

The weekly records were kept until the end of April, when all trees were either in full leaf or dormant. Later, casual phenological observations were made less frequently.

Time and Rate of Flushing in Relation to Duration of Chilling Period

Mean values of bud development are shown in Figure 2 by provenance and inspection date for each of the seven chilling treatments. The curves have the typical S-shape characteristic of growth in leaf area plotted over time (GREGORY, 1956).

When chilling was terminated on October 16 normal bud-break was not induced in trees of any of the four provenances. Some small leaves developed on lower branches of Georgia trees 175 days after chilling, but the upper branches remained dormant. Several months later, upper branches of all these trees were still dormant. By August 1, the lowest buds of Tennessee trees had leafed out, lower buds of Ohio trees were swelling, one Michigan tree had a few lower leaves, and the other Michigan tree was still dormant.

An additional three weeks of outdoor chilling resulted in normal development of Georgia and Tennessee trees. Ohio

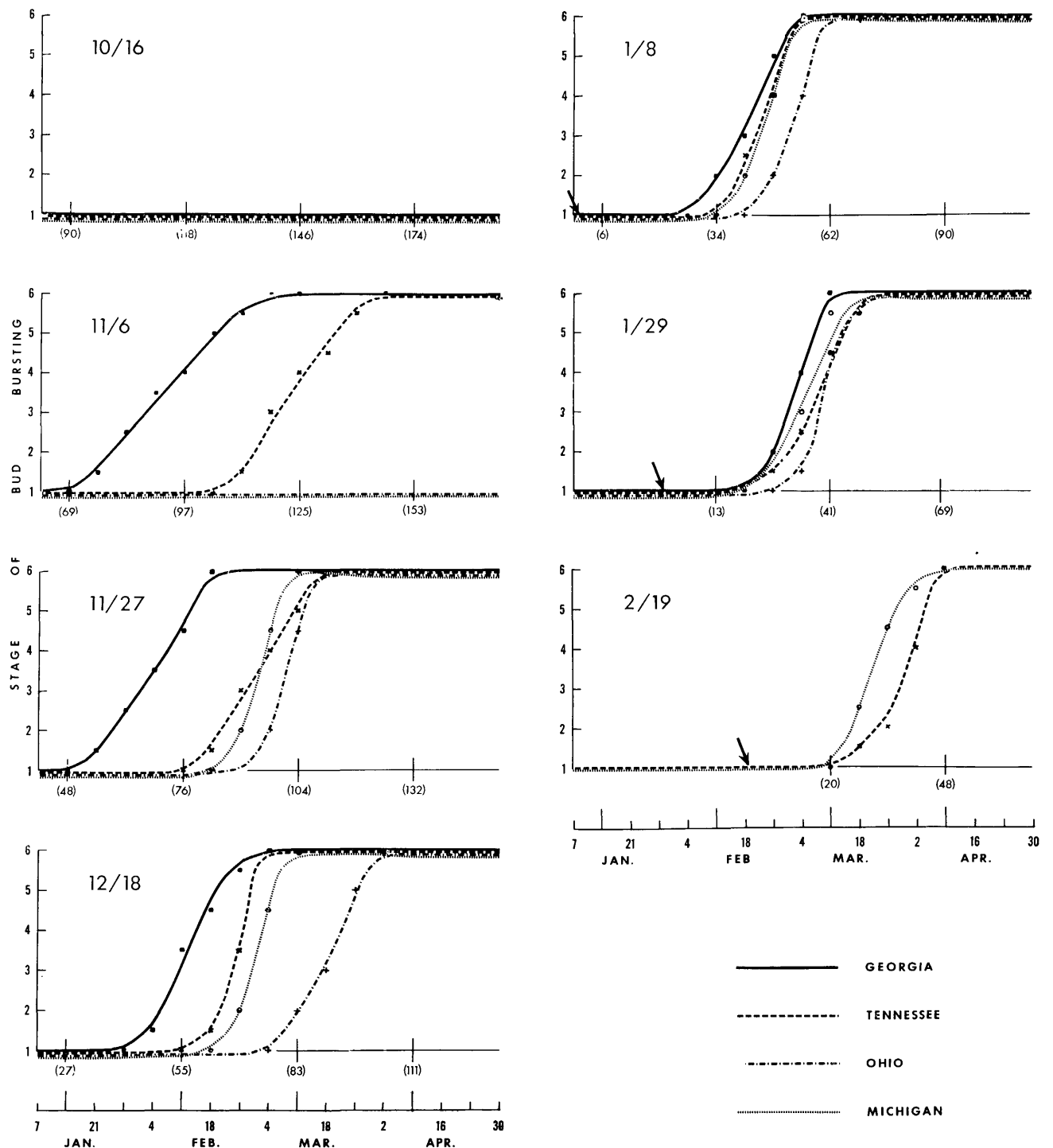


Figure 2. — Time and rate of normal bud-break in the greenhouse, in relation to date of termination of natural chilling (shown by arrow in the last 3 graphs). Figures in parentheses indicate number of days from end of chilling.

and Michigan trees remained dormant, with the exception of abnormal bud-break (lowest buds) on one Michigan tree. Georgia trees leafed out first. Trees from both Georgia and Tennessee developed slowly, as indicated by the slope of the curves in *Figure 2*.

When chilling was terminated on November 27 bud-break was induced in all trees, although the leaves of one Ohio tree were small and restricted to the lower branches. The period after chilling and prior to bud-break was shorter for Georgia trees than for other trees. Rate of flushing (time between Stage 1 and Stage 6) was shorter than for comparable trees in Treatment 2.

In the fourth treatment, the period of post-chilling dormancy was further shortened in trees of all provenances. The time gap between Georgia trees and both Tennessee and Michigan trees was narrowed, although Georgia trees were more advanced than the others. The slowest response was recorded for the Ohio provenance.

In the fifth and sixth treatments, there was further reduction in duration of post-chilling rest, although time required for the actual process of flushing was not reduced very much. There was little difference in date of initiation or completion of leafing-out between trees of different seed sources.

Trees outdoors until February 19 (Treatment 7) were exposed to a period of rigorous winter weather which killed the Georgia and Ohio trees. Thus they were eliminated from the last family of curves. There was no apparent injury to other trees. The Michigan trees were about a week ahead of Tennessee trees in time of leafing out. This relationship was the reverse of that observed in trees subjected to shorter chilling periods.

Normal outdoor flushing of trees of the same progenies is shown in the lower half of *Figure 3*. The broken lines indicate that measurements were not taken before Stage 2. The relative position of each of the four curves was

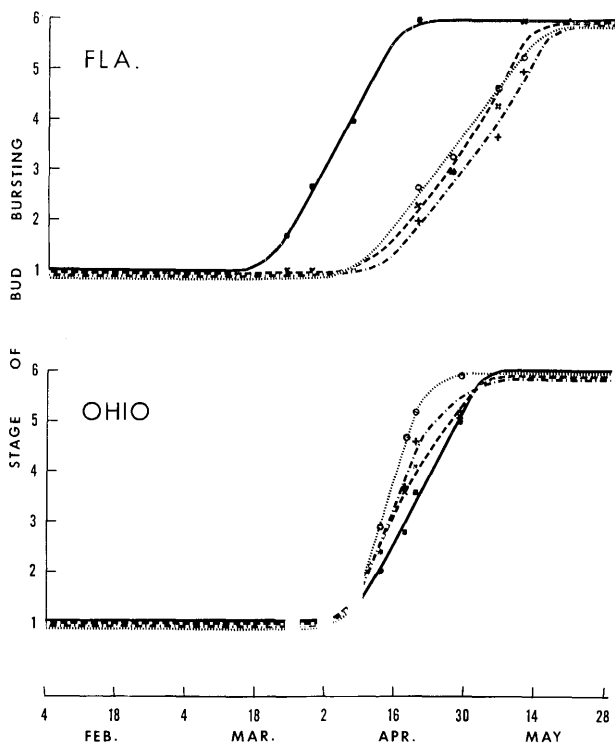


Figure 3. — Time and rate of normal bud-break in the field. Upper curves, Gainesville, Florida; lower curves, Wooster, Ohio. Legend as in *Figure 2*.

Table 1. — Relationship of the duration of dormancy after chilling to the length of the chilling period and the number of hours of chilling below 7° C. — = no bud break; — a = abnormal leafing, on lower branches only; — b = bud break inhibited by cold injury or tree mortality.

Date Chilling Terminated	Hrs. of Chilling below 7° C.	No. of Days to Reach Leafing Stage 4							
		Macon Georgia		Norris Tennessee		Bellefontaine Ohio		Dukes Mich.	
		Tree 1	Tree 2	Tree 1	Tree 2	Tree 1	Tree 2	Tree 1	Tree 2
10/16	211	— a	— a	—	—	—	—	—	—
11/6	457	83	144	116	135	—	—	—	—
11/27	822	69	76	90	104	102	— a	93	97
12/18	1235	58	62	69	71	93	— b	76	79
1/8	1637	44	— a	48	48	55	55	46	48
1/29	2158	34	34	36	44	39	41	34	30
2/19	2662	— b	— b	41	41	— b	— b	34	30

Table 2. — Reduction in post-chilling dormancy obtained by successive increments of chilling.

Total Hours of Chilling Below 7° C.	Chilling Increment Hours Below 7° C.	Reduction in Mean Number of Days Required to Reach Stage 4			
		Macon Georgia	Norris Tenn.	Bellefontaine Ohio	Dukes Mich.
211	246	—	—	—	—
457	365	24	30	—	—
822	413	14	26	8	22
1235	402	14	23	39	26
1637	521	10	7	14	10
2158	504	—	0	—	6

established in earlier studies and indicates sequence in the clinal pattern. This sequence is not affected by seedling age or year of measurement (KRIEBEL, 1957). The upper half of *Figure 3* shows response of trees of the same progenies during their second winter and spring in field plots at Gainesville, Florida.

Table 1 presents comparative measures of the relationship of the duration of post-chilling dormant period to the degree of chilling. *Table 2* shows the influence of additional chilling increments on the duration of the post-chilling dormant period.

Discussion

Time in days is a useful base on which to plot response, as in *Figure 2*. It is also a convenient basis for establishing treatments, using 3-week periods of exposure to outdoor temperatures. While time in days is a suitable measure of post-chilling dormancy in a warm greenhouse and of leaf unfolding from start to finish, it is not an accurate measure of the amount of chilling applied in each treatment, because of wide fluctuations in outdoor temperature.

It is difficult to apply a quantitative measure of chilling, because the physiological relationship of low temperature to bud rest of woody plants is poorly understood. Investigations of the chemical changes associated with rest, the auxin-inhibitor mechanism, and physical factors have been summarized by DOORENBOS (1953) and SAMISH (1954).

Most studies of chilling requirement of trees have been concerned with fruit trees, especially peach (*Prunus persica*). It has been found that extreme cold is not necessary to break rest in peach trees. Temperatures of 7° C. are adequate; a temperature of 10° C. is effective but less efficient. The optimum is probably around 4° C. In climates with long winters the rest is broken long before winter is over, often by early December. Shoots brought into a warm room after this time will develop normally. When peach trees

have had their chilling requirements partly fulfilled, development takes place at favorable temperatures, but at a very slow rate. When chilling is inadequate, abnormal bud-break may take place. In this case, the older buds are the first to break dormancy. These have had two or more chilling periods and need less chilling the second time than 1-year-old buds.

In peaches, the number of hours of chilling below 7° C. required to complete bud rest varies greatly with the variety, ranging from about 200 hours to 1200 hours. The number of days during which the chilling occurs is important. If chilling is concentrated over a shorter period instead of being spread over several months, more hours are required. Continuous chilling permits the shortest time for bud break, but more hours of chilling are required than if chilling is alternated with warmer temperatures and spread over a period of months (WEINBERGER, 1961). Therefore measurements of chilling requirement taken after uniform low-temperature treatment indoors are not a measure of outdoor chilling requirement. However, they can reveal intraspecific variation, as did the analyses by PERRY and WANG of *Acer rubrum* (1960).

Another observation on peach trees should be mentioned, namely that low temperatures in December and January are more effective in breaking the rest of peach buds than are low temperatures in November or February (WEINBERGER, 1961).

The number of hours of chilling required for completion of rest have been ascertained for many species and varieties of woody plants. However, the 7° C. threshold has recognized limitations and should not be applied uncritically to every species (SAMISH, 1961). It does provide a useful standard for evaluating differences in chilling requirement between varieties, or in this case of differences between trees of different provenances. Until the upper limits of temperatures in the chilling range are more intensively studied in sugar maple, a 7° C. value will provide a basis for quantitative measure of degree of chilling which is as useful as another temperature in the range of 7° to 9° C. This was indicated by trial calculations using the data from this experiment.

The measurements in these experiments were taken to Stage 4 in the middle of the flushing period, because the beginning and end of flushing are very difficult to fix. Table 1 shows that: (1) the longer the chilling period, the shorter was the period before flushing, although very long chilling periods had relatively little additional effect over moderately long periods; (2) there was a longer interval to bud-break in northern trees than in southern trees.

In Table 1, the amount of chilling is given in number of hours below 7° C. The minimum requirement for trees of both Georgia and Tennessee origin was between 211 and 457 hours. For Ohio and Michigan trees it was between 457 and 822 hours. One Ohio tree showed abnormal leafing after 822 hours, and one with 1235 chilling hours failed to break bud. In the latter case there was some indication that injury was related to microenvironment and root exposure, rather than to genotype.

Reduction in duration of the post-chilling dormant period obtained after successive increments of chilling varied with seed source. This is shown in Table 2. The greatest reductions among trees of southern origin occurred early in the treatment series, with relatively few chilling hours. Among Tennessee trees, there was a large reduction early in the series, but the effects of adding the third and fourth chilling increments were also large, more so than were the

effects on Georgia trees. This suggests that there is an inherent difference in chilling requirement between trees of these two provenances which the comparison of minimum requirements for bud-break does not reveal.

The effect of successive chilling increments on Ohio trees was similar to the effect on Michigan trees. Table 2 shows that in both cases, the greatest reduction in time to bud-break resulted from the addition of 402 hours of chilling to the previous 1235 hours. There was much less reduction after further chilling. Michigan trees responded more with less chilling than did Ohio trees, though this could be due to experimental error.

Treatments were continued long enough to give a reasonable indication of the diminishing effectiveness of additional chilling as related to seed source. Decreasing effectiveness of additional chilling provided by the last two treatments resulted in northern trees breaking bud at about the same time as southern trees. Table 1 indicates that the minimum time in days from movement into the greenhouse until bud-break was 30 to 40 days for trees of all sources, regardless of how much chilling was applied. The amount of chilling required for a 40-day period was about 1800 hours for Georgia trees, and about 2100 hours for trees of other seed sources. This is as close an estimation of "optimum" or "normal" chilling requirement (distinguished from minimum requirement for bud-break) as the data permit.

It seems clear that trees from all four sources obtained the required amount of chilling well before the end of the winter. Apparently during the period from mid-February to outdoor bud-break in late April some other environmental factor replaced the requirement for additional chilling as the stimulus controlling onset of growth.

In the Florida field test (Figure 3, top), the climate provided sufficient chilling during the winter to induce normal bud-break in all trees. In the Florida locality there were 47 days on which the temperature was below 7° C. for an hour or more, a total of about 430 hours. This was a considerably smaller amount of chilling than was required in Ohio for all but the Georgia trees. Results are quite consistent with evidence previously discussed. The chilling in Florida consisted of a series of cycles with most highs in the range of 15° to 25° Centigrade and lows in the range of -6° to +9° Centigrade. The period with occasional temperatures below 7° C. extended from November to March, according to daily records of the Gainesville weather station (1958-59). In Ohio, the chilling period for the early treatments was much shorter and more concentrated. The results suggest that in maples, as in peach trees, continuous chilling or a concentrated period of chilling requires more actual hours of low temperature than if the chilling is alternated with warmer temperatures and spread over several months. Also, as in the peach, temperatures in December and January seem to accelerate completion of bud rest more than temperatures in November and February. The reversal of the position of the Georgia curve in Figure 3 (top) as compared with Figure 3 (bottom) indicates that although chilling in Florida was adequate for bud break, trees of northern sources were delayed in time of flushing by limited chilling, and that the time required for bud-breaking was extended.

Summary

Experiments on chilling requirement of sugar maple included potted trees from four provenances subjected to

seven durations of outdoor chilling in northern Ohio, and trees from the same seed progenies in field tests in central Florida and in northern Ohio.

Sugar maples of southern origin broke dormancy with less normal outdoor chilling than did sugar maples of northern origin. Only trees of Georgia and Tennessee origin broke bud normally when brought into a warm greenhouse on November 6 after 457 hours of chilling below 7° C. Trees of Ohio and Michigan origin broke bud after chilling was terminated on November 27 (822 hours below 7° C.) although flushing of one tree of the Ohio provenance was abnormal and restricted to lower buds.

Length of the post-chilling dormant period varied with both amount of chilling and seed source. The greater the amount of chilling, the shorter was the subsequent period before bud break. Differences between northern and southern genotypes in length of this dormant period decreased as the amount of chilling was increased. When outdoor chilling was terminated in late January or early February, there was very little difference in duration of post-chilling dormancy between northern and southern genotypes.

The chilling increments were not equally effective in reducing the subsequent time to bud-break. In Georgia trees, the maximum reduction occurred after about 800 hours below 7° C. The time reduction in Tennessee trees was nearly as large after 1200 and 1600 hours as after 400 hours. In Ohio and Michigan trees, the maximum reduction occurred after 1600 hours below 7° C.

Increasing the amount of chilling increased the rate of leaf unfolding by decreasing the number of days between Stage 1 and Stage 6. Chilling beyond early February (about 2300 hours below 7° C.) did not seem to further accelerate rate of development, even in trees of northern origin.

Trees exposed to a full winter in the field in Ohio flushed in a north-to-south sequence with regard to seed source. Among trees exposed to a full winter in the field in central Florida (about 400 hours below 7° C.), trees of Georgia origin flushed first; trees from other sources flushed later and all at about the same time. The time-span in days of the process of leaf-unfolding of trees of Georgia origin was the same outdoors in Florida and Ohio, but for northern genotypes the process was much slower in Florida than in Ohio.

The studies indicated that after mid-February under the test conditions (about 2500 hours below 7° C.) the chilling requirement of trees of all sources had been fully supplied and other factors controlled the time of bud-break.

Zusammenfassung

Titel der Arbeit: *Die Wechselwirkung zwischen Provenienz und der Dauer der Abkühlung bei der Knospenöffnung des Zuckerahorns.*

Versuche über den Bedarf an tiefen Temperaturen umfaßten eingetopfte Pflanzen aus 4 Herkünften, die in Nord-Ohio im Freiland 7 verschieden langen Abkühlungszeiten ausgesetzt wurden, und Pflanzen der gleichen Saatgutnachkommenschaften auf Feldversuchen in Mittel-Florida und Nord-Ohio.

Zuckerahorne südlicher Herkunft beendeten den Ruhezustand schon bei weniger starker natürlicher Freilandabkühlung als Zuckerahorne nördlicher Herkunft. Nur Pflanzen der Herkünfte Georgia und Tennessee öffneten normalerweise die Knospen, wenn sie am 6. November nach 457 Stunden Abkühlung unter 7° C in ein geheiztes Gewächshaus gebracht wurden. Die Pflanzen von Ohio

und Michigan öffneten die Knospen, wenn die Abkühlung am 27. November beendet wurde (822 Stunden unter 7° C), wenn auch der Austrieb einer Pflanze der Herkunft Ohio abnorm und auf die unteren Knospen beschränkt war.

Die Länge der Reaktionszeit wechselte je nach der Dauer der Abkühlung und der Herkunft. Je größer die Dauer der Abkühlung war, desto kürzer war die folgende Periode bis zur Knospenöffnung. Die Unterschiede in der Länge der Reaktionszeit zwischen nördlichen und südlichen Genotypen verringerten sich mit zunehmend stärkerer Abkühlung. Wenn die Freilandabkühlung Ende Januar oder Anfang Februar beendet wurde, bestand sehr geringe Verschiedenheit in der Dauer der Reaktionszeit zwischen nördlichen und südlichen Genotypen.

Die Zunahme der Dauer der Abkühlung wirkte nicht gleichermaßen verringern auf die Folgezeit bis zur Knospenöffnung. Bei den Pflanzen der Herkunft Georgia trat die größte Verringerung nach etwa 800 Stunden unter 7° C ein. Die Zeitverringerung bei der Herkunft Tennessee war nach 1200 Stunden und 1600 Stunden etwa so groß wie nach 400 Stunden. Bei den Herkünften Ohio und Michigan trat die größte Verringerung nach 1600 Stunden unter 7° C ein.

Die Steigerung der Dauer der Abkühlung erhöhte die Geschwindigkeit der Blattentfaltung, indem die Zahl der Tage zwischen Stadium 1 und Stadium 6 verringert wurden. Die Abkühlung bis zu einem Zeitpunkt nach Anfang Februar (etwa 2300 Stunden unter 7° C) schien die Entwicklungsgeschwindigkeit auch von Pflanzen nördlicher Herkunft nicht weiter zu beschleunigen.

Pflanzen, die auf einer Versuchsfläche in Ohio einem ganzen Winter ausgesetzt waren, trieben in einer Nord-Süd-Reihenfolge hinsichtlich der Saatgutherkunft aus. Von den Pflanzen, die auf einer Fläche in Mittel-Florida einem vollen Winter ausgesetzt waren (etwa 400 Stunden unter 7° C), trieben zuerst die Pflanzen der Herkunft Georgia aus; die Pflanzen der anderen Herkünfte trieben später und alle etwa zur gleichen Zeit aus. Die Zeitspanne in Tagen des Vorganges der Blattentfaltung war bei der Herkunft Georgia unter Freilandbedingungen in Florida und Ohio gleich, für nördliche Herkünfte aber war der Vorgang in Florida viel langsamer als in Ohio.

Die Untersuchungen zeigten, daß nach Mitte Februar unter den Bedingungen des Versuchs (etwa 2500 Stunden unter 7° C) der Bedarf an tiefen Temperaturen bei Pflanzen aller Herkünfte voll gedeckt war und andere Faktoren den Zeitpunkt der Knospenöffnung kontrollierten.

Résumé

Titre de l'article: *Interaction entre la provenance et l'intensité du froid nécessaire à la levée de dormance des bourgeons d'Erable à sucre.*

Ces expériences sur les besoins en froid de l'Erable à sucre ont porté sur : des sujets en pot de quatre provenances soumis à sept durées de froid dans le Nord de l'Ohio; les arbres des mêmes provenances établis en plantations comparatives dans le centre de la Floride et dans le nord de l'Ohio.

Le besoin en froid pour la levée de dormance des provenances méridionales d'Erable à sucre est plus faible que celui des provenances septentrionales. Seuls les arbres de Géorgie et du Tennessee débourent normalement lorsqu'ils sont amenés dans une serre chaude le 6 Novembre après 457 heures d'exposition à un froid inférieur à 7° C. Les arbres de l'Ohio et du Michigan débourent

après la fin du traitement au froid le 27 Novembre (822 heures au-dessous de 7° C); cependant, le débouillage d'un arbre de la provenance Ohio était anormal et limité aux bourgeons inférieurs.

La longueur de la période de dormance après l'exposition au froid variait à la fois avec l'intensité du froid et avec la provenance. Plus intense était la réfrigération, plus courte la période suivante avant le débouillage. Les différences entre les écotypes septentrionaux et méridionaux en ce qui concerne la longueur de cette période de dormance ont diminué avec l'augmentation de l'intensité du froid. Lorsque la réfrigération était terminée en fin Janvier ou au début Février, il y avait très peu de différence dans la durée de la dormance après réfrigération entre les écotypes septentrionaux et méridionaux.

L'efficacité de l'augmentation de réfrigération pour réduire la période de dormance avant le débouillage n'était pas toujours la même. En ce qui concerne les provenances de Géorgie, la réduction maxima est intervenue après environ 300 heures d'exposition au-dessous de 7° C. Pour les provenances du Tennessee, la réduction fut presque aussi importante après 1200 et 1600 heures qu'après 400 heures. Pour les arbres de l'Ohio et du Michigan, la réduction maximum est intervenue après 1600 heures au-dessous de 7° C.

L'augmentation de l'intensité du froid augmente la vitesse de débouillage en diminuant le nombre de jours entre le stade 1 et le stade 6. La réfrigération au-delà de début Février (environ 2300 heures au-dessous de 7° C) ne semble plus avoir d'effet sur l'augmentation de la vitesse de débouillage même chez les arbres d'origine septentrionale.

Les arbres exposés à l'hiver normal dans la plantation comparative en Ohio ont débouillé de la façon suivante:

les provenances septentrionales les premières et les provenances méridionales les dernières; toutes, suivant une variation clinale.

Pour les arbres exposés à l'hiver dans la plantation comparative de Floride centrale (environ 400 heures au-dessous de 7° C), les provenances de Géorgie ont débouillé les premières; les autres provenances ont débouillé des provenances de Géorgie a été la même à l'extérieur en Floride et en Ohio, mais pour les écotypes septentrionaux, cette durée était beaucoup plus courte en Floride qu'en Ohio.

Cette étude montre qu'après la mi-Février, dans les conditions de l'essai (environ 2500 heures au-dessous de 7° C), les besoins en froid des arbres de toutes les origines ont été pleinement satisfaits et que d'autres facteurs ont déterminé l'époque de débouillage.

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Interspecific Hybridization in the Genus *Abies*

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Introduction

Artificial hybridization is an important tool in forest genetics. It makes it possible to produce trees with gene combinations that might never occur in nature. Tree breeders around the world have placed special emphasis on interspecific crosses of species in various genera. Fairly detailed information on crossability patterns are available for genera such as *Pinus*, *Picea* and *Larix*. Several lists of species crosses in *Abies* have been reported by workers (JOHNSON, 1939; WRIGHT, 1962¹); ROHMEDEK, 1959 and 1961). However, a search of the literature revealed no current crossability pattern for that genus.

Experiments were initiated in the spring of 1960 at the State University College of Forestry at Syracuse University in an attempt to establish a crossability pattern in *Abies*. The objectives of this study are as follows:

1. The compilation of reported *Abies* crosses into a pattern.

2. The extension of this established pattern by experimental artificial hybridization.
3. The production of interspecific hybrids for future study and evaluation for forestry purposes.

This paper reports the results of the controlled pollinations attempted in 1960 along with the compiled crossability pattern. The results of new crosses carried out in 1962 and data on the putative hybrids produced in 1960 will be reported at a later date.

Review of Literature

General

SARGENT (1926) recognized 33 species of *Abies* existing in the temperate regions of the northern hemisphere. VIGUÉ and GAUSSEN (1929) arrived at a total of 52 species and 12 varieties in their revision of the genus. REHDER (1958) lists 31 species, but states that "about 40 species" of true firs exist in the temperate regions of the northern hemisphere.

Various workers have divided the genus *Abies* into two or three sections. According to McNAB (1876), Bertrand separated the species into two sections based on the position of the needle resin canals. MATTFELD'S (1926) maps divide Mediterranean species into two sections based on

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¹) Personal communication, J. W. WRIGHT, Michigan State University, East Lansing, Michigan (2/28/62).