LAMMAS SHOOT FORMATION IN SCOTCH PINE[1]

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Lammas shoots are second or midseason shoots that develop precociously from buds set earlier in the season (5). These precociously developed shoots are subtended by their own bud cluster. Previous studies have indicated that laminas growth is the main cause of forking (2, 3, 6, 8).

However, little evidence exists on the cause of lammas growth or the influence of site on lammas shoot formation. Some investigators have felt that a factor or factors of weather encourage lammas growth (2, 3, 6, 8). But the cause of the phenomenon is still unknown. Prior investigations have been either unable to demonstrate genetic control , that is a genetic predisposition to lammas shoot formation, or have discounted such genetic control without adequate study (6, 8).

The hypothesis of a genetic variation in disposition to lammas growth has been tested in New Jersey on three Scotch pine (*Pinus sylvestris* L.) plantations of 1050 individuals each representing 35 different native seed sources.

REVIEW OF LITERATURE

Definition of Lammas Shoots

Harlow and Harrar defined lammas shoots in the text of dendrology as "second or midseason twigs" formed from lateral buds which "Within a few days after their maturation they become swollen, open, and then produce a second shoot subtended by its own leaves and axillary buds" (5).

While Harlow and Harrar cite hardwoods in connection with lammas shoot formation, the definition includes the criterion that the lammas shoot bear its own set of buds© Therefore, in the present study, a pine was counted as exhibiting lammas growth if at least one member of a terminal bud cluster commenced growth later the same season, forming a precocious shoot which in turn set a terminal bud cluster of at least two buds. The term "lammassing" is used in this paper to indicate the process of precocious development of a bud into a lammas shoot. A tree is described as "lammassed" if it has exhibited this type of growth. A bud which exhibited post-season elongation without producing a terminal cluster was not consideredto have exhibited lammas growth. The effects of the two cases are usually different.

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Importance of Lammas Shoots

Carvell stated that lammas growth has been noted in white pine (Pinus strobus L.), red pine (Pinus resinosa Ait.), Douglas-fir (Pseudotsuga menziesii Mirb. Franco), maples(Acer spp.) and oaks (Quercus spp.)(3). T he importance of lammassing is due to the forked boles which result Figure 1 (the cover picture) illustrates forking in a three-year—old Scotch pine as result of lammas shoot formation.

The cause of forking in red pine was investigated in detail by Jump in New York (6). He observed that, "The first apparent symptom of forking is the extra-seasonal growth of laterals in the winter-bud cluster of the terminal shoot. " This extra-seasonal growth became noticeable in late June or July. Usually the laterals in the terminal cluster alone exhibit lammas growth. They act as if the terminal had been injured or removed and grow in a vertical direction. These lammas shoots produce buds and needles which extend across the terminal. In the spring when growth is initiated, the laterals are already above the terminal and they often maintain the lead. This condition is shown in figure 2 (p. 27). The terminal faces strong competition since it is forced to grow through the shading mass of needles and secondary branches produced by the precocious laterals. If the terminal survives and prospers, it becomes one member of a fork, opposed by one of the laterals. If the terminal is suppressed, two of the more widely separated laterals become the members of a fork, It is possible to have more than two ascending branches but these usually differ in dominance.

Obviously, forking reduces the possibility that the tree will be suitable for timber, Carvell observed in one 6-year-old red pine plantation in West Virginia that 76% of trees having lammas growth the preceding year had a permanent fork in the bole (3). Of the remaining 24%, the leader had retained dominance but the lammas shoots had produced "large, ascending branches which would ... act as avenues for decay to enter the bole" (3). A forked tree is of little value for timber and is completely worthless as a Christmas tree.

Jump indicated still other disadvantages inherent in forked trees, The forked condition need not be permanent to cause permanent injury to the tree. One fork may eventually achieve dominance; but during the period in which the forks stand at an acute angle to each other, they are "unable to slough off, or push aside, the bark that lies on the inside of the fork between their cambiums, in the manner that the growth of the trunk displaces the bark of a normal lateral branch. This area of non-union of cambium remains in the main axis of the tree as a fissure or pocket that becomes filled with heterogeneous material composed largely of resin and fragments of the bark..." (6). These fissures, in a vertical plane for many years, are easily penetrated by water and provide a favorable environment for "many species of parasitic bacteria and fungi" (6).

Jump also remarks on the increased winter damage to stands of red pine containing a large number of forked trees since the forked branch has less resistance to stresses imposed by the weight of ice or snow. If such a fork breaks, it produces a dow w rd extending cavity in the tree which "may extend almost to the pith"(6). Normal branches snap off at a point beyond the trunk while the forks snap off within the trunk, Both the cavity left by the broken fork and the fissure resulting from the non-union of the cambium in the area of a fork provide entrance to wood destroying rots and diseases. Jump's inspection of sectioned red pine revealed that "Forked areas were almost invariably accompanied by reddish brown streaks within the wood" (6). Forking, therefore, lowers the value of pines directly as a result of crooked boles or indirectly through wood rots, diseases, and wood discoloration.

Causes of Lammas Shoot Formation

1. Site and weather. Littlefield indicated, in a quote of New York District Forester C. E. Baker, that bifurcation of red pine "is pretty closely tied up with site and of course red pine growing on the wrong site is like every other tree, subject to more maladies" (7). However, evidence does not indicate that site, as such, is an important factor in the production of lammas shoots. McCabe and Labisky felt that site could not be disproved as a causative agent of forking (which they indicated was due primarily to lammas growth) but; "The obvious relationship appeared to be between the incidence of forking and some factor or factors of weather"(8).

Peak occurrence of forking in the red and white pine plantations under McCabe and Labisky's observation occurred in the same years as those of two other workers in Wisconsin who studied plantations at other sites (8). "From these data it could be implied that the factors causing forking are associated with the year rather than with intrinsic factors of the plantation itself (e.g. age, soil, slope, pH, etc.)" (8).

Carvell's study also indicates that laminas shoot formation is associated with the year rather than the site, In 1951 and l952 no lammas growth was observed in the red pine plantation which Carvell investigated; while in 1953, 19% of the young trees had one or more lammas shoots (3).

Jump found that, "There appears to be no marked correlation between forking in red pine and site conditions, except a possible relationship with the mean seasonal temperature of the locality" (6). He found, "Degree and aspect of slope ... to be of no significance" (6). In Jump's study the plantation which was the northernmost and the highest in altitude exhibited the least forking.

2. Genetic control. In the plantations of McCabe and Labisky's Wisconsin study (8), 3 trees had been pruned to remove one member of a fork in an attempt to improve the appearance of a demonstration stand. Subsequent observation revealed that only 11 of the trees so pruned had forked again. The percentage was supposedly "no greater than that for unpruned trees" (8). Thus, McCabe and Labisky felt that they were unable to prove genetic differences in disposition to forking, if indeed such differences existed. Though interesting., this experiment has no design or control.

In an attempt to explain the cause of forking, Jump ruled out insects since bud sections and daily observations disclosed no evidence of such disturbance. Physiological disturbance was also considered unlikely as the study covered a wide range of soils. As regards a genetic. cause, Jump discounted this on the basis that: "The wide geographic range of the occurrence of forking, together with the fact that forking in neighboring stands may gradually attain a maximum in different years and at different ages of the plantings indicates genetic influence to be unlikely" (6). However, Jump himself mentions in his dissertation that, "Forking may occur repeatedly in a tree. One 22-year-old specimen, when dissected, showed this phenomenon in at least 12 nodes" (6). Thus, this tree must have exhibited lammas growth in about 60% of its growing seasons.

3. Fungal cause. Jump's conclusion was that a fungus, *Dematium pullulans*, was the cause of lammas shoot formation and therefore of forking also. He was able to isolate this fungus from the buds and forks of red pine which had formed lammas shoots (6). He further showed that Dematium pullulans produced an auxin, It was hypothesized that this auxin would stimulate the laterals, which are normally low in auxin, but not affect the terminal, which is normally high in auxin. However, this was not tested by inoculating normal trees and observing them for subsequent lammas shoot formation; Jump stated that the fact that normal trees might contain this fungus did not invalidate his theory, since forking may be latent in such individuals (6).

Jump's work was published in 1938 and in light of more recent knowledge of auxin control his hypothesis would appear to be untenable, There is a differential response to varying concentrations of auxins by different plant tissues. The apical, or terminal bud, according to Bonner and Galston (1), produces auxin in relatively high concentration. This auxin inhibits lateral buds but does not inhibit the terminal bud. The suppression of the lateral growth by the terminal bud, is known as apical dominance. Apical dominance varies with the type of branching habit of the plant and is very complete in the monopodial branching conifers.

METHODS

In the spring of 1959, three plantations of Scotch pine were established in New Jersey, The three plantations are located at Beemerville, lat. 41° 12' N and long 74° 43' W; Cranbury, lat 40°19' N and long. 74° 31' W; and Green Bank lat. 39° 37' N and long, 74° 34' W. The north-south distances between plantations are 62.5 miles from Beemerville to Cranbury and 49.1 miles from Cranbury to Green Bank. The plantations all lie in an east-west range of 10.7 miles or 12 minutes of longitude. The altitudes of the three plantations are about 800 feet at Beemerville, 115 feet at Cranbury, and 10 feet at Green Bank.

Thirty-five seed sources are represented in the plantings. Seedlings of the thirty-five sources were grown from seed collected from known mother-trees located in established plantings in New York, Pennsylvania and New Jersey.

The plantations were adaptable to the present study because of their planned design which is susceptible to statistical analysis. Each plantation was divided into 30 blocks and each block contained 35 trees, representing the 35 sources. The sources were randomized in each block, Since the seed sources are randomized within blocks, the heterogeneity of site within the plantation has no effect on the statistical analysis, and thus no effect on the ability to infer conclusions.

All 1050 seedlings in each plantation were examined for lammas shoots in 1960 and 1961 and those seedlings exhibiting lammas growth noted by source and block. The results were analysed as a 3 factor analysis of variance. Seed source, the main object of investigation, was at 35 levels; location (plantation) was at 3 levels; and years (1961 and 1962) was treated as a factor at 2 levels, even though it was expected that year would not interact with the other variables. The model was: lammas shoots = b_0 + b_1 (seed source) + b_2 (year) + b_3 (location) + b_{12} (seed source x year) + b_{13} (seed source x location) + b_{23} (year x location) + Error. The analysis was made on the average occurrence of lammas shoots per source in any one year and plantation in order to correct for mortality.

A separate analysis was made within the Beemerville plots since this plantation is located partly on a slope with up to 10 feet difference in elevation within. The occurrence of lammas shoots in a row of 6 blocks on a southeast aspect was analyzed against the row of 6 blocks of a northwest aspect. Thus, the experiment included a test on the significance of aspect as an influence on lammas shoot formation. Aspect was treated as a variable at two levels. The model for this analysis was lammas shoots = b_0 + b_1 (seed source) + b_2 (years) + b_3 (aspect) + b_{13} (seed source x aspect) + b_{23} (years x aspect) + Error.

RESULTS

Table 1 shows the occurrence of lammas shoots. In 1960 the southernmost plantation at Green Bank produced 365 seedlings exhibiting laminas growth. Moving north, the plantation at Cranbury had 152 seedlings with lammas shoots. The northernmost plantation, Beemerville, (which was also highest in altitude) had the least laminas shoots with 108 seedlings bearing the precocious branches. In 1961, the number of cases of lammassing increased by 98 over the previous year in the Green Bank plantation and 89 in the Cranbury plantation. However, there was a decrease of 12 in the Beemerville plantation for the same period.

The repetition of lammas shoot formation in seedlings was lower in Beemerville than in either Cranbury or Green Bank. The percent of seedlings having lammas growth in both 1960 and 1961 was 26.9%, 77.6%, and 86.8% respectively (table 1).

Table 1.--Occurrence of lammas shoots.

	1960		1961		Repeat in 1961		Total in 1960 & 1961
	No.	Percent	No.	Percent	No.	Percent	
Beemerville	108	12.4	96	11.0	29	26.9	204
Cranbury	152	15.5	241	24.6	118	77.6	393
Green Bank	365	35.0	463	44.4	317	86.8	828
Total	625	-	800	-	464	-	-

Table 2.--Occurrence of lammas shoots by selected seed sources.

Coded seed source	Beemerville 1960	Beemerville Repeats in 1961	Beemerville Total 1961	Cranbury 1960	Cranbury Repeats in 1961	Cranbury Total 1961	Green Bank 1960	Green Bank Repeats in 1961	Green Bank Total 1961	Two year Total
9	2	0	2	3	1	5	4	3	7	23
14	2	1	3	0	0	4	8	8	10	27
15	6	1	2	6	6	10	14	11	13	51
17	4	0	0	1	1	7	2	2	7	21
19	7	6	10	10	9	13	16	15	21	77
33	2	1	3	6	5	6	18	14	16	51
29 others	85	20	76	126	96	196	303	264	389	1175
Total	108	29	96	152	118	241	365	317	463	1425

From comparison of the selected seed sources (table 2) it appears that seed source 19 was consistently high across all years and plantations. An analysis of means chart (figure 3) based on figures corrected for mortality verified this and showed other significant variation between sources.

Partitioning of the sums of squares and subsequent F-tests using the mean square of the 3 factor interaction as an estimate of error pointed up the following. The location by years interaction and the seed source by location interaction both proved significant at the 1% level. This indicates that all the three main effects--seed source, location, and years--have important effects on occurrence of lammas shoots. The mean squares for seed source, location, and years almost overshadow the interaction effects and would be themselves significant on the 1% level. However., the factors did not act independently of each other and can not be separated statistically--they exhibit a significant interaction. For example, table 1 reveals that although the year 1961 produced more laminas shoots than 1960, it did not produce the same relative increase in all plantations. In fact, Beemerville dropped for the year 1961. Conversely, although there is an increase in lammas shoots from Beemerville to Green Bank, the relative increase is not the same in 1960 as it is in 1961.

Another statistical aid, an analysis of means chart (9), was prepared for the effect of seed source. This analysis (figure 3) indicates that 6 sources are significantly higher than the average in occurrence of laminas shoots at the 1% level and 6 sources are significantly lower than the average.

In the analysis of the occurrence of lammas shoots between the two aspects on the Beemerville plantation, no significant difference was found between the northwest and the southeast aspects. The sum of the average occurrences of lammas shoots on the northwest aspect was 9.969 as compared to 9.185 on the southeast aspect. Neither were there interaction effects between year and aspect or between seed source and aspect at the 1% or the 5% level of significance. Even in this small test of only a few seedlings, seed sources showed significant differences in the occurrence of laminas shoots.

Figure 2.--Lateral branches of current year extending above the terminal leader (indicated by pencil) as result of formation of lammas shoot growth in previous season in Scotch pine.

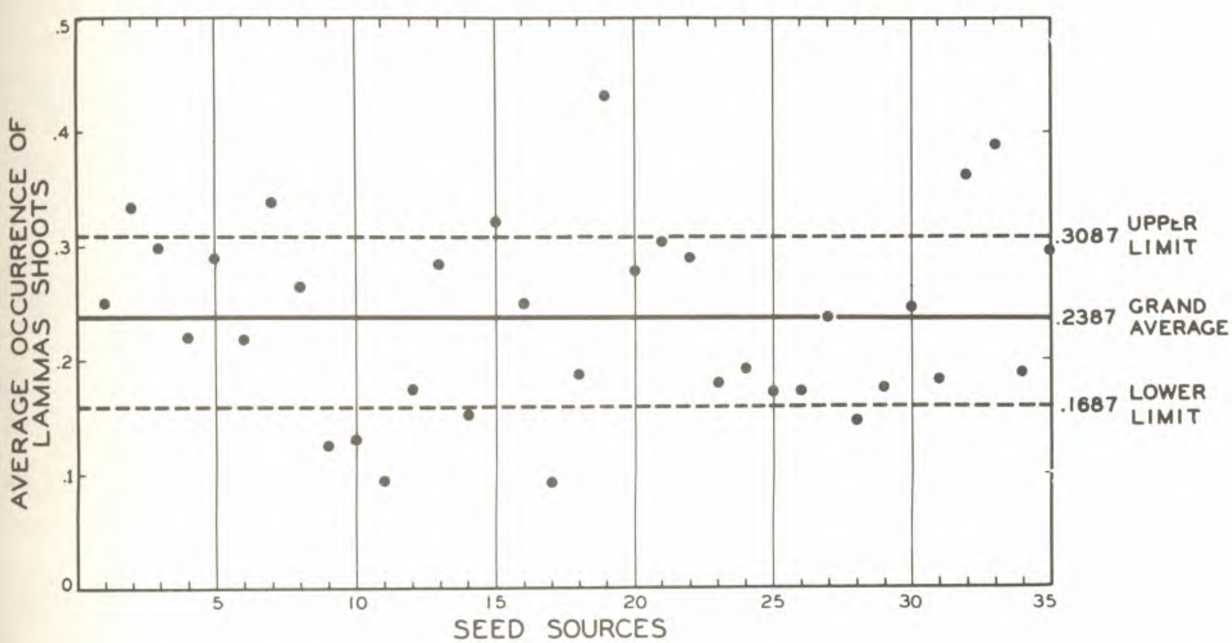

Figure 3.--Analysis of Means Chart. Any seed source above the upper limit or below the lower limit is significantly higher or lower, respectively, than the average at the 1% level in formation of lammas shoots.

DISCUSSION AND CONCLUSIONS

Genetic Variation in Lammas Shoot Formation

The results of this experiment show that occurrence of lammas shoots is different between seed sources. Analysis of variance shows that seed source is an important factor in the occurrence of lammas shoots.. Analysis of means chart for seed sources shows that sources 9, 10, 11, 14, 17 and 28 produce significantly fewer lammas shoots than the average and that sources 2, 7, 15, 19, 32 and 33 have significantly more laminas growth than the average. Within the Beemerville plantation, seed source was shown to be the single most important factor in occurrence of laminas shoots by an analysis of variance on two aspects of that plantation. The basic difference which is understood to exist between seed from different mother-trees is that of genotype. Therefore, genetic differences exert an influence on occurrence of lammas shoots.

McCabe and Labisky (8) found: "Of 275 17-year-old red pines only 7.3% showed multiple forking, and 4.5% occurred in 337 white pines of the same age". They felt that this did not indicate genetic inheritance of the phenomenon, However, these data are greatly at variance with that of the present study. Even in the Beemerville plantation, which is lowest in repeat lammas shoots for 1961, the proportion of repeats is 26.9%. The Cranbury plantation had a repeat rate of 77.6% and in Green Bank 86.8% of the seedlings which had laminas shoots in 1960 had lammas shoots again in 1961, Using this measure as an indication of genetic influence, then these data substantiate the conclusion that lammas shoot formation is genetically controlled in the sources studied.

In one 22-year-old red pine sectioned by Jump (6), forking was evidenced at 12 nodes. But this is evidence of forking only. Carvell (3) estimated that of the pines he studied which had lammassed, only 76% would become forked. Thus, Jump's red pine indicates a high degree of repetition which would be accounted for on a genetic basis.

Evidence also exists in the literature which may support the hypothesis of genetic control of lammas shoot formation. McCabe and Labisky (8) presented a history of forking in the University of Wisconsin Arboretum and elsewhere in Wisconsin. Their study produced a significant difference between amount of forking in white pine as compared to red pine--22% and 46% respectively. An adjacent plantation which had been established 8 years later than the first, however, produced values of 21% and 10% in forking of white and red pines respectively. There is a good chance that plantations established 8 years apart may draw on seedlings of different sources, What would then be expected under the proposed hypothesis is what occurred--a difference in the amount of forking.. The same argument may be applied to other figures which this study quotes- in still another plantation J. R. Been had found 88% of white pine and 84% of red pine forked while elsewhere in Wisconsin, Honey found 38% of plantation white pine and 57% of natural white pine forked.

There is a long list of unaccountable variation in forking between adjacent plantations. This variation is evidence that differences exist between planta tions--and plantations are more likely to be genetically similar within than between. Results of the present study force the conclusion that there is a genetic influence on the occurrence of lammas shoots.

Phenotypic Expression

The experiment points up another fact concerning the genetic control of laminas shoot formation. Foresters have found in practice that trees exhibiting good form and growth in one location may not reproduce individuals equally as well suited to other locations. For instance, the U. S. Forest Service specifies that seed for its plantings originate at the same altitude (within a certain range) as that on which it is to be planted (4). Similarly, this experiment has shown that the phenomenon of lammassing varies with location of the plantation. Though one seed source may produce many lammassed individuals compared to another source at one location, it may produce relatively fewer lammassed individuals when the two sources are transferred to a new environment. The interactive effect, dependent on both the seed source and the environment, was significant in this experiment although the range of latitude tested was only 1° 35' and that of longitude only 12'.

Influences on the Development of Lammas Shoots

The factor location is synonomous with geographic position. Geographic position determines many variables. Some of these are soil, slope, aspect, and pH. Another factor determined by geographic position is weather.

In the present study it is hypothesized that the only difference between the two levels of year, 1960 and 1961, is the factor of weather. There is no statistic to describe a difference in weather between any two periods and the present experiment contained no method of measure to separate individual components of weather.

If the significance of location was really due to influences of soil, pH or slope, the two factors, year and location, would probably not interact to such a highly significant degree (1% level). The effect of year could then be separated from the effect of location. Inability of the experiment to separate year from location represents an inability to separate the influence of climate from that of local weather.

The one factor of site that was deliberately tested in the present experiment was aspect. This proved non-significant in effect on lammas shoot formation and was separable from the effect of years at the level of 1%. The fact that other conditions, notably soil texture, varies between plantations makes it impossible to completely rule out intrinsic site conditions as an important factor.

It may be inferred, therefore, that the climate of any given area is an important influence on the occurrence of lammas shoots subject to yearly weather variation as it is modified by local influences.

Most investigators have felt that weather is an important variable in forking or lammas production. The study made by McCabe and Labisky (8) indicated that although site could not be disproved as a causative factor in forking, the relationship seemed to be connected with a factor or factors of weather. The years of peak forking in their study coincided with those reported by other investigators in Wisconsin. They stated that this implied forking was associated with the year rather than with intrinsic site factors.

Carvell (3) reported no lammas growth in 1951 and 1952 but 19% in 1953. In 1953 he observed weather conditions had been much different than in the two years preceding, Jump (6) was unable to find any marked correlation between forking and site conditions, "except a possible relationship with the mean seasonal temperature of the locality".

The present study and previous investigations indicate that factors of weather might exert a strong influence on occurrence of lammas shoot formation.

SUMMARY

The present study, utilizing three plantations designed for progeny testing of 35 different seed sources of Scotch pine established in 1959, allows a definite conclusion to be drawn as to the genetic basis of lammas shoot formation, Results of this study indicate that there is a significant difference between seed sources in amount of lammassing. Genotype is therefore an important factor in amount of Lammas shoot formation.

A significant variation in phenotypic expression of the phenomenon between the seed sources at the three different locations was found to exist. Influence of aspect within the one location tested was not significant.

Location and year could not be separated as simple effects on lammas shoot formation, They interact and effect the phenomenon as a combined factor. The inability to separate the effects of these two factors is indicative that both are measuring weather.

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