DEGREE DAY REQUIREMENTS FOR BUD FLUSHING IN WHITE SPRUCE-VARIATION AND INHERITANCE

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Plantation management of white spruce *(Picea glauca* [Moench.] Voss) can be highly profitable when improved strains are planted on suitable sites (Carlisle and Teich, 1970). The species, however, is highly susceptible to late spring frost injury, and site selection must therefore consider not only soil quality but also microclimate. In the extreme continental climate of the northern Lake States and adjacent Canada, even the most careful selection of a suitable microclimate cannot prevent occasional severe damage from late spring frost. Risk of damage, however, can be materially reduced if late flushing strains are used. The correlation between time of flushing and frost damage has been described previously for white spruce (Nienstaedt and King, 1970) and other species (Busgen and Munch , 1929; Sweet, 1965; Kiellander, 1970).

It is possible that in exceptional years early flushing trees may attain a degree of frost resistance while late, recently flushed trees are still highly susceptible. In such years with unusually late frosts, the late trees may in fact suffer more damage than those with early budbreak (Langlet, 1960). No critical research has been done on white spruce relating specific stages of shoot elongation to frost damage; it is sorely needed but outside the scope of this report.

Early research (Nienstaedt and King, 1970) reported degree day requirements for selected clones of white spruce and heritability estimates based on the growth of progenies of some of the clones in growth rooms and the greenhouse. The following summarizes results with parental clones and their progenies during three additional seasons.

METHODS AND MATERIAL

Details of the origin of the clonal selections, the controlled pollinations, and the early development **of the** progenies have been described (Nienstaedt and King, 1970). In general, the study has involved a clonal field test with five replications at a single location and a progeny test under a variety of conditions indoors as well as in the nursery. Sixteen "late" and nine "early" clones were used in the field test; female parents for the progenies were nine "late" and one "early" clone from the field test plus three "early" clones from another study. No field data are available for the last three clones. The females were crossed with three pollen mixtures—unrelated early, late, and randomly selected pollen parents. The progenies were tested in two growth rooms and a greenhouse throughout the winter of 1969. The 1970 paper reported only results with 27 progenies of the "late" clones; in a few instances, the results in this paper will involve the 39 progenies of all 13 parent clones.

On February 5, 1969, the seedlings from the greenhouse were moved to a growth room (Growth Room #21, Nienstaedt and King, 1970) and, with all other seedlings, exposed to a dormancy inducing 13-hour photoperiod (item #5 below).

On April 2, 1969, all plants were then moved to the cold room where they were chilled at 36°F. and exposed to a 13-hour photoperiod until June 3 (item #6 below). In summary, the entire treatment between germination in the greenhouse in February, 1968, and planting in the nursery in August, 1969, was:

1. February, 1968—July, 1968
   Germination and early growth in the greenhouse.

2. July—End of September, 1968
   Growing under outdoor conditions modified by 50 percent shade in the lathhouse.

3. September—November, 1968
   Artificial chilling in order to break dormancy.

4. November, 1968—February, 1969
   Growing under controlled conditions in growth rooms and greenhouse.

5. February 5—April 2, 1969
   Dormancy inducing short-day treatment in the growth rooms.

6. April 2—June 3, 1969
   Artificial dormancy—breaking **chilling** in the cold room.

7. June 3—August, 1969
   Growing under outdoor conditions modified by 50 percent shade in the lathhouse.

8. August 11-15, 1969
   Transplanting to the nursery. All subsequent treatment was equivalent to standard nursery procedures and field planting.

For the progenies, Nienstaedt and King (1970) treated data on flushing in controlled environments in

November-December, 1968, and total height in March, 1969. In addition, this paper reports data on:

1. Flushing in the lathhouse measured on June 18, 1969. The scoring was based on 6 grades-the score "6" signifying dormancy and "1" active elongation (for details see Nienstaedt and King, 1970).

2. Total height in the nursery in August, 1970.

3. Flushing in the nursery in May, 1971. Scores for five dates of scoring were averaged and presented here.

4. Total height in the nursery in August, 1971.

Nienstaedt and King (1970) reported degree day (d.d.) requirements in the clonal test for one year. In addition, this paper discusses degree day requirements in the growth rooms and nursery for the progenies.

RESULTS

Figure 1 summarizes the flushing of 27 progenies in the lathhouse in 1969 and in the nursery in 1971, and compares these data with the flushing in the greenhouse in 1968. The graph groups the progenies of the three pollen mixtures (E = early; L = late; R = randomly selected males) by female parents.

The male effect is particularly clearcut for the responses in the nursery. In every one of the nine groups of related families, development followed the expected pattern. The families with the "late" pollen mixture as male parent were the slowest to develop in all cases. Also, the correlation with the parental clones was highly signficant (Table 1). These correlations represent only the narrow, 7-day spread in flushing of the late clones. If correlations could have been determined for a complete sample of flushing types, they undoubtedly would have been even larger. The pattern was less clearcut, but still recognizable in the greenhouse-five of the nine family groups followed the pattern.

In the lathhouse, the pattern was completely different: the families with the "late" male parent developed first in eight of the nine groups of families.

In March, 1969, at the end of the growth in the greenhouse and growth rooms, the heights ranged from 6.4 to 8.5 cm. By August, 1970, after one season's growth in the nursery, the range was 26.6 to 33.6 cm. and one year later 41.4 to 50.7 cm. The three measures of height were all correlated.

It is important to relate height growth of the progenies to the flushing characteristics of the clonal parents and to the flushing of the progenies themselves; this is done in Tables 1 and 2. All the correlations are negative, and three of the 12 values reach significant levels; all are relatively large, probably real, and may have important implications in selection. Average heights for the nine female groups in August, 1971, were not significantly related to the flushing of the clones (Table 1). They were highly significantly (1-percent probability level) related to the flushing of the progenies in the greenhouse in 1969, but not to the flushing in the nursery in 1971 (Table 2). Heights in 1969, but not in 1970 and 1971, were significantly related to the 4-year averages for clonal flushing (Table 1).

Heritabilities were computed on the basis of means of the 27 progenies from 9 female parents for flushing and height measurements in the nursery. It was relatively high for the variation in flushing, $h2 = .536$; for height it was $h^2 = .207$ in 1970, and $h^2 = .406$ in 1971 (for the model used see Nienstaedt and King, 1970).

Degree day requirements (+ 40° F.) for the clonal test were computed as averages for three weather stations located within 20 miles of the test. The following compilation summarizes the data for all the clones:

	1968	1969	1970	1971
16 LATE CLONES: [1]				
Date of Flushing	**29.9**	27.0	29.4	33.8
Degree Days	580	569	560	504
9 EARLY CLONES:				
Date of Flushing [1]	**15.3**	12.1	17.1	18.6
Degree Days	411	351	344	315

[1] Number of days after May 1st.

Data for the nine parental clones and their progenies are summarized as follows:

CLONAL DATA (AVERAGE OF 9 LATE CLONES):

1. 4-Year Average (1968-1971) 546 d.d.
2. 1971 Requirements 499 d.d.

PROGENY DATA (AVERAGE OF 27 PROGENIES):

1. Nursery 1971 285 d.d.
2. Cool Growth Room #19
   60° Day - 55° Night 258 d.d.
3. Warm Growth Room #21
   65° Day - 55° Nights 423 d.d.
4. Greenhouse
   75° Day - 65° Night 510 d.d.

[1] For details, see Nienstaedt and King (1970).

The latest average date of flushing was in 1971, the year with the lowest degree day requirement-504 d.d. for the late clones and 315 d.d. for early clones. That same year, the average for 27 progenies in the nursery was 285 d.d. (data from the same three weather stations). In the growth-room phase of the study, the requirement was the lowest in the coolest environment -258 d.d., and almost twice that amount in the greenhouse, which had the warmest environment.

DISCUSSION

Continued observations on the clones and progenies have verified the strong genetic control of the time of flushing, and, at the same time, have thrown some light on the modifying effects of environment and the developmental phase of the trees. The year-to-year

differences between the earliest and latest average dates of flushing over the 4 years of observations were 6.5 days for the early clones and 6.8 days for the late clones. This is about half the difference observed in young Douglas-fir by Irgens-Moller (1967) and less than one-quarter of the range observed in two Douglas-fir clones over a period of 14 years (Morris, Silen and Irgens-Moller, 1957). Although it would be reasonable to expect the difference to be smaller in the continental climate of northern Wisconsin, added years of observation probably will prove the spread to be greater in white spruce also.

It is perhaps significant that the lowest degree day requirement was recorded in the year with the coolest spring, and the latest recorded date for flushing. It appears to agree with the observation in the two growth rooms and the greenhouse; there the lowest degree day requirements were also recorded in the coolest environment. The verification of these observations and the clarification of their physiological significance would be an important contribution.

Of the three indoor environments, the coolest (60°F. day — 50° F. night) yielded the degree day requirements that were nearest the values determined two years later in the nursery. When the study originally was planned, the cool environment was included with the expectation that the lower temperature would accentuate the differences between the progenies, and therefore yield the highest estimates of heritability for flushing. This was not the observed result; the highest heritabilities were obtained using the greenhouse data—the warmest of the three environments. Spring was cool in 1971, and the heritability estimate was relatively high—$h^2 = 0.536$, but not as large as $h^2 = 0.705$, computed on the basis of the greenhouse data. The results leave unanswered the question: What is the best test environment for studies of genetic variation in the time of flushing?

How strongly the use of controlled environments can influence results and lead to erroneous conclusions is demonstrated by the flushing data from the lathhouse in 1969. The correlation between the flushing in the greenhouse in 1968 and flushing in the nursery in 1971, $r = 0.6510$ (d.f. = 7, based on nine female averages), approaches significance at the 5-percent level; (computed on the basis of 13 female group averages, $r = 0.709$ is significant). The correlation between flushing in the lathhouse in 1969 and flushing in the nursery in 1971 is negative; not significant on the basis of female group means ($r = -0.5739$; d.f. = 7), it is highly significant when computed on the basis of 27 individual families $r = -0.6334$; d.f. = 25.

Previous research has demonstrated that 4 to 8 weeks of chilling white spruce at 36° to 40° fulfills chilling requirements and assures prompt breaking of dormancy under greenhouse conditions (Nienstaedt, 1966). Other studies have indicated that the length of the photoperiod during bud formation materially effects the formation of needle primordia (Dormling, Gustafson, and von Wettstein, 1968); one experiment in white spruce has indicated that 6 to 8 weeks of short day exposure are required for normal development of the new shoot (Nienstaedt, unpublished manuscript).

The treatments after February 5, 1969, were designed to meet these requirements and assure normal subsequent flushing. They failed to do so. The reasons for this are not clear. They are probably related to the hardening-off period rather than to the chilling treatment during which dormancy is broken. Conditions during hardening can, as mentioned, affect primordia formation and also chilling requirements (Nienstaedt, 1966), while the chilling simply acts to release dormancy. The results do emphasize the importance of follow-up field studies to verify observations in controlled environments. Follow-up tests should be conducted in environments resembling the sites of eventual commercial planting.

The time of flushing becomes progressively later as a tree ages. This is clearly shown by the data for degree day requirements in 1971; the average requirement was 499 d.d. for the parental clones, but only 285 d.d. for the progeny. This difference equals 10 days to two weeks of degree day accumulation, and is substantially shorter than the differences of 2 to 4 weeks reported for other species (Irgens-Moller, 1957; Busgen and Munch, 1929).

In their paper, Nienstaedt and King considered as encouraging the possibilities of simultaneous selection for late flushing and superior growth. This conclusion was based on the superior performance of the late flushing clones. However, the growth of the progency brings the conclusion in doubt. The negative correlation between time of flushing and height growth would suggest the contrary. To this can be said: (1) That female parents of the progenies involved in the correlations only represent the narrow spread of about seven days between the earliest and latest of nine *late* parent clones. Had they represented the entire three-week spread of the clones in the field test, perhaps they would have supported the earlier clonal data. (2) The fact that the correlations are non-significant indicates considerable scatter around the regression line (and few degrees of freedom). This may mean that the development of late flushing, fast growing types, in spite of the very high heritability for flushing, may require large-scale progeny testing in order to identify the relatively few individuals that combine late flushing and fast growth.

Table 1. Simple correlations [1] between clonal flushing and the heights and flushing of the progenies

Progeny characteristics	Clonal Characteristics	
	Flushing Date 4-Year Ave.	*D.D. Requirement 4-Year Ave.*
Flushing score in greenhouse	0.780*	0.739*[2]
Flushing score in nursery	.851**	.873**
Height March 1969	-.690*	-.649
Height Aug. 1970	-.529	-.441
Height Aug. 1971	-.653	-.579

[1]Correlations based on averages for 9 female groups (d.f. = 7).

[2]* = significant at 5-percent level and ** = significant at 1-percent level of probability.

Table 2. Simple correlations [1] between flushing characteristics and heights of white spruce progenies

Flushing Score	Heights		
	March 1969	*Aug. 1970*	*Aug. 1971*
greenhouse	-0.589	-0.622	-0.802**[2]
nursery	-.733*	-.457	-.567

[1]Correlations based on averages for 9 female groups (d.f. = 7)

[2]* = significant at 5-percent level of probability and ** = significant at 1-percent level

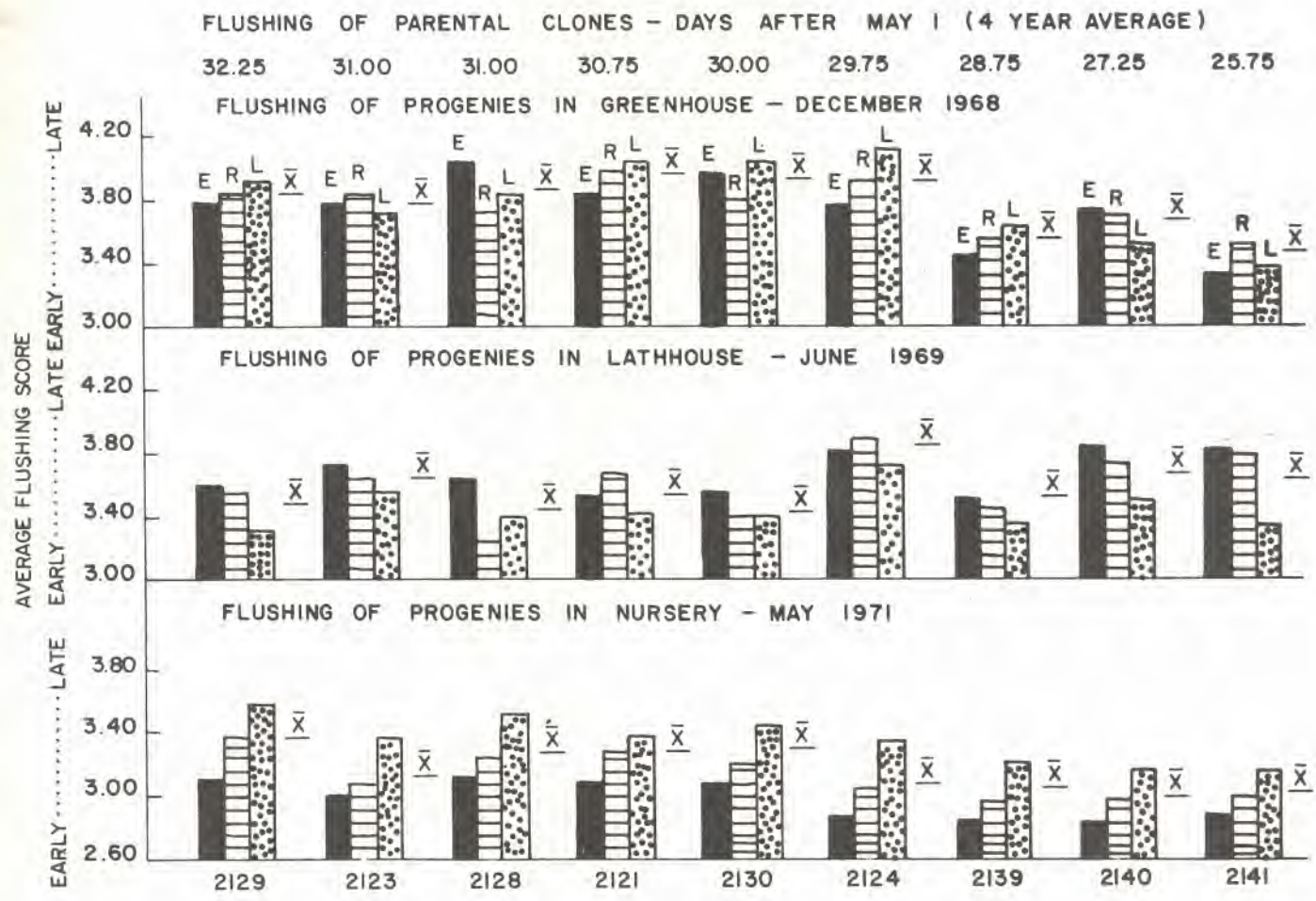

Figure 1. Flushing of the progenies of nine late-flushing selections of white spruce growing under greenhouse conditions, in the lathhouse, and in the nursery. The three progeny means in the individual female (e.g., 2129) groups were the results of pollinations with early (E), random (R), and late (L) mixtures of pollen. The average flushing dates (days after May 1st) of the female parental clones are shown as numbers on the top of the diagram. Means for the nine groups of three progenies are at the right of the individual family groups ($\bar{x}$).

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