of lammas and fixed growth, without increasing the risk of frost damage.

Introduction
Sitka spruce (*Picea sitchensis* (Bong.) Carr.), is the most important commercial tree species in Britain. A large number of Sitka spruce provenance trials dating back to 1929 (Fletcher and Faulkner, 1972) has shown the Queen Charlotte Island (QCI) origin from British Columbia, Canada to be the most suitable in terms of growth rate and autumn frost hardiness for most sites in Britain (Edwards, 1953; Streets, 1962; Lines, 1964; Fletcher, 1992). Within-origin improvement has involved the selection of good quality phenotypes (plus-trees), which were believed to be of QCI origin, and then estimating their breeding values based on the mean performance of half-sibling progeny planted in replicated field trials (Lee, 1990; Lee, 1992). Reselection of parent trees for Breeding and Production Populations is based on multi-trait performance of the progeny (Lee, 1995).

Samuel (1991) estimated the genetic parameters for growth and stem-form over a 15-year period from planting in a $7 \times 7$ complete diallel cross of Sitka spruce and concluded that there could be as much as 50 per cent of the total genetic variation for height from non-additive sources (cannot be predicted from additive
breeding values). The scope for increased genetic gain through exploitation of non-additive genetic variance is therefore large and could potentially double the gain achieved from exploitation of additive genetic variance alone. However, technological problems associated with meristem ageing prevent commercial-scale propagation of superior clones selected within clonal tests (John and Mason, 1987) and so the breeding programme remains sexually based as it progresses into the second generation (Lee, 1993).

Frost damage to Sitka spruce has been assessed since early species trials in the 1830s (Streets, 1962). Sitka spruce is prone to leader damage by frost in both spring and autumn (Aldous, 1962; Lines, 1964) but low variation among origins for flushing times leaves little scope for avoiding spring frost through choice of origin (Lines and Mitchell, 1966). Susceptibility to autumn frost damage is dependent on the timing of growth cessation (Glerum, 1976), which can vary greatly among different Sitka spruce origins in Britain; southerly origins with inherently long vegetative periods are more susceptible (Lines and Mitchell, 1966). Site factors, particularly critical day-length or photoperiod, are important determinants of severity of autumn frost damage (Burley, 1966a, b; Edwards, 1953) as they determine the onset of winter dormancy. In black spruce (Picea mariana (Mill.) B.S.P.), the incidence of autumn frost damage has been shown to be positively correlated with the amount of lammas growth and decreasing latitude of origin (Pollard and Logan, 1974).

Lammas growth is the free-growth that takes place towards the end of the growing season once predetermined growth is complete. In Sitka spruce, lammas growth is restricted to young trees although it can last for up to 10 years from germination (Joblanczy, 1971). The amount of lammas growth varies greatly with site, origin of the trees and between trees within origin. Pollard et al. (1975) found that the rate of free-growth in Sitka spruce was more dependent on site factors than on latitude of origin. However, Cannell and Willer (1975) found lammas growth for Sitka spruce in Britain to be well correlated with latitude and date of first frost at the provenance of origin.

Under favourable conditions lammas growth may constitute a significant proportion of annual height growth in Sitka spruce (Lines and Mitchell, 1966; Cannell and Johnstone, 1978). Pollard and Logan (1974) found good correlations between height growth in 4-year-old black spruce seedlings and the amount of lammas growth, suggesting that trees were taller by virtue of the length of lammas growth produced.

The relationships between lammas growth and total early height growth, and lammas growth and frost damage are important in the Sitka spruce breeding strategy because of the implications for early selection. Sitka spruce breeders are constantly attempting to reduce the age of indirect selection for final rotation volume. Six-year height is currently used as the indicator trait for mid-rotation diameter (Gill, 1987) and parent trees are accepted or rejected for further breeding work based partly on the mean height across sites of their progeny at this age. Breeders have to be sure that (1) selections made on early height growth are sustained once free-growth ceases and (2) trees selected at the early ages are not more frost susceptible as a result of possible indirect selection for increased amounts of lammas growth.

Between 15 and 19 October 1993 air temperatures in the forests surrounding Newcastleton village (55° 11’ N, 2° 46’ W) consistently dropped to between −6°C and −8°C (A. Furlong, personal communication) causing damaging frosts across the area. On a routine visit to a research clonal test in Newcastleton forest later that month, Forestry Commission staff observed symptoms on the 1993 needles of some trees which were typical of autumn frost injury (Redfern and Cannell, 1982 and Redfern, personal communication). The clonal test contained randomly selected progeny from within full-sib crosses (i.e. both parents known) between genotypes previously selected for the breeding population, and an unimproved QCI control seedlot. The incidence of frosting therefore provided the opportunity to investigate (1) the variation of, and relationships between, lammas growth, total

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height and frost damage in this 4-year-old clonal trial, and (2) the amount of lammas growth and frost damage in a selected population compared with the unimproved QCI control.

Materials and methods

Selection of clonal material

In March 1988, cuttings were taken from eight one-year-old seedling stock plants randomly selected from within each of six unrelated full-sib families. The clones that made up the full-sib families had all been selected for the Sitka spruce General Breeding Population considered suitable for all sites where QCI origin would normally be planted. All stock plants had been grown in a glasshouse under extended day conditions using high pressure sodium light. Up to 100 6–10 cm cuttings were taken from each stock plant and rooted in a heated mist house (Mason, 1984) before lifting and planting in clonal trials in the field during March, 1990.

Test sites

The clonal tests were established at Newcastleton (55° 11’ N, 2° 46’ W) and Wauchope forests (55° 20’ N, 2° 42’ W). Both sites are situated in the Borders Region of Scotland, close to the border with England, and are only about 40 km apart. Rainfall (1300–1400 mm) and slope (7°) are similar at each site although soil varied, being a peaty gley at 320 m at Wauchope and brown earth at 180 m at Newcastleton. Mean monthly daylengths for both sites were estimated from latitudes and the computerized meteorological tables of Beer (1990). The maximum difference between the two sites in any given month between May and November was only 3 minutes, suggesting a high degree of similarity of photoperiod.

Clonal test design

Experimental design at both sites was single plant plots with 15 complete replications. The control was an unimproved seedlot of QCI origin, which occurred twice in each replication. Sufficient rooted cuttings were raised for 48 clones to be planted at the Newcastleton site and 42 at Wauchope; 40 clones were common to both sites.

Field assessments

Each clonal test had already been assessed for height (in centimetres) after the second (HTCM02) and third (HTCM03) growing seasons. Frost damage (FRSC04) was assessed on a 1–4 subjective scale (1 = no trace of frosting; 2 = very slight signs of frosting on bud tips or underside of the branch needles; 3 = clearly visible signs of frosting on bud tips and on the top side of branch needles; 4 = highly visible signs of frosting from a distance) in October, 1993 at the Newcastleton site only. There were no temperature records for the Wauchope site. Four-year height (HTCM04), 3–4 year increment (INCM04), and fourth year lammas growth (LGCM04) and fixed growth (FGCM04) were all measured in May, 1994 before the onset of fifth year bud flushing. Lammas growth was identified from changes in needle size, and stem size and colour as defined by Cannell and Johnstone (1978).

Statistical methods

Estimation of variance components

Analysis of variance was carried out for all traits at each site using PROC GLM within SAS (SAS, 1982) assuming random additive effects. Expected mean squares (EMS) models adapted from Mullin et al. (1992) and Park and Fowler (1987) were used to calculate the genetic variance components. EMS models were adjusted for missing values and the residual variance effects were assumed equal to the replicate clone (within family) interaction. Eighteen per cent of trees at Wauchope and 5 per cent of trees at Newcastleton were excluded from the analyses due to missing leaders in their fourth growing season.

The model for the analysis of traits was:

\[ Y_{ijk} = \mu + B_i + F_j + C_{kj} + BF_{ij} + e_{ijk} \]

where:
- \( Y \) = the observed value of the \( k \)th clone from the \( j \)th family growing in the \( i \)th replicate;
- \( \mu \) = overall mean;
- \( B_i \) = effect of the \( i \)th replicate (\( i = 1, \ldots, 30 \));
- \( F_j \) = effect of the \( j \)th family (\( j = 1, \ldots, 6 \));
C_{kj} = the effect of the k\textsuperscript{th} clone within the j\textsuperscript{th} family (k = 1, \ldots, 8);
BF_{ij} = the interaction of the j\textsuperscript{th} family in the i\textsuperscript{th} replicate;
e_{ijk} = residual effect

Estimates of additive and non-additive vari-
ances (\sigma_{A}^2 and \sigma_{NA}^2) were derived using the follow-
ing simplified genetic models from King and
Johnson (1991):
\[
\sigma_{F}^2 = \frac{1}{2} \sigma_{A}^2 + \frac{1}{4} \sigma_{NA}^2
\]
\[
\sigma_{C(F)}^2 = \frac{1}{2} \sigma_{A}^2 + \frac{3}{4} \sigma_{NA}^2
\]
where:
\sigma_{F}^2 and \sigma_{C(F)}^2 are the variation between family
means and variation of clone within family
respectively.

Solving equations (1) and (2) simultaneously
gives
\[
\sigma_{A}^2 = 3 \sigma_{F}^2 - \sigma_{C(F)}^2
\]
\[
\sigma_{NA}^2 = 2(\sigma_{C(F)}^2 - \sigma_{F}^2)
\]

Heritabilities

Heritability is a measure of the ratio of estimated
genetic variance to the estimated phenotypic vari-
ance (Falconer, 1989). There are a number of ways
of measuring heritability depending on the for-
m of selection (standing tree in the forest, progeny or
clonal test mean) and degree to which additive and
non-additive genetic variances are included.

Three types of heritability were estimated
according to Mullin and Park (1992):
1. \(H^2\) for mass selection and cloning;
   \[
   H^2 = \frac{\sigma_{F}^2 + \sigma_{C(F)}^2}{\sigma_{ph}^2}
   \]
2. \(h_{FS}^2\) for selection based on full-sib family means;
   \[
   h_{FS}^2 = \frac{\sigma_{F}^2}{\sigma_{ph(FS)}^2}
   \]
3. \(H_{C}^2\) for selection based on clonal means;
   \[
   H_{C}^2 = \frac{\sigma_{C}^2}{\sigma_{ph(C)}^2}
   \]
where \(\sigma_{C}^2, \sigma_{ph}, \sigma_{ph(FS)}^2\) and \(\sigma_{ph(C)}^2\) are the total
clonal variance, the total phenotypic variance, the
phenotypic variance for full-sib family means and
the phenotypic variance for clone means respec-
tively, and \(\sigma_{C}^2 = \sigma_{C(F)}^2 + \sigma_{F}^2\) (Burdon and Shelbourne, 1974).

Correlations

Estimates of the full-sib family variances and
covariances between traits were derived from the
MANOVA option for the SAS GLM procedures.
Genetic and phenotypic correlations between
paired traits were calculated using equations
adapted from Falconer (1989), and Zobel and

1. Genetic correlation for traits x and y:
   \[
   r_{G(xy)} = \frac{\sigma_{Fxy}}{\sqrt{\sigma_{Fx}^2 \sigma_{Fy}^2}}
   \]
   \(\sigma_{Fxy}, \sigma_{Fx}^2\) and \(\sigma_{Fy}^2\) are the full-sib components of
covariance and variance for traits x and y
respectively.

2. Phenotypic correlation for traits x and y:
   \[
   r_{P(xy)} = \frac{\sigma_{xy}}{\sqrt{\sigma_{x}^2 \sigma_{y}^2}}
   \]
   \(\sigma_{xy}, \sigma_{x}^2\) and \(\sigma_{y}^2\) are the phenotypic covariance and
variances for x and y respectively.

Results

Family and clonal performance

Table 1 shows that height growth at Wauchope
was initially better than at Newcastleton
(HTCM02 and HTCM03) although there was
effectively no difference between the two sites by
the end of the fourth growing season (HTCM04).
While absolute values varied between sites, the
performance of the selected material relative to
the QCI control for HTCM04 ranged from 120
to 166 per cent at the family-mean level, and from
94 to 193 per cent at the clonal-mean level.

The clonal-mean performance of the selected
material for lammas growth (LGCM04) was 6.5
and 32.7 times greater than the QCI control value
at Newcastleton and Wauchope respectively.
Lammas growth accounted for an average of 23
per cent and 21 per cent of current incr ement
(INCM04) at Newcastleton and Wauchope
respectively compared with just 5 per cent and 2
per cent for the QCI controls. The greater propor-
tion of lammas growth at Newcastleton compared
with Wauchope, reflected the more favourable
growing conditions of the Newcastleton site.
Family ranks for lammas growth were identical at both sites, with top ranked families and clones having high proportions of lammas growth (Figures 1 and 2).

The clonal mean value for frost damage (Newcastleton only) was the same as the QCI control, although approximately 33 per cent of the clones and families had frost damage scores higher (i.e. more frost damage) than the QCI control.

**Variance components and heritabilities**

Table 2 gives the heritabilities and estimated variance components expressed as a proportion of the total phenotypic variance for the two sites. Additive and non-additive variances are expressed as proportions of the total genetic variance. Negative variances were equated to zero as in Mullin et al. (1992).

![Figure 1. Breakdown of 4-year height (HTCM04) across sites, at the family mean level. Black, white and grey shades = 3-year height (HTCM03), fourth year fixed growth (FGCM04) and fourth year lammas growth (LGCM04) respectively.](image-url)
There was a slight increase in the proportion of genetic variance ($\sigma^2_G$) at both sites for HTCM04 relative to HTCM02 and 03, although $\sigma^2_G$ was consistently higher at Newcastleton. These differences are reflected in heritability values (e.g. $h_{FS}^2 = 0.88$ and 0.44 respectively). Genetic control for HTCM02, HTCM03, HTCM04 and LGCM04 was exclusively additive ($\sigma^2_A$) at Newcastleton, but at Wauchope, non-additive control ($\sigma^2_{NA}$) made an important contribution. Fixed growth seemed to be controlled entirely by $\sigma^2_A$ at Wauchope although $\sigma^2_A$ and $\sigma^2_{NA}$ effects were equally important at Newcastleton. Genetic control for INC04 varied greatly between the two sites, being under a large amount of genetic control (mainly $\sigma^2_A$) at Newcastleton, and only a small amount of genetic control (mainly $\sigma^2_{NA}$) at Wauchope.

Lammas growth was under the greatest genetic control of all the measured traits; $\sigma^2_G = 57$ per cent at both sites. In each case the source of genetic variation for lammas growth was exclusively additive. Frost damage, while having similar total genetic control to HTCM04 ($\sigma^2_G = 43.7$ per cent), was mostly under non-additive control.

Correlations between traits

Phenotypic and genetic correlations between traits at Newcastleton, Wauchope and combined across sites are presented in Table 3. Correlations are interpreted according to Fowler and Cohen (1992).

Lammas growth was more closely genetically correlated with HTCM04 than fixed growth at both Newcastleton and Wauchope. Fixed growth (FGCM04) was, in general, either very weakly or weakly correlated with other traits, except for the modest positive correlation with INC04 at Newcastleton ($r_G = 0.61$) and a modest negative correlation ($r_G = -0.68$) with lammas growth at Wauchope. INC04 was more positively correlated with height than either lammas growth or fixed growth. Correlation of frost damage at Newcastleton with lammas growth and increment approaches zero but is weakly correlated with fixed growth.
Table 2: Variance components and heritabilities at Newcastleton and Wauchope

(a) Newcastleton

<table>
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<tr>
<th></th>
<th>HTCM02</th>
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<th>HTCM04</th>
<th>INCM04</th>
<th>FGCM04</th>
<th>LGCM04</th>
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<td>$\sigma^2_{ph}$ (%)</td>
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<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
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<tr>
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<td>44.1</td>
<td>44.0</td>
<td>47.0</td>
<td>35.7</td>
<td>17.8</td>
<td>57.2</td>
<td>43.7</td>
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<td>$\sigma^2_B$ (%)</td>
<td>1.4</td>
<td>4.4</td>
<td>4.2</td>
<td>2.0</td>
<td>1.4</td>
<td>1.3</td>
<td>0.3</td>
</tr>
<tr>
<td>$\sigma^2_F$ (%)</td>
<td>27.7</td>
<td>23.7</td>
<td>24.2</td>
<td>15.6</td>
<td>7.1</td>
<td>34.5</td>
<td>4.4</td>
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<tr>
<td>$\sigma^2_{C(F)}$ (%)</td>
<td>16.4</td>
<td>20.3</td>
<td>22.8</td>
<td>19.8</td>
<td>10.8</td>
<td>22.6</td>
<td>39.3</td>
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<td>0.0</td>
<td>2.4</td>
<td>3.4</td>
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<td>$\sigma^2_F$ (%)</td>
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<td>51.5</td>
<td>46.4</td>
<td>58.9</td>
<td>75</td>
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<td>100.0</td>
<td>78.4</td>
<td>58.6</td>
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<td>$h^2_{FS}$</td>
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<td>0.89</td>
<td>0.88</td>
<td>0.83</td>
<td>0.77</td>
<td>0.91</td>
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<tr>
<td>$H^2$</td>
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<td>0.46</td>
<td>0.49</td>
<td>0.36</td>
<td>0.19</td>
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<td>0.89</td>
<td>0.75</td>
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(b) Wauchope

<table>
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<th></th>
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<td>16.4</td>
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<td>$\sigma^2_F$ (%)</td>
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<td>$\sigma^2_{C(F)}$ (%)</td>
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<td>0.0</td>
<td>2.3</td>
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<td>$\sigma^2_F$ (%)</td>
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<td>81.1</td>
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<td>$\sigma^2_A$ (%)</td>
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<td>$\sigma^2_{NA}$ (%)</td>
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<td>$h^2_{FS}$</td>
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<td>$H^2$</td>
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<td>$H^2_C$</td>
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<td>0.93</td>
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$\sigma^2_{ph}$ = total phenotypic variances (equivalent to $\sigma^2_B + \sigma^2_F + \sigma^2_{C(F)} + \sigma^2_{FB} + \sigma^2_E$); $\sigma^2_G$ = total genetic variance (equivalent to $\sigma^2_F + \sigma^2_{C(F)}$); $\sigma^2_B$ = variation between blocks; $\sigma^2_F$ = variation between family means; $\sigma^2_{C(F)}$ = variation between clones within families; $\sigma^2_{FB}$ = family by block interaction; $\sigma^2_E$ residual effects; $\sigma^2_A$ = additive genetic variance; $\sigma^2_{NA}$ = non-additive genetic variance; $h^2_{FS}$ = full-sib family heritability; $H^2$ = individual clone heritability; $H^2_C$ = clonal mean heritability.
The effect of selection and breeding on the amount of lammas growth

The increase through selection and breeding of lammas growth relative to the unimproved QCI control was investigated by estimating the proportion of lammas growth among the top 10 clones selected for a number of different traits (Table 4).

Lammas growth accounted for over 27 per cent of the fourth year height gain among the top 10 clones ranked for total HTCM04 (selection trait 1 in Table 4). When clones were ranked for the ability to produce lammas growth (selection trait 4 in Table 4), the average proportion of lammas growth for the top 10 clones rose to 34 per cent and 36 per cent at Newcastleton and Wauchope respectively, compared with 18 per cent and 8 per cent when clones were ranked and selected for FGCM04 (selection trait 3 in Table 4). This is in comparison with an across sites mean of just 3 per cent lammas growth for the QCI control.

Table 5 compares the frost damage relative to the QCI control of the top 10 clones when selected according to the same traits in Table 4. The top 10 clones ranked for lammas growth (selection trait 4) had 5 per cent more frost damage relative to the QCI control, while frost damage was reduced by 8 per cent and 11 per cent for clones selected for absolute height after four growing seasons...
Discussion

Despite early differences, height growth at both sites was similar by the end of the fourth growing season. Clonal mean superiority relative to the QCI control averaged 46 per cent across sites. The proportion of genetic control increased with time and most of this was additive. The scope for further improvement of Sitka spruce through multiplication of tested clones would seem considerable.

The results show that lammas growth is an important component of 4-year height among clones selected for the General Breeding Population, accounting for an average of 22 per cent of current growth across the two sites, and up to 37 and 43 per cent in some families and clones respectively. The proportion of lammas growth in the top 10 clones ranked for each of HTCM04, LGCM04, INCM04 was consistently over 26 per cent compared with just 3 per cent for the unimproved QCI control. Even for those clones ranked for FGCM04 the amount of lammas growth (8 per cent) was more than twice the QCI control. Lammas growth is under strong genetic control, most of which is additive. In absolute terms, more lammas growth was produced among the clones at the more favourable Newcastleton site than at Wauchope but relative to the control, there was no difference between the two sites. Similar proportions of lammas growth have been reported by several authors for Sitka spruce and other conifers. In a 4-year-old clonal trial of *Picea mariana*, Pollard and Logan (1974) found that lammas growth accounted for up to 37 per cent of total growth, and Lines and Mitchell (1966) found 25 per cent for Sitka spruce in Britain.

The similarity between the sites for proportion of growth attributable to lammas growth can be explained by the strong genetic control of this trait. However, differences in the absolute values between the sites is likely to be environmental. Photoperiod and temperature are the key determinants of the occurrence of lammas growth (Pollard and Logan 1974, 1976). Estimates of photo-periods for the two sites differed by only 3 min (according to the method adopted by Beer, 1990), which is less than the critical photoperiod difference required for differences between sites to be expressed (Pollard and Logan, 1976). It is therefore likely that the reduced lammas growth at Wauchope is related to lower temperatures at this high elevation site.

Although there were significant differences between families and clones within families for lammas growth, the range of variation was greater between clonal means. Such patterns of variation have often been observed with lammas growth, e.g. Kleinschmit and Sauer (1976).

It would appear that large proportions of

| Table 4: Proportion of lammas growth (%) among the top 10 clones |
|----------------------|----------------|----------------|----------------|
| Selection trait      | Newcastleton  | Wauchope       | Across sites   |
| 1 Four year height (HTCM04) | 26.4          | 27.9          | 26.7          |
| 2 Fourth year increment (INCM04) | 27.9          | 27.0          | 26.8          |
| 3 Fixed growth (FGCM04)     | 17.7          | 8.1           | 7.8           |
| 4 Lammas growth (LGCM04)    | 33.7          | 36.2          | 33.4          |
| Control                    | 4.8           | 0.9           | 3.1           |
| Site mean                  | 20.3          | 18.5          | 19.1          |

Proportion of lammas growth = \( \frac{LGCM04}{INCM04} \times 100\%

| Table 5: Mean frost damage for top 10 clones compared with QCI control |
|------------------------|----------------|
| Selection trait        | Frost damage (%) |
| 1 Four year height (HTCM04) | 96          |
| 2 Fourth year increment (INCM04) | 92          |
| 3 Fixed growth (FGCM04)   | 89          |
| 4 Lammas growth (LGCM04)  | 105         |
| Control                  | 100         |
| Clonal mean              | 101         |
Lammas growth improve rankings for 4-year height. Similar results were obtained by Cannell and Johnstone (1978), who suggested that the ability to produce lammas growth could be exploited through the selection of such genotypes.

Selecting clones for the ability to produce lammas growth or 3–4-year increment would produce more potential gain in height at the end of the fourth growing season than would selecting for fixed growth alone. The good correlations between lammas growth and earlier heights suggest consistency of lammas growth in seedlings across years 1 to 4. Although lammas growth is only known to last for up to 10 years in spruce, Joblanczy (1971) and Pollard et al. (1975) estimated that the cumulative gains in growth during this period can provide lasting advantages. Burley, (1966a) also found that future height growth was dependent on current ‘capital’, so increased gains in the first few years, due partly to lammas growth, could result in trees with a greater proportion of mature fixed growth.

Results presented here show that on average, selected Sitka spruce clones were no more frost susceptible than the unimproved QCI control. An examination of the frost scores presented in Table 5 suggests that frost damage might be increased by 5 per cent if clones were selected exclusively for the ability to produce lammas growth. However, ranking and selecting clones for absolute height at 4 years old reduced frost damage by 4 per cent despite a fivefold increase in lammas growth relative to the control.

The weak correlation between lammas growth and frost damage ($r_G = 0.15$) is interesting and may have a number of explanations. First, both traits differ in their modes of genetic control; lammas growth is predominantly under additive genetic control, and frost hardness is under non-additive genetic control and correlations presented here are derived from the additive component of covariance. Second, the likelihood of frost damage is governed by the date of growth cessation, and the rate of hardening rather than by growth rate per se; damage will therefore only result if the growth period is extended as opposed to a higher daily rate of lammas growth.

Table 4 suggests that future generations of improved Sitka spruce will have higher proportions of lammas growth compared with unimproved QCI. To exploit the potential of this important component of early height growth in Sitka spruce fully without increasing the risk of autumn frost damage, more information is required on the seasonal growth cycle and the duration of lammas growth for selected genotypes before mass multiplication and deployment.

**Conclusions**

Lammas growth is an important component of early height growth in improved Sitka spruce and on average could account for 22 per cent of early height in improved planting stock at four years of age.

While the selection of clones exclusively for the ability to produce lammas growth would marginally increase potential frost damage compared with the unimproved control, there was no evidence to suggest increased frost damage is an indirect effect of selection based on absolute height.

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