Environmental and Genetic Control of Dormancy in *Picea abies*

By

JOHN WORRALL and FRANÇOIS MERGEN

Yale School of Forestry, New Haven, Connecticut

(Received November 26, 1966)

Abstract

The effects of temperature, photoperiod and chilling on the leafing-out of Norway spruce, *Picea abies* (L.) Karst. were studied. High temperature promotes breakage of post-dormancy, long photoperiods having no such effect. Photoperiod and chilling cause the breakage of true dormancy. However, under field conditions, photoperiod will have no effect on leafing-out date in the spring.

By use of clonal material it was possible to show substantial genetic differences between individuals in response to temperature and photoperiod. When the effect of clones was accounted for, treatments could be compared more precisely. Differences between clones were apparent in heat-sum required for leafing-out, in rapidity of response to favorable post chilling conditions, and in chilling requirement. This latter quantity was given a new definition, applicable when both chilling and post chilling temperatures are controlled and specified. This is that period beyond which a further 10 days of chilling accelerates leafing-out by less than one day, *i.e.* the point at which the slope of the line relating days till leafing-out to chilling period, is equal to minus 0.10.

Differences in leafing-out date were shown between provenances taken from throughout the range of Picea abies. These differences were related to latitude with provenances of high latitude leafing-out first.

Introduction

As has been repeatedly emphasized in the literature, discussions of dormancy in woody plants are often misleading because of the lack of a standard nomenclature. Samish (1954) stated that "it is important to distinguish between stages of rest and quiescence in reporting experiments on dormancy." Doorenbos (1953) pointed out that "many authors do not make a clear

distinction between various types of dormancy." These same statements are still valid.

Doorenbos recognized three types of dormancy for temperate zone woody plants. These are summer dormancy, winter dormancy and induced dormancy. The latter is caused by adverse environmental conditions. Woody plants are in a state of induced dormancy from perhaps January to a few weeks before leafing-out. The other types of dormancy are not caused directly by the environment, but are the result of the internal physiological condition of the plant. Winter dormancy is a state of the tissues themselves, so that a normally favorable environment will not cause breakage of dormancy, *i.e.* a passing over to the condition of induced dormancy. Summer dormancy, which is of less interest in the present discussion, is an interaction between plant parts, *e.g.* the dormancy of laterals caused by terminals, or of axillary buds caused by leaves. The terms used by Vegis (1963, 1964) — predormancy, true dormancy and post dormancy — are essentially equivalent to those of Doorenbos, and will be used in the present report. Romberger (1963) has given a comprehensive and analytical review on the subject and his book also included a section on the nomenclature of dormancy.

Many factors govern the breakage of dormancy, and these have been reviewed by the authors cited above. In our experiments we were concerned with the effects of photoperiod, chilling, and temperature, and with tree-to-tree and racial variation. Although the several experiments that were conducted are reported under separate headings, they are all interrelated.

General Methods

In determining the effects of different environmental conditions, clonal material, or highly inbred lines should be used, otherwise response to environment may be masked by genetic differences. Conversely, several clones per species should be studied, if the results are to be validly extrapolated to the species as a whole. Clones of tree species, particularly conifers, have not been used to any great extent in research, because vegetative propagation is often difficult. Clones have been used mainly with herbaceous species, such as the grasses (*e.g.* McMillan 1959). There is also a large body of data for fruit tree varieties, which are vegetatively propagated. In the first two parts of this study, clones of Norway spruce, *Picea abies* (L.) Karst. were used. These were derived by rooting cuttings from individual trees of a mature stand growing in New Haven, Connecticut. The same cuttings were used in a previous experiment by Mergen, Burley, and Yeatman (1964). As with most older plantations in North America the seed source was unknown. It is likely, however, that the trees were grown from one seed collection rather than several, so that the differences between clones reported below are within-provenance rather than between-provenance differences. The age of the ramets from rooting, was eight years, and they have been grown in plastic pots in the nursery, year round. The plants showed little or no apical dominance, so that they were designated as having broken dormancy when the bud scales had separated sufficiently to show the fresh green needles in 50 percent of the viable buds.

I. Effect of Temperature

a) *Field Temperature*

Review

Because photoperiod in a specific area is constant on any date from year to year, providing cloud-cover is ignored, control of the breakage of dormancy by photoperiod alone should ensure that "spring" would always arrive on the same date. On the contrary, it is well known that there is a wide year to year variation in date of breakage of dormancy. Such variation is generally related to difference in temperature. The phenological behaviour of both vegetative and reproductive buds in different years has been recorded for many species. Perhaps the most striking data were reported by Williams (1953). Leafing-out date of oak and ash in Hevingham, England, ranged 54 and 63 days respectively, over the period 1751 to 1947. Data of this type do not support the idea of photoperiodic control of breakage of dormancy.

Experimental

Phenology of rooted *Picea abies* cuttings was followed in the nursery in New Haven, Connecticut, in 1965 and 1966, and their leafing-out date recorded. In this group (1) there were 12 ramets per clone. Additional data were collected on young material (2 years), with fewer plants per clone (1 to 6 each). These plants, designated as group 2, also differed from the first group in their location in the nursery, and in the soil and pot type in which they were growing.

Results and discussion

Mean leafing-out dates per clone for group 1 were calculated, and these are shown in Figure 1 a where 1966 leafing-out date is plotted on 1965 leafing-out date. The data from group 2 are shown in Figure 1 b. The mean dates of leafing-out in 1966 were significantly later than those of 1965, and the mean April and May temperatures in the two years were respectively $7.8°C$ and $6.7°C$, and $15.6°C$ and $12.2°C$, so that later leafing-out could be attributed to the lower temperature. More definite is the pronounced effect of genotype. The regression data show that there is consistency in the relative date (*i.e.* order) of breakage of post-dormancy from year to year. The r^2 values are estimates of broad-sense heritability. Because the slope of both lines is greater than one, (respectively 1.3 and 2.0), these data confirm the findings of Oksbjerg (1954) who showed that cool springs delayed the flushing of late flushing forms of Picea abies, more than that of early flushing forms. The separation of the plants into clones greatly increased the precision of the estimate of the difference in leafing-out between years. The overall standard deviation was about five days, as can be seen from Figure 1, whereas the mean standard deviation within clones was less than two days. In fact, mean dates of flushing were barely significantly different between years if the plants were treated as one population.
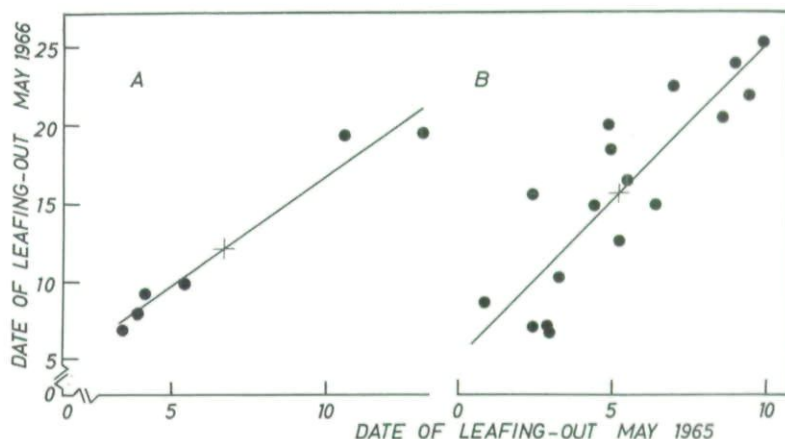
Figure 1. *The relationship between dates of leafing-out in the nursery in two years, in Picea abies.* Each point represents the mean of several plants per clone. r^2 is the coefficient of determination and measures the amount of variation accounted for by the fitted line. *A:* Group 1, $r^2 = 0.96$; *B:* Group 2, $r^2 = 0.75$.

b) *Controlled Temperature*

Review

Differences in rate of response to temperature are often explained in terms of the heat sum. This quantity, which is thought to be a constant, is required for the initiation of various plant and animal processes. It is discussed with respect to trees, by Hellmers (1962), and may be defined as the summation of the products of temperature above a certain base level, t_0, and the time of duration of that temperature. It is expressed in degree-hours, or degree-days. Numerous experiments have shown the promotive effect of high temperature in breakage of dormancy, and greenhouse forcing is, of course, a common horticultural technique.

Experimental

Three clones (A, B, and C), were brought into controlled environment rooms from the nursery on February 10th, *i.e.* after a substantial amount of chilling had occurred, and the plants were presumably post-dormant. Fifteen plants of each clone were placed in the following three temperature regimes, with days being 16 hours long — 30°C day, 30°C night; 30°C day, 20°C night; and 30°C day, 10°C night. These temperature regimes correspond to 720, 640, and 560 degree-hours per day if the heat sum is calculated from 0°C. The effect of temperature was further investigated using ramets of clone D, brought in from the nursery on March 12th and again on April 13th. In the first case there were 10 plants per treatment, in the second case 5 plants. The temperature conditions used were 20°:30°C, 20°:20°C and 20°:10°C day:night, with a sixteen-hour day. In addition, in the March 12th experiment, 5 plants were placed in complete darkness in the controlled environment room with the 20°:30°C regime. The heat sums per day were 560, 480 and

400 degree-hours. In the case of the plants in the dark, however, shielded from the radiation of the light source, the "day" temperature was reduced 1.5°C on the average next to the foliage. Consequently, heat sum per day for the plants in the dark was 536 vs. 560 degree-hours, for the light grown plants.

Results and discussion

The results for clones A, B, and C were plotted in Figure 2 as means for each clone and temperature regime, and an analysis of variance of the data was calculated. Temperature regimes and clones were both highly significantly different; high temperatures promoted breakage of post dormancy. Clones accounted for 16.5 % of the variation within each temperature regime, so that again, a considerable degree of precision is gained, for treatment contrasts, by using clonal material. In a subsidiary, less well replicated experiment along the same lines, clones accounted for 29 % of the variation within temperature regimes. The results for clone D are shown as means, in Figure 3. There are again significant differences between temperature regimes with high temperatures promoting leafing-out. Also, leafing-out re-
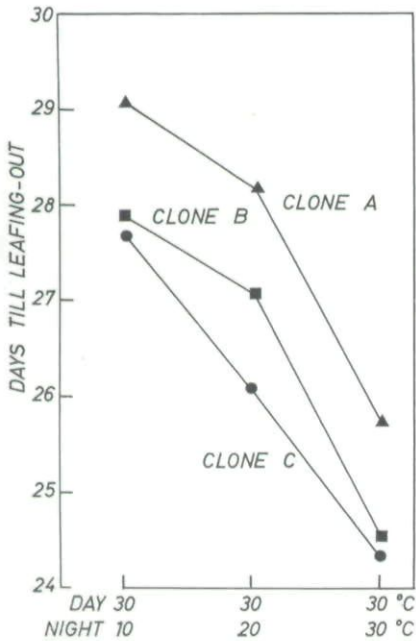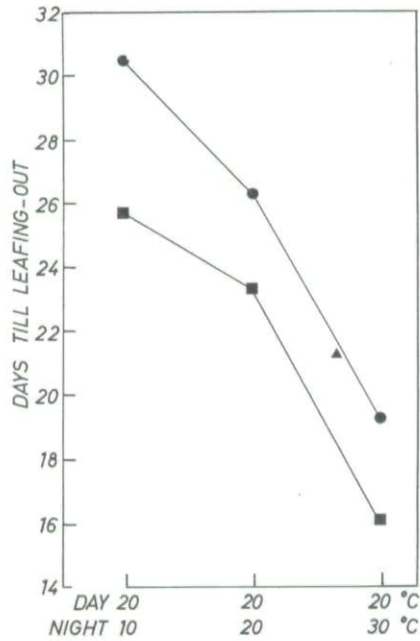

Figure 2.   Figure 3.

Figure 2. *The effect of day:night temperature and clone on leafing-out of Picea abies.* Each point is the clonal mean for fifteen plants.

Figure 3. *The effect of day:night temperature on leafing-out of a single clone of Picea abies on two dates.* Clone D: (●) on March 12th (▲ grown in darkness) and (■) on April 13th. Each square is the mean for 10 plants, other points represent the mean of 5 plants.

quired less time when the plants were brought in later. This may be due to the increased period of chilling, or more likely, to the contribution made to the required heat sum for breakage of dormancy between March 12th and April 13th. Calculations of heat sums from our data are quite inconsistent. This may be due to the very high temperatures used (designed for a different experiment being run concurrently). The different clones did require different heat sums, however.

Of particular interest is the fact that the plants of clone D grown in complete darkness broke dormancy at close to the time expected from the temperature conditions. Photoperiod had no effect on the breakage of post-dormancy in these plants. Temperature on the other hand has an extremely great effect.

II. Photoperiod and Chilling

Review

Many plant species require a chilling period before dormancy can be broken. Among trees that fail to break dormancy, if unchilled, are, for example, sugar maple *Acer saccharum* Marsh. (Olmsted 1951), and black walnut, *Juglans nigra* L. (Bode 1961). These species survived dormant for periods over a year, and broke dormancy only after a chilling period. Without a chilling period, dormancy may be broken, but abnormal growth results. Thus *Abies* species grown year round in the greenhouse in New Haven (*i.e.* never subjected to chilling), abort their terminal buds and the laterals take over. This is a serious problem when fruit tree varieties from northern areas are grown in warmer regions. Performance is poor because of lack of chilling, and subsequent failure to properly break dormancy (*e.g.* Overcash and Loomis 1959). With fruit trees, the proportion of buds that grow is important, and chilling increases this proportion, as well as accelarating the response.

There are also many reports of the effect of photoperiod in the promotion of leafing-out, but in all cases noted by the authors it seems that such effects in forest trees only occurred in unchilled or partly chilled plants, *i.e.* plants in the true dormant conditions. The marked photoperiod chilling interaction has led to the uncertainty as to the effect of photoperiod in the breakage of dormancy in the spring.

Experimental

Two clones of Picea abies were brought into the cold room, on October 14th (clone E) and on October 20th (Clone F), before any significant amount of chilling had occurred in the nursery beds. The cold room was maintained at a temperature of $4 \pm 0.5^\circ$C, and the photoperiod was eight hours. Sylvania VHO fluorescent lamps were used, supplemented by incandescent lamps to yield about 27,000 lux, as in Ib. At various intervals after the commencement of chilling, 10 plants of each clone were placed in a growth chamber with a temperature of 23°C for 16 hours, and 14°C for eight hours. Two photoperiods were used, 16 hours or eight hours, so that there were five plants per photoperiod, per clone, per chilling period.

Results and discussion

The mean dates of leafing-out are plotted in Figures 4 and 5, and the fitted lines are rectangular hyperbolas. The methods of Bliss and James (1966) were used. For clarity, only the means for the 8-hour photoperiod are shown where they did not differ from the long photoperiod means.

From these curves it can be seen that after about fifty days of chilling, there is no difference in date of breakage of dormancy between photoperiods differing by even 8 hours. In unchilled stock, leafing-out had not occurred in the short photoperiods even after 7 months (so that this point is not shown in the Figures). These plants, after one month of chilling, broke dormancy fairly quickly, but rather abnormally (resulting in very long needles well separated on the twigs). The conclusion is that both chilling and photoperiod cause breakage of true dormancy. Even a short chilling period, which will always occur under natural conditions, rapidly breaks true dormancy, leafing-out (breakage of post-dormancy), occurring when suitable conditions return. Photoperiod can also break true dormancy, but long photoperiods, occurring in nature before the date of leafing-out only in extremely high latitudes, are required.

Reworking of data in the literature, *e.g.* that of Olmsted (*op. cit.*) for sugar maple, shows that in general, the relationship between rapidity of leafing-out and amount of chilling is of hyperbolic form. In addition, it is general that, as chilling periods increase, the promotive effects of photoperiod rapidly decline to zero. Some of the most interesting data on the subject of photoperiod-chilling interaction is that of Roberts and Main (1965) who worked with American elm, *Ulmus americana* L. We have reworked their data originally presented in tabular form only, to yield Figure 6. This shows the acceleration, in days, in the date of flushing caused by a 9-hour increase in photoperiod (10 versus 19 hours), after varying periods of (nur-
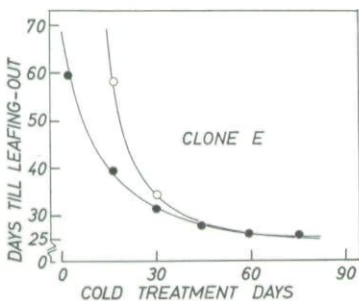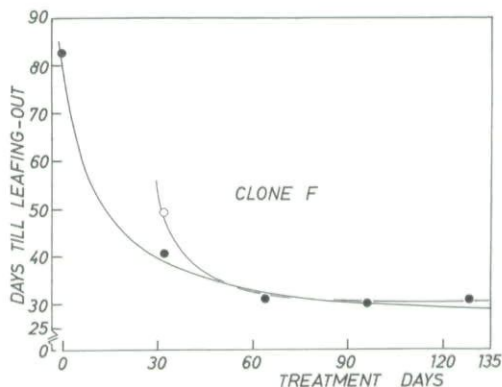

Figure 4.

Figure 5.

Figure 4 and Figure 5. *The effect of chilling and photoperiod on leafing-out of Picea abies.* Each point is the mean of 5 plants. The fitted lines are rectangular hyperbolas. Where there was no effect of photoperiod the 8 hour points were omitted for clarity, as is the point at 15 days (these plants did not leaf-out). (●) 16 h, (○) 8 h photoperiod.
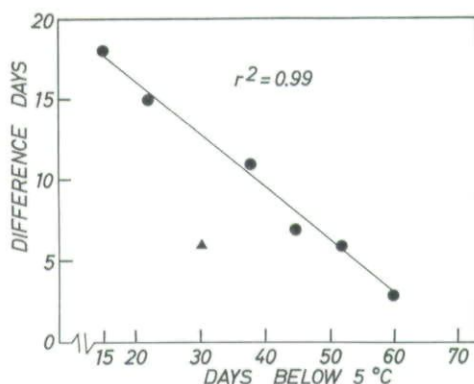
Figure 6. *The relationship between promotive effect of long photoperiods and chilling period, in the leafing-out of Ulmus americana.* The triangle is an outlying point and was not used in fitting the line. The data were derived from the report of Roberts and Main (1965). Ordinate: Difference in leafing-out date between 10 and 19 hour photoperiods.

sery bed) chilling. An extremely good correlation is evident. One point, at 15 days chilling was omitted as an outlier (P < 0.05). The promotive effect of long photoperiods tends to zero as chilling progresses. Such results cast doubt on the validity of the claims that "day length, in addition to temperature, may control the breakage of winter dormancy" (Hiesey and Milner 1965). These authors cited Hellmers (1959), who applied various photoperiods to Coulter pine *Pinus coulteri* D. Don, and big cone Douglas-fir *Pseudotsuga macrocarpa* (Vasey) Mayr, seedlings in the fall, *i.e. before* chilling. Similarly, Billings (1964) inferred a "photoperiodic timer" from the promotive effects of long photoperiods on *unchilled* alpine sorrel. *Oxyria digyna.* The extrapolation of such data to plants in their spring (chilled) condition is dangerous.

III. Determination of Chilling Requirement

Review

Chilling requirement is usually recorded in very general, often qualitative terms. Samish and Lavee (1962) have discussed this problem with respect to fruit tree species and varieties, and have pointed out that breeders need more precise information. Often the number of hours below a threshold temperature which cause breakage of dormancy is used. This however does not specify what percentage of buds must break, nor how fast they break.

Method

The Figures 4 and 5 show a slight tendency to a minimum, *i.e.* there is a small rise above the hyperbolic prediction after extreme periods of chilling. To determine if this effect is real, ramets of clone G were brought into the cold room in mid-January, after a period of natural chilling, and five ramets were placed in the growth chamber generally at two-week intervals. Days till leafing-out was recorded.

Results and discussion

Mean response is plotted in Figure 7, and fitted with a quadratic curve. The presence of the minimum is not conclusive, because for the very long
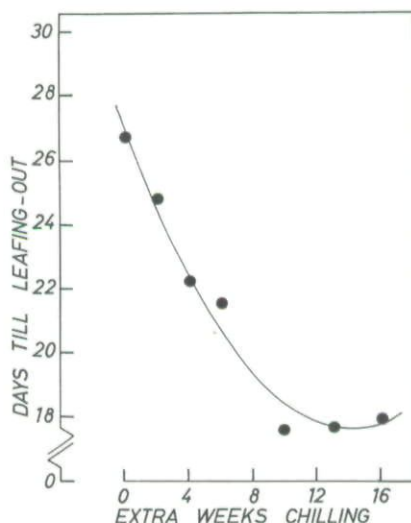
Figure 7. *The effect of extended periods of chilling on leafing-out of a single clone of Picea abies.* Each point is the mean of five plants; the fitted line is a parabola.

chilling periods, scatter about the mean increased almost threefold. Generally the five plants broke dormancy within a range of 4–5 days, but the last group ranged over 12 days. The reason for this is unknown. The adverse effect of "over-chilling" is so slight that it may be merely due to loss of vigor caused by continuing respiration in the cold room.

If there were a definite minimum in the curve, this would allow a definition of chilling requirement as that period which allows most rapid leafing-out (under a given set of post-chilling temperature conditions). Because the curves relating rapidity of breakage of dormancy to chilling period are more generally hyperbolic, with no minimum, chilling requirement can be better defined (quite arbitrarily) as that period of chilling at which a further 10-days of chilling produces less than one day acceleration in breakage of dormancy. Use of such a definition, or a similar one, will allow more precise discussion of this topic than has been possible previously. Under this definition, clones E and F differ in their chilling requirement by about 2 weeks. Note also that after their chilling requirement is satisfied they differ significantly in their rapidity of response to favorable conditions. Clones accounted for about 26 percent of variation in date of leafing-out. The data of Perry and Wang (1960), which do show real minima, can be used as an example of the calculation of chilling requirement by this new definition. Using several provenances, they applied 0, 1 and 2.5 months of controlled chilling. We have fitted to their data on leafing-out response either rectangular hyperbolas (where applicable), or quadratic curves. The equations of these lines were calculated. These are $(x - x_0) (y - y_0) = c$ for the hyperbola, $y = a + bx + cx^2$ for the quadratic curve, where x is the chilling period, y the days to break dormancy, and a, b, c, x_0 and y_0 are constants. The x value where the slope of the line is -0.10 (chilling requirement), was obtained by putting the first differential of y, $\dfrac{dy}{dx}$, equal to -0.10, and solving for x. These
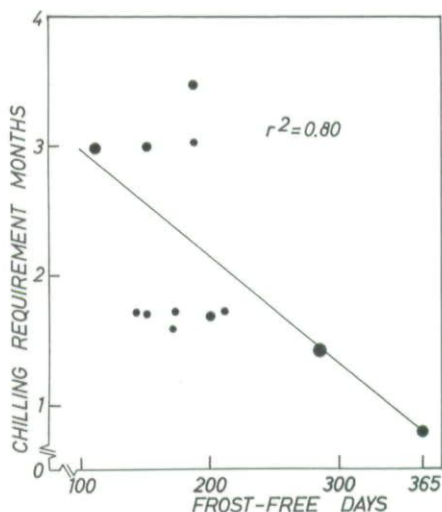
Figure 8. *The relationship between chilling requirement and frost-free days at the origin of the seed source, for Acer rubrum.* The data was derived from the report of Perry and Wang (1960). Chilling requirement is defined in the text. Size of the points represents the degree of replication. Abscissa: Frost-free days at seed source.

values have been plotted in Figure 8 against frost free days at the provenance origin. The areal size of the points represents the degree of replication. The highly significant regression indicates that chilling requirement depends on the severity of the winter at the provenance origin, as might be expected.

This racial variation allows the last evidence cited by Hiesey and Milner (*op. cit.*) supporting photoperiodic control of breakage of post-dormancy to be re-interpreted. Irgens-Moller's (1957) provenance test of Douglas-fir, run at low elevation, showed that high altitude races responded to photoperiod, low altitude ones did not. Perhaps the relatively mild winter at the low elevation (Corvallis, Oregon) did not provide adequate chilling for the high elevation sources, which therefore retained a residual response to
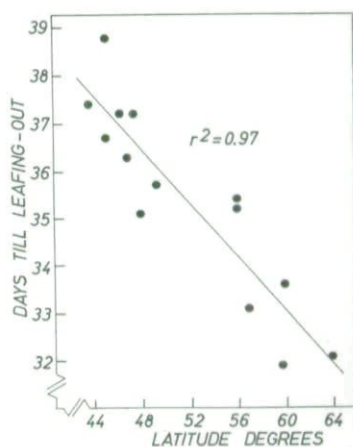

Figure 9. *The relationship between date of leafing-out and latitude of origin of the seed source in Picea abies.* See text for details.

photoperiod. Such racial variation also shows how location by provenance interactions can occur in leafing-out results. In Ohio, the northern sources, in the sugar maple provenance study of Kriebel and Wang (1962), broke dormancy before the southern ones. In Florida the reverse was true. Evidently in Ohio, southern sources were chilled for too long a period and their response perhaps retarded, and in Florida, northern sources were inadequately chilled and were slow to respond to spring conditions. Similarly, Samish and Lavee (*op. cit.*) described how the apple variety "Red Astrachan", which has a relatively long chilling requirement, blooms before "Calville San Sauveur" in a cool climate, but blooms after it in a warm climate, since it is inadequately chilled.

IV. Effect of Genotype

Review

Genetic control of leafing-out date of individuals, and of races within species has been demonstrated by provenance and progeny tests, and by transplanting and grafting techniques. Much has been published in Europe, notably on oak and beech, showing that it would be possible to breed for frost resistance (late flushing), and also to produce strains whose delicate initial stages of growth are out of synchronization with the population peaks of defoliating insects and pathogens.

General phenological observations also show that genotype has a great influence on leafing-out date. Data of this type was obtained in I. Figure 1 showed some genotypes leafing-out consistently early and others consistently late.

Experimental

To test for geographic variation in date of flushing, material from the 1938 International Union of Forest Research Organizations provenance test in Deering, New Hampshire, was used. Mergen, Burley and Yeatman (1964) have shown that field flushing can be adequately estimated by the flushing of cuttings planted in sand in the greenhouse. Consequently, on February 15, 1965, 40 cuttings from each of ten trees of fourteen provenances were taken, from comparable crown positions, and planted in sand in the greenhouse. On March 21st, three more provenances were sampled, so as to supplement the latitudinal range. In the first case, the 5600 cuttings were planted in two randomized blocks, in rows of 20. In the second case, with only 600 cuttings available, 10 cuttings per row were planted. There was appreciable mortality, and the worst 3 rows per block and provenance were discarded. Number of days for 50 percent flushing in each row was recorded, and was used for the analyses of variance.

Results and discussion

Sources differed significantly in date of leafing-out, as was shown by analysis of variance. The differences were not large, and the variance components indicated that there was more variation within provenances than between provenance means. Similarly, Ruden (1965) showed that leafing-

out date in *Picea abies* varied more between progeny of individual mother trees then between provenances (and that there was very little variation within clones).

Both sets of data show that northern provenances leaf-out first, as previous workers have shown (*e.g.* Langlet 1960). The reason for this is not clear. Presumably, northern provenances are adapted to a cooler growing season, and respond to temperatures that do not affect more southerly provenances. A linear relationship between leafing-out date and latitude of origin of the seed source is shown in Figure 9, for the first set. Correction of latitude for altitude did not improve the regression.

References

Billings, W. D.: Plants and the Ecosystem. — Wadsworth, Belmont, California. 1964.

Bliss, C. I. & James, A. T.: Fitting the rectangular hyperbola. — Biometrics 22: 573–602. 1966.

Bode, H. R.: Über die Abhängigkeit des Knospenaustriebs bei Juglans nigra von der vorangegangenen Wintertemperatur. — Ber. Dtsch. Bot. Ges. 74: 288–291. 1961.

Doorenbos, J.: Review of the literature on dormancy in buds of woody plants. — Medelingen van de Landbouwhogeschool 51: 1–24. 1953.

Hellmers, H.: Photoperiodic control of bud development in Coulter pine and big cone Douglas-fir. — For. Sci. 5: 138–141. 1959.

— Temperature effect on optimum tree growth. — In Tree Growth (ed. Kozlowski). Ronald Press, New York. 1962.

Hiesey, W. M. & Milner, H. W.: Physiology of ecological races and species. — Ann. Rev. Plant Physiol. 16: 203–216. 1965.

Irgens-Moller, H.: Ecotypic response to temperature and photoperiod in Douglas-fir. — For. Sci. 79: 83. 1957.

Kriebel, H. B. & Wang, Chi-Wu: The interaction between provenance and degree of chilling in bud break of sugar maple. — Silv. Genet. 11: 125–130. 1962.

Langlet, O.: Mellaneuropeiska granprovenienser i svenskt skogsbruk. — Kungl. Skogs- och Lantbruksakad. Tidskr. 99: 259–329. 1960.

McMillan, C.: The role of ecotypic variation in the distribution of the central grassland of North America. — Ecol. Mon. 29: 285–308. 1959.

Mergen, F., Burley, J. & Yeatman, C. W.: Variations in growth characteristics and wood properties of Norway spruce. — Tappi 47: 499–504. 1964.

Oksbjerg, E.: Om udspringstid og skudstrækning i grankultur. — Hedeselsk. Tidsskr. 75: 49–55. 1954. (Forestry Abstracts 15: 3365.)

Olmsted, C. E.: Experiments on photoperiodism, dormancy, and leaf age and abscission in sugar maple. — Bot. Gaz. 112: 365–393. 1951.

Overcash, J. P. & Loomis, N. H.: Prolonged dormancy of pear varieties following mild winters in Mississippi. — Proc. Amer. Soc. Hort. Sci. 73: 91–98. 1959.

Perry, T. O. & Wang, Chi-Wu: Genetic variation in the winter chilling requirements for date of dormancy break in red maple. — Ecology 41: 785–790. 1960.

Roberts, B. R. & Main, H. V.: The effect of chilling and photoperiod on bud break in American elm. — J. For. 63: 180–181. 1965.

Romberger, J. A.: Meristems, growth, and development in woody plants. — U.S. Dept. Agr. For. Serv. Tech. Bull. 1293. 1963.

Ruden, T.: Ein Nachkommenschaftversuch aus dem Jahre 1951 mit Picea excelsa (Lam.) Link nach freiem Abblühen und seine Ergänzung durch Stecklingsversuche. — Tagungsberichte, Deutsche Akademie der Landwirtschaftwissenschaften zu Berlin 69: 133–138. 1965.

Samish, R. M.: Dormancy in woody plants. — Ann. Rev. Plant Physiol. 5: 183–204. 1954.
— & Lavee, S.: The chilling requirement of fruit trees. — XVIth Int. Hort. Congr., pp. 372–388. Brussels, Belgium. 1962.
Vegis, A.: Climatic control of germination, bud break and dormancy. — In Environmental Control of Plant Growth (ed. Evans). Academic, New York. 1963.
— Dormancy in higher plants. — Ann. Rev. Plant Physiol. 15: 185–224. 1964.
Williams, C. B.: Graphical and statistical methods in the study of insect phenology. — Trans IX Int. Congr. Entom. 2: 174–188. 1953.