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# INTRODUCTION

The process of bud bursting or leaf flushing in the spring is not completely understood. In general, temperature triggers spring phenological events, such as bud break, flowering, and greening of bark, whereas photoperiod initiates fall events, including growth cessation and cold hardening (Smithberg and Weiser, 1968).

When seeds of a species are collected from different sources throughout its range and seedlings raised in a common garden, there is usually variation in the time of bud burst among sources. What causes these differences and the general patterns of these differences will be considered in this paper. The avoidance of freezing of the vegetative plant parts seems to be the selective force responsible for the observed variations in leaf flushing adaptations (Sharik, 1970).

Very early papers related spring phenological events to temperature summation (Reaumur, 1738). More recent papers (Garner and Allard, 1920) attributed the differences for many herbaceous and small woody plants to photoperiod. The most recent studies show a heat summation as being of primary importance in the North Temperate Zone, after a minimum of chilling during the winter (Nienstaedt, 1974a). Photoperiod is a "second line" trigger, only important in unusual circumstances, such as inadequate winter chilling (Irgens-Moller, 1957). Laboratory studies showing flushing in complete darkness (Wareing, 1956), or simultaneously in the same temperature regime but with different photoperiods (Worral and Mergen. 1967), support this theory. If photoperiod, which exhibits a constant yearly cycle, completely controlled bud bursting, one would expect leaves to flush on the same date every year regardless of temperature. Instead, we find variation in the start of flushing from year to year, although the sequence of sources flushing remains the same (Bey, 1973a).

## OBJECTIVES

The general objective was to study the phenomenon of flushing in woody plants and determine what mechanisms affect and control it. The problem was broken down into the roles of four components as follows:

1. Latitude and altitude
2. Species differences in the genus *Betula*
3. Age of *Betula species*.
4. Heat summation.

Besides an extensive literature review, flushing was observed in populations of various species of the genus *Betula*. Four birch plantations were monitored during the spring of 1974, and flushing was scored. These plantings comprised a wide range of seed sources (populations) from the northern and southern Appalachian mountains, as well as from the upper and lower peninsulas of Michigan. The plantations were started in different years, allowing comparisons of some of the same seed sources at different ages.

Seed sources were compared in rate and timing of flushing. Relationships evidenced in flushing patterns along elevational and latitudinal gradients were analyzed to determine the general patterns of their response.

## STUDY SITES AND METHODS

Four plantations were observed. Two were located at the University of Michigan Matthaei Botanical Gardens in Ann Arbor, and two were located at the Southern Michigan State Forest Nursery near Brighton, Michigan.

### Plantation 1

The oldest plantation, planted in 1969 at the Botanical Gardens, consisted primarily of yellow birch saplings from souteastern Michigan. Other yellow birch sources from Michigan and West Virginia were also included. Four bog birch sources from the lower peninsula of Michigan, one hybrid yellow X white birch, one putative polyploid derivative of Betula Xpurpusii, and two hybrid crosses of yellow birch x the putative polyploid were also included. Betula platyphylla, a Japanese paper birch was the only non-native species in this planting. (See Appendix A for the exact sources).

The seeds were collected from birch mother trees and germinated in 1968 in a greenhouse at the Botanical Gardens. They remained in pots one year before being outplanted at the field site in 1969. The plantation consisted of 15 rows, eight feet apart. There were 53 plants per row, spaced six feet between plants. A completely randomized design, with three replicates of each source was used. Three seedlings from each mother tree formed each replicate. A buffer row surrounded the plantation, leaving 51 plants, or 17 mother tree replicates of three trees per row.

## Plantation 2

The second plantation was established as part of a genecological study of Appalachian birches (Sharik, 1970). Seed sources originated from the northern Appalachians in New Hampshire and Vermont, the southern Appalachians in North Carolina, Virginia, West Virginia, and from the Ohio plateau area. Three Michigan sources were included. A number of trees from a plantation near College Park, Pennsylvania (established by Schreiner, 1949), was also included in the plantation. They were scored for flushing but were not included in the analysis since their exact origins were unknown. This study comprised 24 sources of yellow birch and 15 of sweet birch. Many source areas had both species. A complete list of the sources is shown in Appendix A.

The seeds were germinated in March of 1968 and planted at the Southern Michigan Nursery in June. They were transplanted from Brighton to the Botanical Gardens in March 1971, directly west of Plantation 1. The plantation has 13 north-south rows, eight feet apart. Rows 1 and 13 were buffer rows and the first and last plants in rows 2 to 12 were buffer plants. There were a maximum of 15 individuals per mother tree. A completely randomized design of the progeny of mother trees was used. Three mother trees per seed source were planted adjacent to each other and constituted a single replicate.

## Plantation 3

The third plantation was established in 1972 at the

Southern Michigan Nursery to study phenology, growth, biomass, and relative tolerance of yellow birch sources from Michigan and the Appalachians (Hart, 1974). The experiment comprised 10 seed sources of yellow birch and three of sweet birch, each with two mother trees. Two sources of paper birch and one yellow X paper birch source, each with one mother tree, were also included. Populations from the eastern and western upper peninsula of Michigan, as well as populations from northern and southeastern lower peninsula of Michigan, were included. Both high and low elevation populations in the northern and southern Appalachians were represented. (Appendix A).

The birch seeds for this study were collected in the fall of 1970 and 1971. They were germinated in April 1972 in a greenhouse of the Botanical Gardens and planted in June at the Southern Michigan nursery in three blocks of three plots each. Each of the nine plots contained four seedlings from each mother tree for the yellow and sweet birches, completely randomized in each plot. For the two paper birches and the one hybrid birch, there were eight seedlings from the single mother tree of each of these sources. There were originally three blocks or replications of three plots each; in each block one plot receiving 100% sun, one plot receiving 45% sun, and one plot receiving 25% sun. Shade frames, constructed of slats, were used to control the amount of sunlight received on the latter two plots. The shade frames were placed up over the trees in spring, and removed after the leaves fell in the autumn. One replication of three plots was harvested in the fall of 1972. The second replication was harvested in fall, 1973. I observed seedlings in the spring of 1974, the three remaining plots, one of each light intensity. Each plot was 24 feet by 4 feet in size. The birches were planted in eight rows 6" apart with 12" between plants. Buffer plants surrounded the test trees in each plot.

### Plantation 4

The fourth plantation, a common garden test of yellow birch was also located at the Southern Michigan Nursery. Thirty yellow birch populations and three hybrid yellow x paper birch sources were used. Most of the sources were from Michigan, both upper and lower peninsulas. Four northern and southern Appalachian sources were included. Twenty eight of the yellow birch populations had five mother trees, one population had four mother trees, and one population had three mother trees. All three hybrid sources had one mother tree. See Appendix A for a list of the sources.

The seeds were germinated in February 1973 in the Botanical Gardens and planted at the Southern Michigan Nursery in June of 1973. Seedlings of each mother tree were replicated 20 times and grown in Jiffy peat pots in a bench at the Botanical Gardens. Of the 20 original replications, 16 were planted at Brighton, 141 trees per replication. The position of the individual trees in each replicate followed the original randomization used in the Botanical Gardens.

There were 288 rows in the plantation; the rows were 12 inches apart. There were eight seedlings in each row, and the seedlings were planted five inches apart in a row. There were no border rows.

## Scoring Methods

Scoring of the seedlings started on April 10, 1974 and continued until May 26, 1974. The scoring system used in describing the flushing of leaves was modified slightly from that used by Sharik (1970) and Hart (1974).

1= at rest: buds closed, no leaves visible, no observable activity

2= breaking rest: bud scales swelling, no leaves visible

3= semi-rest: buds opening, leaves visible, expanded less than $\frac{1}{4}$ the length of the bud scales

4= expanding: leaves $\frac{1}{4}$ to $1\frac{1}{2}$ times the length of the bud scales

5= $\frac{1}{4}$ flushed: leaves $1\frac{1}{2}$ times the length of the bud scales to leaf blade 20 mm.

6= $\frac{1}{2}$ flushed: leaf blade 21 mm. to 60 mm.

7= more than $\frac{1}{2}$ flushed: leaf blade greater than 60 mm.

The first visit was to Plantation 3 on April 10, 1974. All the seedlings were scored 1, at rest. Plantation 4 was also observed and no activity was noted. Thereafter, the two Brighton plantations were observed every three days until May 13. One final observation was made on May 20 on the 100% sun plot of Plantation 3, which contained the latest flushing seedlings.

The two Botanical Garden plantations were first observed April 29 and then once every week thereafter until May 19 for Plantation 1 and May 26 for Plantation 2. Leaves of the trees were already partly flushed on April 29. A table of the dates on which trees were scored is presented in Table 1.

A value for the start of flushing was calculated for the Brighton plantings. The number of days from April 10 until flushing score 2, i.e., the first sign of flushing, was determined as the start of flushing. In the case where the score changed from 1 to 3, and 2 was bypassed, the number of days one day before the 3 score was recorded was assigned as the start of flushing. Where the score changed from 1 to 4, bypassing 2 and 3, the number of days two days before the score of 4 was recorded was designated as the start of flushing.

From the individual flushing scores and start of flushing scores for each tree on each scoring date an average flushing score was calculated. All the individual scores from each source on each date were averaged together by species in each plantation to give an average flushing score for that source e.g., ADC on May 6 in Plantation 4 or LCC on April 29 in Plantation 2. The same method was used to calculate the average start of flushing score. The average scores are listed by source for each plantation in Appendix B.

Table 1. Dates of scoring for each birch plantation in spring, 1974.

| | Plantation | | | |
|---|---|---|---|---|
| Date | 1 | 2 | 3 | 4 |
| 4/10 | | | X[a] | |
| 4/13 | | | X | |
| 4/16-17 | | | X | X |
| 4/20-21 | | | X | X |
| 4/23 | | | X | |
| 4/24 | | | | X |
| 4/27 | | | X | X |
| 4/29 | X | X | | |
| 4/30 | | | X | X |
| 5/3 | | | X | X |
| 5/5 | X | X | | |
| 5/6 | | | X | X |
| 5/10 | | | X | |
| 5/12 | X | X | | |
| 5/13 | | | X | X |
| 5/19 | X | X | | |
| 5/20 | | | X[b] | |
| 5/26 | | X | | |

[a] X= seedlings scored

[b] On this date only the 100% sun plot was scored.

## Methods of monitoring temperature

Temperatures were monitored at ground level and at three feet above the ground each time the trees were scored. Temperatures were taken three times during the scoring of Plantation 4 and twice during each scoring of Plantation 3. Hart (1974) suggested that the shorter seedlings, closer to the ground, tended to flush earlier than might be accounted for by their source because of higher temperature near the ground. The purpose of the temperature monitoring was to determine if the ground temperature was different than the temperature three feet above the ground and could therefore be having a differential effect upon smaller seedlings or lower branches. Two thermometers were used; they were held out of the direct sunlight at each level simultaneously until the temperature stabilized. Then the temperature was recorded.

To calculate heat sums, it was not possible to obtain records of continuous or hourly temperature readings for either the Brighton Nursery site or the Botanical Gardens. Maximum and minimum daily temperature from January 1974 through May 1974 were obtained for the Milford GM Proving Grounds in Livingston county and the University of Michigan in Ann Arbor (U. S. Environmental Data Service, 1974). The GM Proving Grounds is 5¼ miles from the Brighton Nursery. The University weather station is only 2¼ miles from the Botanical Gardens.

## Statistical methods

For Plantations 1 and 4, the average flushing score of each source on each scoring date was regressed on latitude as the independant variable. For Plantation 4 the average score for the start of flushing was also regressed on latitude. The correlation coefficient was calculated for each regression.

In Plantation 2, the average flushing score on each scoring date for yellow birch, sweet birch, and yellow and sweet birch together were regressed on latitude, latitude adjusted for elevation, and elevation as the independant variables. Two latitude adjustment factors were used, 1.61° and 1.52° for every 1000 feet of elevation. These were determined by Sharik (1970) for length of growing season and mean July temperature data from the Appalachian mountains. A regression of the differences between species (yellow and sweet birch) on each scoring date was also done. The correlation coefficient was calculated for each regression.

Flushing differences among sources in Plantation 3 (the light intensity study) were analyzed by analysis of variance. The effects of light intensity among the three plots upon the start of flushing and on flushing at successive dates were tested for both yellow and sweet birch, and both species together. The average flushing score on each date and the start of flushing score were regressed on latitude and latitude adjusted for elevation as the independant variables for yellow birch, sweet birch, and both species together. The correlation coefficient was calculated for each regression.

Flushing dates of yellow birch from all four plantations (only the 100% sun plot of Plantation 3) were analyzed using multiple regression analysis to test the effects of latitude and plantation upon flushing scores for three dates, April 29-30, May 5-6, and May 12-13.

# LITERATURE REVIEW

## Historical aspects and early thoughts

### Heat sums

It has long been recognized that temperature strongly influences phenological events. In the 1730's, Reaumur invented a temperature scale and summed up mean daily temperatures in April, May and June. He found this sum to be nearly constant for the onset of a given developmental stage of any plant from year to year. He assumed that his thermometric constant expressed the amount of heat required for a plant to reach a given state of maturity. This sum was known as "Reaumur's thermal constant of phenology" (Réaumur, 1738; Garner and Allard, 1920; Wang, 1960; Newman et al., 1967).

Wang (1960) reviewed the historical development of heat sum methods. In 1750, Adanson modified Reaumur's idea. He disregarded temperatures below 0°C and used only positive temperatures and termed it the "remainder index" method. Since this time, many other workers have used the "remainder index" method, calculating positive heat sums, and not subtracting degree hours for the temperatures below freezing early in the season.

Alexander Humboldt considered sunlight an important physiological factor and initiated the idea of the actinometric constant, measuring the direct heating power of the sun. Edwards and Colin, in 1834, called attention to the upper limit of temperatures that inhibited plant growth in calculating the thermal sum during their germination studies. In 1844, Gasparin considered the influence of sunlight, and conducted studies on a thermal constant above 5°C, a heat summation, computed over the time period from planting to harvest of cereals.

Brendel (1859) calculated heat sums accumulated by the time of flowering of several tree species. He added together the daily mean temperatures from the day each year when germination occurred for seeds, or the sap started moving for trees, until a given phenological stage was reached, and compared these summations over many years. He found that 0°C was the best threshold for most tree species. According to Wang (1960), in 1861, Fitch determined thermal constants for the blossoming and ripening of 889 different plant species by totaling the mean daily temperature above 0° Reaumur scale (0° Reaumur=0° C) from January onward until blossoming or ripening occurred.

Julius Sachs, in 1860-1862, laid the foundation for the idea that germination, budbreak, and growth in general occur within a defined upper and lower limit of temperature (Wang, 1960; Vegis, 1963). Linsser, in 1867-1869, studied interrelationships between climate and plant development. He found that the sum of temperatures above 0°C for each of two places, which correspond to a given physical stage, are proportional to the accumulated heat summation of all positive temperatures at each of the two locations. For example, the total annual heat sums for Brussels, Belgium, and

St. Petersburg, Russia, were 3687°C and 2253°C respectively. Early spring flowers began flowering at 184°C and 93°C, or 5% and 4% of the annual sums in Brussels and St. Petersburg, respectively (Langlet, 1970, 1971). Thus, over one hundred years ago, Linsser had linked the occurrences of phenological phases to the proportionality of the annual heat sum.

Brendel, in 1887, investigated heat sums for a number of species in Illinois. He demonstrated that the date of flowering might vary by as much as 20 days from year to year, but the sum total of daily mean temperature until flowering was approximately the same from year to year (Brendel, 1887; Lamb, 1915).

Wang (1960) mentions many workers in the late 1800's and early 1900's who added refinements to heat sum methods. Coutagne, in 1882, believed that the plant growth rate depended upon a certain maximum temperature which was determined by interactions of irradiance, wind, and soil moisture. From 1919 to 1952, many workers applied the "remainder index" method to many native and cultivated plants.

Photoperiod

In 1852, a hypothesis was published by Henfrey, suggesting that the natural distribution of plants is at least partially tied to latitudinal variation in the relative lengths of day and night (Naylor, 1961). Kjellman, in 1885, carried out experiments on the effect of the duration of the light period on the rate of increase in size, speed of maturation, and possible requirements of a rest period north of the Arctic circle, on the northern Siberian coast, where daylength would not be limiting (Naylor, 1961). Jost, in 1894, demonstrated that continuous light was occasionally able to bring beech out of its winter rest (Thorup, 1957). Klebs, in 1914, used continuous illumination to obtain uninterrupted growth all winter in beech, oak, ash, and hornbeam. He also used continuous light in the laboratory to break dormancy of Fagus sylvatica. Provided the shoots received the neccessary preliminary period of illumination, the subsequent leaf unfolding could take place equally well in light or dark (Wareing, 1948). Klebs thought that the quantity of light (intensity x time) was more important than the length of illumination alone (Kramer, 1936; Wareing, 1948; Thorup, 1957).

Garner and Allard (1920) conducted many photoperiod experiments. They found that the flowering and fruiting stages of herbaceous plants and some shrubs and dwarf trees could be attained only when the length of day fell within certain limits which were reached only during certain seasons of the year. Some species of herbaceous plants flowered in short days, and others in long days. They concluded that daylength was an important factor in budbreak and growth cessation of woody as well as herbaceous plants.

Kramer (1936) concluded that daylight should be regarded as an indirect rather than a direct causal agent of growth initiation and cessation. Since this time, many experiments have been conducted to test the response of plants to photoperiod.

## Flushing

In the 1820's, Pierre-Phillippe- André de Vilmorin raised many different seed sources of Scots pine in a common garden, and observed variation of many morphological characteristics. He also observed the time of flushing. He found sources which were strikingly different from each other in many characters, including flushing. However, between these extremes there was an unbroken chain of gradations, i.e., a cline (Langlet, 1970). Keinitz, in 1879, observed that seeds of Picea excelsa from trees at high elevations germinated "better" at lower temperatures than seeds from lower elevations (Vegis, 1963; Langlet, 1970). Brendel noticed that during warm spells in the winter, buds of many trees in Illinois swelled considerably. When cold weather followed, this swelling ceased, until the next warm spell. He postulated that the time of blooming might partly depend upon soil moisture, the dryness of the atmosphere, and the quantity of direct sunlight, as well as the air temperature (Brendel, 1887).

Engler, in 1905, and Cieslar, in 1907, found in common garden tests that trees from northern localities began leaf and shoot growth earlier in the spring than trees from southern localities when planted at central European sites. They also noted that trees from higher elevations leafed out earlier and became dormant earlier than trees from low elevations (Kriebel, 1957). Lamb (1915) noted that trees go through their sequence of events in a definite yearly pattern. He calculated that the season was about four days later for each degree of latitude north of a point, although local influences might more than offset this influence. He stated that increasing altitude had the same influence as latitude in retarding growth.

Winter chilling

In 1910, Howard conducted an extensive experiment on chilling and flushing of leaves. Collections of twigs of 283 species of plants were brought into a greenhouse at various intervals and many treatments were applied to force them into bloom, including freezing, drying, applying chemicals, and a control with no treatment. He found different levels of ease in breaking dormancy. In 1906-1907, he brought collections of twigs inside every 10 days from October through February. Very few species broke dormancy at the beginning, but as the experiment continued more species would break bud and in fewer days after being brought inside. In another experiment, Quercus penduncul ata that had been exposed to freezing temperatures in a cold frame before being brought into a warm greenhouse broke dormancy whereas those that had been inside all winter stayed dormant (Howard, 1910). Although not mentioned by Howard, the amount of cold received during the winter outdoors is obviously involved. Coville (1920) found that trees and shrubs that were kept continuously warm during the winter started growth later in the spring than chilled plants. The stimulating effect of cold was limited to the portions of the plant that were chilled. One branch of a blueberry bush extending out of a hole in the greenhouse flushed in the spring, while the rest of the plant did not. Another blueberry bush grown outside with one branch extending into the greenhouse had the exposed portions flush, but not the single branch that had been inside. Coville associated the stimulating effects of cold with the transformation of stored starch into sugar.

## Summary

Many principles involved in leaf flushing were studied for over two hundred years. Various scientists worked on the summations of temperatures. Experimenters carried on where their predecessors left off, working with increased accuracy in predictions as methods improved. Over one hundred years ago, the concept of a proportionality of the total annual sum of temperatures required for each phenological stage was recognized. Workers discovered that even though the date of flushing changed from year to year the amount of heat needed for a given stage did not change.

The concept of photoperiod, the effects of relative daylength, was not studied as early as heat summations. In the laboratory, daylength was hard to increase until the introduction of the electric light. Kjellman solved this problem by moving his experiments to the Siberian coast where the daylength was as long as he needed it. He then shortened the day for his experimental plants by placing them in dark boxes. Many of the extensive early experiments were done with herbaceous plants and may not relate to woody plants. These experiments were mainly on the flowering process and showed the length of the day affected the timing of flowering. At some daylengths only vegetative growth occurred.

Early common garden experiments were mostly the work of Europeans, studying economically valuable conifers. They noticed trends in flushing as well as in morphological characteristics. Generally, seedlings from northern and high elevation sources flushed earlier than southern or low elevation sources in a common garden. Two American workers noticed trends in nature in the yearly flushing cycle. Brendel noted the effects of a warm spell quickening flushing and a later cold spell inhibiting flushing. Lamb connected the timing of trees flushing and the native latitude of the tree, southern trees flushing earlier than northern trees. He postulated a retarding effect of high altitudes on flushing.

In 1920, Coville was the first to connect the amount of cold received during the winter with the rate and timing of flushing later during the warmer weather of spring. He realized that a cold period was required before growth could resume for most species. Others before had done experiments showing the same trends but had overlooked the importance of winter chilling in breaking dormancy.

## Dormancy and winter chilling

### Definitions

Dormancy in plants has been studied by many authors; the term has been defined in several ways. Howard (1910) stated that the rest period or dormant period was the time when plants did not grow, usually during the winter in the northern hemisphere. He noted that some dormant plants would start to grow when brought into a warm room, whereas others would not. He did not differentiate between the rest period and dormancy. Weldon (1934) differentiated between dormancy and rest. He defined dormancy as a state in which a plant could respond to favorable conditions and flush its leaves. Rest, in contrast, was an extremely profound condition not affected quickly by temperature, moisture, and other factors favorable for growth, unless sufficient winter chilling had preceeded these favorable influences. These definitions are not currently in use today.

Worral and Mergen (1967) differentiated three types of dormancy; summer, winter, and induced. The first two are results of internal physiology of the plant, the latter is caused by adverse environmental conditions. Perry (1971) defined dormant plants as those having a period of markedly reduced growth rate, with little or no cell division in the plant meristems, and requiring a chilling treatment before resuming growth.

Vegis (1963) subdivided the continuum of dormancy into three stages, "pre-dormancy" (early rest), "true-dormancy" (winter rest), and "post-dormancy" (after rest). Pre-dormancy is induced by gradually shortening days. Plants in this stage are not yet fully dormant and can resume growth under favorable conditions. When plants are in true-dormancy, metabolic changes have taken place, and even with favorable conditions of light and temperature growth does not take place. True-dormancy is ended once the chilling requirement has been met; then post-dormancy commences. When in post-dormancy, plants exposed for a period of time to warm temperatures, within a given range, are stimulated to grow. Temperatures above the effective range are detrimental and may counteract previous chilling. The range of effective temperatures for growth resumption is narrow immediately after the chilling requirement has been met and gradually widens until all temperatures above freezing and below the lethal point are effective. Once growth starts in the spring, the post-dormant stage is ended (Vegis, 1963).

In this paper, the term dormancy (unless otherwise specified) will be used according to the more general definition of Perry; a period of markedly reduced growth, requiring a winter chilling treatment before breakage.

### Studies of winter chilling

Many experiments on winter chilling have been carried out since the first ones in the early 1900's. Most authors agree that for most temperate zone trees, a winter chilling requirement must be met before they resume growth (Bennett and Skoog, 1938; Daubenmire, 1949; Downs and Borthwick, 1956; Wareing, 1956; Naylor, 1961). Temperatures of approximately 5°C are most effective in fulfilling the chilling requirement. Temperatures above 10°C and below 0°C are not as effective. High temperatures during the post-dormant period can negate the effects of a previous chilling (Naylor, 1961; Vasil'yev, 1961; Perry, 1971; Flint, 1974; Hart, 1974). The duration of low temperature needed to break dormancy varies by species. Six to ten weeks is sufficient for many woody species (Flint, 1974). In experiments with 123 species of ornamental trees growing outside in the Leningrad Botanical Gardens and 116 varieties of fruit trees from the European USSR, Moroz found some trees require 60 days of chilling temperatures to break bud. A second group required 30 to 45 days and a third group 15 days of chilling. A few species flushed without any additional chilling as soon as they were brought into a warm room (Vasil'yev, 1961).

Most winter chilling experiments involve many tree seedlings or cuttings being brought from the cold outdoors or a cold room into a warm greenhouse at regular intervals (treatments) from autumn through the winter. The number of days until flushing occurred was counted for each treatment. Species involved in these studies were Pinus resinosa (Gustafson, 1938), Hardy pear trees (Bennett, 1950), sugar maple (Olmstead, 1951), eastern hemlock (Olson and Nienstaedt, 1957), yellow and white birch (Wang and Perry, 1958), hemlocks (Olson et al., 1959), red maple (Perry and Wang, 1960), Tilia (Ashby, 1962), sugar maple (Kriebel and Wang, 1962), white pine (Mergen, 1963), and oaks (Longmann and Coutts, 1974). The general trend was that chilled seedlings flushed sooner than unchilled, and in some cases the unchilled seedlings did not break bud until the next year. If many successive lots of seedlings were taken into suitable growing temperatures, each lot took less time to flush than the one before it. In those unchilled plants that broke bud, growth was often abnormal or only occurred on the basal branches.

Delayed foliation, a problem for fruit tree growers in mild climates, is caused by insufficient winter chilling (Weldon, 1934; Bennett, 1950). In one friut tree orchard in California, a border of tall eucalyptus trees provided winter shade and low temperatures allowing the first few rows of peach trees in the shade to leaf out normally while the other trees in the orchard did not (Weldon, 1934).

The chilling requirement of different seed sources of the same species has been found to occur in predictable patterns. For example, Perry and Wang (1960) found clinal patterns in red maple chilling requirements. This chilling requirement could be correlated (r=.96) to the frost free period in the native habitat. Those seed sources from the northern part of the range required longer chilling than those from the southern part of the range. Wilcox (1968) found a clinal response in the foliation date of sweetgum to the location of the seed sources in Mississippi. The northern sources required longer chilling than the southerly sources.

## Latitudinal differences in chilling requirements

Genetic variation in the winter chilling requirement has been demonstrated along a north-south latitudinal gradient. Many workers have found that seedlings of southern origin needed longer chilling in winter than seedlings of northern origin (Vasil'yev, 1961; Nienstaedt, 1967; Irgens-Moller, 1968; Flint, 1974). In 1948, Moroz found that woody subtropical plants and those from the far south in regions characterized by mild winters, had no dormancy or chilling requirements (Vasil'yev, 1961). Kriebel and Wang (1962) found clinal variation in the amount of chilling required to break dormancy of sugar maple in a northern Ohio common garden test with provenances from a 1500 mile long north to south transect. Northern sugar maple cuttings required a longer period of chilling before flushing than southern sources when brought into the laboratory at three week intervals. However, the northern and not the southern sources were the first to flush in the Wooster, Ohio common garden site. This showed that more than the chilling requirement alone had an influence.

In a midwest black walnut provenance test, the northern black walnuts were the last to break buds (Bey, 1972). Bey hypothesized that the northern sources needed a longer period of chilling, and this caused them to flush later.

## Photoperiod interactions with chilling

In some studies, long days have been found to compensate for lack of winter chilling (Olmstead, 1951; Olson and

Nienstaedt, 1957; Wareing and Black, 1958; Olson et al., 1959; Naylor, 1961; Jenson and Gautherum, 1965; Nienstaedt, 1967, 1974a). In laboratory experiments with eastern hemlock, chilled seedlings grown under both short and long photoperiods resumed growth when returned to suitable temperatures. Unchilled seedlings grown under long day photoperiods resumed growth when returned to warm temperatures, although more slowly than chilled seedlings, whereas those seedlings grown in short days remained dormant (Olson and Nienstaedt, 1957). A more extensive eastern hemlock experiment showed that all the chilled seedlings broke dormancy regardless of photoperiod. Unchilled seedlings with 16, 20, and 24 hour days broke dormancy more slowly than chilled seedlings. Unchilled seedlings with 12 and 8 hours of daylength did not break dormancy at all (Olson et al., 1959). Birch buds that had been chilled broke dormancy with long or short days and also in complete darkness. Unchilled buds broke dormancy only with long days or very warm temperatures (Wareing and Black, 1958).

In a provenance study of basswood sources from the midwest grown in Chicago, Ashby (1962) found that slightly chilled plants placed under long day conditions exhibited delayed flushing, compared to short day slightly chilled plants. This is opposite to the general trend of long days compensating for underchilling. The slightly chilled plants showed a decrease in vigor and slower growth through the season compared to the fully chilled seedlings.

Since Jost brought beech out of dormancy with continuous light in 1894, other laboratory experiments employing various photoperiods have been performed. Downs and Borthwick (1956) found that in some species, such as catalpa, development of the cold requirement occurred gradually in the fall and winter. Before this buildup of the chilling requirement reached a level adequate to maintain dormancy, long photoperiod alone could induce resumption of growth. It appears these catalpas were not in true-dormancy according to Vegis's definition, but were still in pre-dormancy. Perry (1971) stated that only those plants subjected to short photoperiods and cold nights developed true-dormancy. In his studies, when box elder and viburnum were treated with long photoperiods and cold nights, active growth ceased. When these species were returned to a warm environment, growth was renewed without winter chilling. Thus, the plants had not reached true-dormancy, but were in the predormant state, and could be affected by favorable conditions.

In many experiments dormancy was induced in the laboratory through short day treatments and then growth was renewed with long day treatments or warm temperatures. Populus euroamericana cv. robusta cuttings stopped growth after short day treatments, even in warm temperatures. Dormancy was not broken by high temperatures as long as there were short days. When placed under continuous light, growth was resumed (Veen, 1951). The chilling requirement was not needed, but it is not certain that true-dormancy had been reached. Wareing (1959) found that certain species of trees could be brought out of short-day-induced dormancy by long day treatments. Even such leafless dormant seedlings responded to long days. Villiers (1966) reported that a minimal number of short day cycles were neccessary for induction of dormancy. The first few cycles were reversible, but after a certain number, there was no reversibility, i.e., true-dormancy was attained. Downs (1958) found marked differences in the requirements for breaking the short day induced dormancy in the laboratory. Several levels of dormancy were measured. Some species resumed growth immediately when placed under long days. Others could not have their dormancy broken by long days alone, i.e., they were in true-dormancy. Between these extremes were all variations.

Weiser (1970) differentiated between the first stage of cold acclimation induced by short days (pre-dormancy) and the second stage of cold acclimation (true-dormancy) which was induced by low temperatures. Frost appeared to trigger this second stage. Naylor (1961) reported that *Fagus sylvatica* had no cold requirement and the time of budbreak under natural conditions in some regions might be controlled by seasonal changes in light-dark cycles.

### Summary

In summary, dormancy is the stage in which most temperate zone plants pass through adverse conditions, usually cold or dry periods. Dormancy is induced by the progressive shortening of daylength together with low temperatures in late summer. Pre-dormancy, a stage where favorable conditions can trigger growth, gradually deepens to true-dormancy, a stage where growth cannot be induced by favorable conditions. For most species in nature, a chilling requirement at temperatures slightly above freezing must be satisfied at which point a post-dormant stage is reached. The length of the chilling requirement neccessary varies by seed sources within each species as well as by different species themselves. In many temperate species, seedlings of southern origin required a longer chilling period than seedlings of northern origin. This might be a protective mechanism against warm spells in the south inducing growth, followed by cold weather again, which kills the new growth. Many times, far northern regions stay cold until the spring thaw with no late freezes after growth has begun. When planted in common gardens outside their native range, some northern sources of temperate zone species seem to require longer winter chilling than southern sources. Subtropical and tropical species often have no winter chilling requirements or dormant period. Possibly in temperate species that grow into subtropical or tropical regions in the southern extent of the range, the southern sources require less chilling because normally there is no freezing weather to avoid. One might hypothesize that in those species that range far to the north and slightly south, the southern sources need more chilling. In those species that range far to the south and slightly north, the northern sources require more chilling.

When chilling is inadequate, plant growth may not occur at all, or it is abnormal or slow. During post-dormancy, favorable, warm conditions within a certain range of effective temperatures can stimulate resumption of growth. In some cases, such as eastern hemlock and birch, long day-lengths can compensate for winter chilling, although it is not certain whether this is true for plants that are in true-dormancy or only in plants that are not yet fully dormant.

## Heat summations

### Methods of calculation

The heat unit approach to plant phenology has been in use for over two centuries. Starting with Reaumur in 1735, many different methods have been used. With the invention of more sophisticated instruments and development of new methods predictions have become more accurate.

A heat sum is the summation of the product of temperature above a certain base level (threshold) and the time duration of that temperature (Worral and Mergen, 1967). For example, if the temperature was 50°F for six hours during the day, with the remainder of the day's temperatures below the 45°F threshold, the sum would be 5°F for each of the six hours, or a total of 30 degree-hours accumulated heat during the day.

To find the exact number of degree-hours accumulated for an individual tree it is neccessary to use a thermometer attached to a recording device to get the exact minute to minute temperature (thermograph). Using planimetry, one can then measure the area under the temperature curve and above the threshold (Boyer, 1970). However, this is not often done. Most experimenters calculate equations approximating the exact temperature summation. For example, Hellmers (1962) used the term heat sum in degree-hours to mean the numerical value of temperatures over 0°C multiplied by the length of time in hours that the plants were at each temperature during the 24-hour day. An example is, if the temperatures were 2°C for three hours, and at 4°C for two hours, with the rest of the temperatures below 0°C, one would have 2°C X 3 hours + 4°C X 2 hours= 14 degree-hours.

Moss (1960) defined a degree-day as one degree per day of mean temperature above a certain threshold temperature. For summing, the maximum temperature minus the threshold temperature. the quantity multiplied by the number of days equals the total number of degree-days. If the threshold were 42°F, and the maximum temperature was 45°F for two days, then one would have (45°F-42°F) x 2 days= 6 degree-days.

Lindsey and Newman (1956) developed the "duration-summation" method, which attempted to improve the simple daily mean method of accumulation heat units. Their method was designed to reflect the approximate durations of different temperature levels during the day. They used both daily minimum and maximum temperatures in addition to the threshold. The equation was: $24(w-t)+24(h-w)/2=$ the number of effective degree hours in one day, when $w=$ daily minimum temperature, $h=$ daily maximum temperature, and $t=$ the threshold temperature. When comparing the heat sums calculated by the formula to the actual tracings of a hygrothermograph, the approximations were within 1% and 3% of the exact heat summations (Lindsey, 1963). A chart compiling heat sums for all combinations of daily minimum and maximum temperatures for five different thresholds was developed by Lindsey and Newman (1956) to simplify further experimentation using their method.

## Threshold temperatures

Most heat sum systems are based on units of degree-hours or degree-days which are calculated by summing together the number of hours of each temperature above a certain threshold. There are different threshold temperatures for each species (Taylor, 1974). Bassett et al. (1961) studied early flowering of woody plants near Ottawa, Ontario, Canada from 1936 through 1960. Starting with March 1, temperature sums were accumulated. Repeated thresholds were used, starting low enough to include all temperatures, then successive approximations were calculated until the threshold that best explained variations in the year to year flowering was found. For *Betula papyrifera*, the maximum apparent threshold for flowering was 4.2°F, with -2.0°F the minimum. Ritchie and Lichti-Federovich (1963) found thresholds of 10°C day and 0°C night temperatures for the flowering of *Populus*, *Alnus*, and *Ulmus* species in Manitoba. Stearns (1970) reported a threshold of 32°F for lilac flowering in the northeastern United States. Lindsey (1963) studied the blossoming of the Japanese cherry trees at the Tidal Basin in Washington, D. C. He found a threshold temperature of 42°F gave the most constant summations from February until flowering occurred over a 40-year period. In 1952, Thornewaite pointed out that one of the flaws in the degree-hour approach was the difficulty of establishing correct values for the threshold temperatures (Newman et al., 1967).

Heat-sum thresholds for leaf bud bursting have also been calculated, and vary by species and geographic area. For three southern pines, Hellmers (1962) used a threshold of 32°F. In Finland, degree-days with a 5°C threshold have been employed frequently. Calculations were started in spring when the mean daily temperature exceeded 5°C for the first time (Sarvas, 1967). In northern Sweden, Erlandsson found a very high correlation between the annual radial growth in pine and the number of days when the maximum temperature exceeded 19°C (Mikola, 1962). Boyer (1970) studying Pinus taeda tried thresholds of 40°F, 45°F, 50°F, and 55°F along with planimetering the area between the temperature trace on a hygrothermograph and the four different thresholds mentioned above. The degree-hour heat sum above 50°F was found to be the best single variable regression explaining shoot growth timing.

Other methods

Other methods have been devised to take factors other than only heat summation into account. Padol'skiĭ, in 1958, found neither heat sum nor the threshold temperature a constant in his studies of cotton phenology. By constructing a phenology-temperature nomogram to eliminate non linearity, he aquired a greater accuracy in phenological prognosis (Wang, 1960).

Formulas incorporating total radiant heat or energy from the sun have also been developed. Newman et al. (1967) calculated net heat accumulations in cal./cm.$^2$/min. and cal./cm.$^2$/day in studies of Valencia orange growth and maturity. They combined air temperature, wind speed, and black body absorption temperature in their figures. Caprio (1974) developed the "solar thermal unit" (STU) based on lilac observations. This unit is a product of temperatures higher than 31° F and the daily amount of solar radiation in langleys (1 STU=1 ly-°F-day).

Stearns (1970) found that air temperature was the most important influence on woody plant phenology; the next most important factor was diurnal temperature gradients 20 inches below the soil surface. He reported Newman's 1967 findings that suggested that the soil temperature relationship to phenological events was a result of the shift of water from surface liquid to vapor state diurnally, resulting from heating above and residual stored heat from below. This effect was found to be most influential on phenology in early spring. Herman (1956) related the start of leader elongation for four Arizona junipers with soil temperature. Growth started when soil temperature reached 50°F. At the end of the growing season, growth stopped when soil temperatures dropped below 50°F, even when soil moisture was not lacking.

Ahlgren (1957) found a relationship between spring bud initiation and temperature per se, rather than a temperature summation. Bud swell in mountain ash, yellow and paper birch, and trembling aspen began with a slight warming but when minimum temperatures might still be below freezing.

Other species such as black and white spruce, and red pine began activity in the first spell with minimum temperatures above 30°F. American elm and red maple did not begin activity until maximum temperatures reached 60°F, and a fourth group, including black and red ash, balsam fir, and white pine, began growth when maximum temperatures reached 70°F. Basswood, bur oak, bigtooth aspen, and silver maple he found swelled over a wide range of temperatures.

Heat sum interactions with photoperiod

Photoperiod and temperature (absolute or heat sum) are often cited as having a concommitant influence on plants. Robak and Magnesen (1970) stated that daylength and temperature were among the most important factors controlling the yearly alternation of active growth and dormancy in trees. Dormling et al. (1968) found that for Picea abies daylength and temperature during maturation of the terminal bud determined the degree of dormancy attained, the time of bud-breaking, and the growth attained the following year.

Pauley and Perry (1954) found that temperature rather than photoperiod was effective in breaking dormancy. Later in the season, however, daylength had to be greater than a certain minimum for height growth to continue.

Some authors mention daylength and temperature acting antagonistically. Romberger (1963) cited the work of Vegis who proposed that in most woody species investigated light and temperature acted in opposition. In the laboratory, high temperatures promoted induction of rest in buds whereas long photoperiods promoted continued growth near the end of the growing season. Vaartaja (1960) mentioned that in nature, photoperiodic growth cessation responses in trees were likely masked and modified by many factors, especially temperature.

Data presented by Kaszkurweciz and Fogg (1967) appeared to reflect a causative relationship between photoperiod and growth initiation, which was considerably affected by the interaction of other environmental factors, especially temperature. They hypothesized that these other environmental factors restrain the photoperiodic response under certain circumstances.

Roberts and Struckmeyer (1938) studied various herbaceous plants in two temperatures and two photoperiods. They found that a number of species gave unlike responses to the same photoperiod at different temperatures. Some plants which were unfavorably affected in their growth and fruiting responses by the warm environment were frequently further injured by the long daylengths. They concluded that for many herbaceous plants, photoperiod might be a dominant requirement, but not essential for flowering. Photoperiodic effects could be modified by other external factors, i.e., temperature.

### Studies supporting the heat induction of flushing

**Coincident flushing with the same temperatures but different photoperiods** Many studies support the theory that it is the accumulation of heat, expressed as a heat sum, that induces bud bursting in the spring for both conifers and angiosperms. One series of experiments that supports this theory instead of photoperiodic induction of flushing involves plants flushing at the same time with different photoperiods but with the same temperature regime (*Acer negundo* and *A. rubrum*, Garner and Allard, 1923; *Populus*, Pauley and Perry, 1954; birches, locusts, maples, poplars, and white ash, Pauley, 1954b,1958; *Quercus*, McMillan, 1957; black and white spruce, Fraser, 1966; Norway spruce, Worral and Mergen, 1967; red-osier dogwood, Smithberg and Weiser, 1968).

Chilling of birch buds was found to remove the requirement of light for breaking dormancy, since chilled buds expanded even in complete darkness at 20°C (Wareing and Black, 1958). Pauley (1954b) found many species of angiosperms (yellow, paper, black, and grey birch; pin and black cherry; striped, red, and sugar maple; and white ash) broke dormancy at the same time with varying photoperiods when under the same temperature regime. However, species in the Fagacae (red, black, and white oak; American chestnut; and beech) failed to break dormancy in the continual dark. Wareing (1948) reported Klebs use of continuous light to break dormancy in beech. Provided the shoots received a period of light first, their subsequent leaf unfolding could take place equally well in the light or dark. McMillan (1957) reported no variation in the time of opening of *Quercus* buds under a series of different light periods. However, oak displayed wide variations under a series of different temperatures.

Wareing (1956) summarized results of these experiments by saying that in those species that showed a chilling requirement, budbreak was probably determined by rising temperatures in the spring, since chilled buds broke independant of daylength when transferred to warm conditions.

Flushing on different dates each year Another piece of experimental evidence supporting the theory of a heat sum inducing flushing in the spring rather than photoperiod is the variance from year to year in flushing dates. If photoperiod, which has the identical pattern of change each year, was the sole trigger one would expect a tree to flush on the same date every year regardless of temperature. However, many workers report flushing differences from year to year. Fraser (1966) found black spruce growth initiation varied by two weeks during the period 1960 to 1963. Kramer (1943) working at Duke University, and Keinholz (1941) working in Connecticut both studied the growth initiation of a variety of conifers and deciduous trees. Both noted that growth began earlier in the 1938 season than in 1939. Kramer mentioned that March weather of 1938 was about 6°F warmer than average, and March 1939 weather was about 3°F warmer than average. The flushing of Quercus robur in Giessen, Germany varied by 29 days over a 20 year period (Longmann and Coutts, 1974). This phenomenon has been reported for other species including Douglas-fir (Munger and Morris, 1936; Morris et al., 1957; Walters and Soos, 1963), Ulmus (McMillan, 1957), Norway and white spruce, hemlock, red pine, and balsam fir (Kozlowski and Ward, 1957a), western hemlock, western and red cedars, and western white pine (Walters and Soos, 1963), mesquite (McMillan and Peacock, 1964), yellow birch and sugar maple (Jacobs, 1965), cottonwood and sycamore (Kaszkurewicz and Fogg, 1967), oak and ash (Worral and Mergen, 1967), and black walnut (Bey, 1973a).

Some studies mention that flowering dates also vary from year to year. Lilac flower buds have appeared as early as March 30, 1945 and as late as May 13, 1950 in Minnesota (Hodson, 1954). Lindsey (1963) found a spread of almost a month in 40 years of observations of flowering of Japanese cherry trees around the Tidal Basin in Washington, D.C.

Constant heat sums induce flushing. Some workers have not only noted differences from year to year in flushing, but have calculated heat summations each year to see if the same heat sum was attained by the different dates. Brendel did this in 1887 for a number of species. Lindsey's (1963) studies of the Japanese cherry blossoms revealed that the single flower needed a temperature sum of 4,749 degree-hours over 42°F. The double blossom cherries required 9,297 degree-hours over 42°F before full bloom was attained. These average heat summations held true for 40 years of observations.

Mowbray and Oosting (1968) observed flushing along a transect across a north and south slope in the southern Appalachian mountains. They found very rapid leafing in all the species along the transect (*Pinus rigida*, *Acer rubrum*, *Liriodendron tulipifera*, *Quercus coccinea*, *Betula lenta*, *Magnolia fraseri*, *Gaylussacia baccata*, and *Galax* spp.) during a clear, warm, dry spring. The next year, cool, cloudy, and wet weather prolonged the entire leafing season. The heat sum for each species at flushing time was approximately the same both years.

Experiments with different temperatures in the laboratory have been conducted to test the effects of different temperatures on flushing. Garner and Allard (1923) found that lower temperatures delayed the time of flowering. In later experiments, they showed that variation in temperature caused variation in the date of flowering (Garner and Allard, 1930). A close correlation between the mean temperature and the length of the pre-flowering period was found. A decrease of 1° F in the mean temperature caused a delay of two or three days in the date of flowering. Jenson and Gatherum (1965) found the mean date of Scots pine flushing in the laboratory was 15 days earlier at 71° F than at 56° F.

*Yearly flushing sequence* Although plants may break buds on different dates during different years, individual plants or populations usually flush in the same sequence relative to other individuals or populations of the same species. This has been noticed both for seed sources in plantations and in nature. Munger and Morris (1936) found the order of bud bursting of Douglas-fir seed sources in plantations nearly identical in two consecutive years. Morris et al. (1957)

ranked vegetative budburst in Douglas-fir sources about in the same rank order over many years. Bey (1972), studying black walnut, reported that the seed sources that flushed first on an upland site also flushed first on a bottomland site 15 miles away.

Vaartaja (1959) stated that seasonal earliness is peculiar even to individual trees. This was evidenced by Morris et al. (1957) who observed the flushing of two Douglas-fir trees less than 200 feet apart. These trees flushed in the same sequence every year for 14 years. The greatest interval was 12 days apart; the smallest interval was two days apart. This consistancy in order indicates a strong genetic control over the time of budbursting.

Summary

Many authors have observed phenological differences among species and among different seed sources of the same species. The environmental effects on the genetic makeup of a plant cause the variations year to year in flushing, as well as other phenological events. In common garden and laboratory tests, the environmental factor of temperature, as expressed by a summation of heat after the chilling requirement has been met, best explains these yearly differences in flushing times.

A heat summation is usually measured in degree-hours or degree-days, and is the summation of the product of temperature above a certain base level, and the time duration of that temperature. Many methods of measuring temperature summations have been calculated, some using temperature alone, others incorporating soil moisture, radiant energy from the sun, and other factors into the equation.

There are many different types of studies that support the heat induction of flushing, as opposed to photoperiod. Some laboratory experiments showed that plants growing under different photoperiod treatments but at the same temperatures flushed simultaneously. Plants with different temperatures but the same photoperiod did not flush at the same time. This second experiment is what happens in nature: i.e., the photoperiodic regime is the same each year but temperatures vary. In nature, trees typically flush on different days each year, therefore a photoperiodic induction theory is not supported. When workers have calculated heat sums of the temperatures above freezing until flushing occurs, the summation is fairly constant from year to year, even though the dates of flushing might be different.

When different provenances of a species are raised together in a common garden, differences can be seen each year between provenances. However, over many years, the same sequence of sources flushing can be seen. This shows the strong genetic control of flushing. Different requirements must be met for different provenances and individuals, once the chilling requirements have been met.

## Major flushing trends

### North to south cline

Differences in flushing among provenances have been observed in many common garden studies. One of the major trends observed is a north to south clinal pattern. Often latitude is used as a basis upon which to measure this north to south variation. In most studies the northern sources flushed before the southern sources when all plants are grown in an intermediate common garden. Worral and Mergen (1967) hypothesized that northern sources flushed earlier because they were adapted to a cooler growing season and responded to temperatures that did not elicit a response from seed sources of more southerly origin. Many deciduous and conifierous trees exhibit this genetically based north to south cline (sugar maple, Kriebel, 1957, Kriebel and Wang, 1962, Worral and Mergen, 1967; Ponderosa pine, Squillace and Silen, 1962; *Prosopis laevigata*, McMillan and Peacock, 1964; yellow birch, Clausen and Garrett, 1969; yellow and sweet birch, Sharik, 1970, Hart, 1974; Norway spruce, Langlet, 1970; white pine, Wright, 1970; many species, Stearns, 1970; sugar maple, yellow birch, *Pinus strobus*, Nienstaedt, 1974a).

In a sitka spruce study by Burley (1966a), the north to south variation pattern was found to be generally true, but there were exceptions. Forty seven sources in nine groups of seedlings from Alaska through California were grown in New Haven, Connecticut. Five groups fell into the pattern of northern sources flushing first; four groups flushed earlier or later than what might be expected when based on latitude alone. Two of the sources in the sixth group, from southern California in an area with rare spring frosts, flushed earlier than expected. The four sources in the seventh group were from Alaska. The two coastal sources flushed early, but two inland sources, near ice fields flushed late. These two groups as well as the eighth and ninth groups were adapted to local conditions rather than the general trend.

South to north trend

Some other provenance studies show a reverse trend, with southern sources flushing first in the common garden (Douglas-fir, Ching and Bever, 1960; tulip tree, Sluder, 1960, Farmer et al., 1967; sugar maple, Kriebel and Wang, 1962; white pine, Sluder, 1963; Prosopis glandulosa var. glandulosa, McMillan and Peacock, 1964; black spruce, Morgenstern, 1969a; black walnut, Bey, Toliver and Roth, 1971, Bey, 1972, 1973a; sweetgum and sycamore, Nienstaedt, 1974a). Worral and Mergen (1967) reviewed the common garden tests that resulted in the southern trees flushing first. They found most of these tests had been carried out in the southern part of the range of the species. They hypothesized that the northern plants in the study had not recieved sufficient chilling, and were therefore slow to respond to the warming conditions in the spring. Another possibility was that the spring temperatures rose too quickly, leading to a narrowing of the acceptable temperature range for early growth.

Kriebel and Wang (1962) raised sugar maple seedlings from many seed sources in two common gardens, one in Ohio, the other in Florida. They found opposite trends at each site. In Ohio, northern sources flushed first, while in Florida, the southern sources flushed first. They hypothesized that in the northern test, the southern sources were "over chilled" by the low winter temperatures, retarding their growth response, or else possibly the spring temperatures were not high enough in early spring to allow an early budbreak. The probable reason the northern sources flushed later than the southern sources in the southern test was that they were not sufficiently chilled.

Bey (1972) found that midwestern black walnut sources at an Illinois plantation flushed earlier than the same sources at a plantation in Michigan. However, the rate of flushing was slower in the Illinois plantation. They hypothesized that the soil warmed more gradually in the southern plantation, thereby magnifying seed source differences. They expected flushing in each plantation to be delayed approximately four days for every 100 miles to the north that the plantation was established.

Nyland (1974) found that conifers stored over the winter at 28°F to 30°F did not flush as soon after planting as those freshly dug in the spring from a nursery in Syracuse, New York. The unstored conifers had been exposed to natural winter temperatures in an outdoor plantation. Once flushing occurred, the stored stock showed a slower rate of leaf expansion. Slower leaf expansion in the plants that warmed more quickly, i.e., the plants that went from storage directly to spring warmth and did not undergo gradual conditioning from normal seasonal temperature rises, showed a trend opposite to the one observed by Bey that the seedlings in a plantation that warmed up more gradually were the ones that flushed at a slower rate, The differences could be due to under chilling of the stored stock.

Length of the growing season

Some studies have found significant interrelationships between the date of flushing and the length of the growing season at the origin of the seed source. Generally, seed from areas having a shorter growing season flushed earlier in a common garden. The length of the growing season was often more significant then the latitude. The length of the growing season could take into account site differences that were not evident when using latitude alone.

Mergen (1963) found the average period of time neccessary to break bud in white pine after warm conditions began was related to the length of the growing season at the source. Seedlings from areas having shorter growing seasons broke dormancy more rapidly than those of longer growing seasons. In general, a shorter growing season is found at higher latitudes and elevations.

Smithberg and Weiser (1968) noticed that red-osier dogwood clones in a common garden had a closer relationship between the onset of dormancy and the length of the growing season than latitude or minimum temperature. Clones with shorter growing seasons went into dormancy sooner than those with longer growing seasons.

Experiments with tamarack seedlings in Wisconsin indicated a significant correlation (r=.65) between the date of bud set and the frost free period of the seed origin. The seedlings having a shorter frost free season set bud earlier (Rehfeldt, 1970).

Mesquite populations grown in Texas showed that early spring flushing activity and short dormancy requirements were positively correlated with the long growing periods of the most southern (sub-tropical) habitats (McMillan and Peacock, 1964). This trend was the reverse of that found by Mergen (1963) with white pine and by other workers with different species. Mesquite ranges from temperate Oklahoma to sub-tropical Mexico, the southernmost areas without frost. Thus, this example is not exactly comparable to that of white pine, which grows in a cold season of varying intensities in all parts of its range.

Sluder (1960) found the date of growth initiation of tulip trees in a North Carolina common garden was negatively correlated with the length of the growing season (r=-.90); the correlation with latitude was r=.58. Those seedlings with a longer growing season or more southern origin flushed first. This case is also opposite to the general trends and is a tree of the Temperate Zone.

Morgenstern (1969a) found a strong and significant correlation (r=.78;p<.01) between the length of the growing season and flushing of black spruce from Canada and northern Wisconsin. Those seedlings from sources with shorter growing seasons flushed earlier.

Temperatures during the growing season at the origin of the seed provenances have been related to flushing patterns expressed in a common garden. The pattern of sitka spruce flushing in a Connecticut common garden was related to the temperature regime during the growing season in the native habitat (Burley, 1966b). The seedlings from warmer habitats generally flushed later than those from cooler sites.

### Elevation effects

Lamb (1915) hypothesized that higher elevations would have the same effect as higher latitude upon phenological events. He expected the seedlings from higher elevations would flush first, just as many seedlings from higher latitude flush first. Some studies of flushing have established this correspondence. This trend would be expected because often as elevation increases, conditions become more extreme. Temperatures are colder and the winds can be stronger. At very high elevations, the atmosphere is thinner, so radiation and reradiation would occur more quickly. Munger and Morris (1936) found that in Douglas-fir grown at 1100 feet in an Oregon common garden, trees from several high elevation sources burst their buds one or two weeks before those from low elevations. Lines (1970) reported that high elevation European larch sources were early flushing in a Scottish common garden. Medium elevation Swiss sources were later flushing, and low elevation Polish and Czechoslovakian provenances were the latest to flush.

However, this trend is not always found. In some areas, the highest elevation may not have the most severe conditions, and the low elevations may not be the mildest. Mirov et al. (1952) found a middle elevation Sierra Nevada (1850 feet) site milder than higher (5650 feet) or lower (960 feet) common garden sites. Cold air flowing down the mountain chilled the lower plantation. Hart (1974) cited the findings of Stephens (1969) that the lengths of the frost free season at four elevational stations in the Smoky Mountains were similar. At elevations of 1460, 3850, 5000, and 6300 feet, the frost free seasons averaged 156, 152, 148, and 152 days. Some Douglas-fir experiments carried out in Corvallis, Oregon, have shown low elevation sources flushing before high elevation sources (Irgens-Moller, 1957, 1967; Ching and Bever, 1960; Hermann and Lavender, 1968). Two plantations in Idaho also showed this trend (Rehfeldt, 1974) in contrast to the findings of Munger and Morris (1936).

High elevation sources of Douglas-fir have shown photoperiodic responses in budburst, whereas the low elevation sources have not (Irgens-Moller, 1957). This might indicate that the high elevation sources when grown at low elevations did not receive enough winter chilling, and photoperiod acted as a "second line" trigger, eliciting a flushing response. When adequately winter chilled, photoperiod usually does not affect flushing.

Other trends have displayed trends of lower elevation sources flushing before high elevation sources, including Populus trichocarpa (Pauley, 1954a) and northern red oak (McGee, 1974). McMillan and Peacock (1964) found Prosopis laevigata from the northern Mexican coast flushed before sources from more southern mountain populations when grown in Austin, Texas.

In an attempt to compensate for elevation along latitudinal gradients, different equations have been formulated to adjust latitude for elevation when comparing the performance of populations of different latitudes and altitudes. These relationships depend upon the species and physiographic area. Sharik (1970) calculated an adjustment factor of 1.52° for every 1000 feet of elevation for yellow and sweet birch in the Appalachians. This formula was based upon association with the mean annual temperature. Another compensation factor of 1.61° for every 1000 feet of elevation was based upon the length of the growing season. He mentioned adjustment factors of 1.40° for 1000 feet of elevation on the Atlantic seaboard calculated by Spurr, and 1.50° for every 1000 feet of elevation in the mountainous regions of the western United States used by the U. S. Forest Service. Hamrick and Libby (1972) also used 1.5° of latitude for every 1000 feet of elevation for white fir in the west.

These formulas help compensate for the differences in the length of the growing season at different elevations at the same latitude. Generally, going up in elevation has the same effect as going north in latitude. By adjusting the latitude, more precise comparisons can often be made (Spurr and Barnes, 1973, p. 37).

Tests monitering plants in nature show different trends than in a common garden. Common purple lilacs blossomed in Stanford, California (98 feet in elevation) in late March, compared to late June at timberline (10,004 feet) (Caprio, 1967). Galax and Gaylussacia in the Smoky Mountains flushed one to five days sooner near the top of an elevational transect than near the bottom (Mowbray and Oosting, 1968). Kaszkurewicz and Fogg (1967) found high elevation cottonwood and sycamore flushed at lower temperatures than at low elevations.

Photoperiod affecting flushing

Some research workers stated that photoperiod affected or caused budbreak (Vaartaja, 1954; Wareing, 1956; Nienstaedt and Olson, 1961). Daubenmire (1949) stated that daylength was more important than temperature in stimulating trees to resume growth after winter dormancy during his studies of 17 tree species at the University of Idaho at Moscow arboretum. The daylength was more closely related to the start of growth than the daily minimum and maximum temperatures.

Peacock and McMillan (1965) hypothesized that south of some latitude in the Northern Hemisphere, photoperiod, if critical at all, would cease to control tree responses. This is because without frost being a lethal factor to growth, it would not be necessary to have a cue such as photoperiod to cause growth to cease.

The theory of photoperiodic control of flushing does not have too much support today, but photoperiodic control of growth cessation is strong. There is much more evidence supporting a heat summation following fulfillment of the winter chilling requirement.

## Summary

Most common garden studies showed gradients in flushing according to the origin of the seed sources. The most common pattern is that the northern sources flush first, followed by sources of progressively southern origin. This occurred when the common garden was located in the northern or central portion of the range. Sometimes the southern sources flushed first. In some cases this appeared to be due to insufficient winter chilling of the northern sources when experiments were carried out in more southern test sites. Another exception to the generally north to south trend occurred when species from the far south, including sub-tropical areas, were tested. In the most southern regions, no spring frosts or very rare frosts occurred, therefore, no selective forces were at work to cut the growing season off during part of the year.

Some common garden experiments showed a correlation between the length of the growing season and the time of flushing, with the sources having a shorter growing season flushing first. Generally, long growing seasons are found in the more southerly latitudes and lower elevations. Short growing seasons are usually found in the north. However, microsite differences can be revealed that are often overlooked in the more general latitudinal approach.

The effects of elevation in common garden studies were not as clearcut as those of latitude. Some tests showed trends of higher elevation sources flushing first, comparable to the general relationship of high latitude sources flushing first. However, in some tests the lower elevation sources flushed first when grown at low elevation gardens. This could be due to inadequate chilling of high elevation plants at the low elevations. Also, in some mountainous regions, the highest elevations did not always have the most severe conditions. Therefore, one would not expect the higher to lower elevation trend to always be true. An important factor that should be considered is the length of the growing season at each elevation and the specific environmental conditions at each elevation.

In some of the tests carried out at low elevations, where the low elevation sources flushed first, the high elevation sources showed photoperiodic responses. This response to daylength is an indication that the winter chilling requirements were not met at the milder test site. Without sufficient winter chilling, the responses of plants to warm weather would have been retarded.

Some authors have stated that photoperiod is a causative agent in flushing, however, more of the evidence tends to indicate that it is a heat summation after sufficient winter chilling that is by far the significant environmental factor. Photoperiod is possibly a "second line" trigger, important only in unusual cases e.g., if the winter chilling requirement was not met.

In nature, as opposed to common garden tests, the plants of southern areas and lower elevations flush first. this is because these areas warm up more quickly, and the temperatures meet the adaptive requirements of the plants sooner than plants farther north when it is still relatively colder and the temperature requirement is not yet met.

## Genetic variation in flushing

### Introduction

In differing common garden environments, the flushing trends of seed sources may differ greatly. It is primarily the underlying differences in the genetic makeup of the sources that allow these differences to be expressed. In 1882, Kasan said, "every form or species may be regarded as a mean product resulting from all the influencing mechanical, physiological, and climatic factors of a site" (Langlet, 1970). Obviously, in nature we cannot separate out the environmental and genetic compounds of phenotypic variation. Thus, in the common garden site we are holding the environment constant in order to observe differences due to the genotype.

### Heritability

Control of flushing behavior seems to be strongly genetically controlled. Many studies have shown very high heritabilities of flushing. Wilcox and Farmer (1967) reported a heritability of .97 on an individual basis, and .99 on a clonal basis for two year old cottonwoods in a natural stand. Wilcox (1970) reported broad sense heritabilities total genotypic variation/phenotypic variance) that were very significant for sweetgum flushing in Mississippi ($h^2$= 1.27 and .98 in two plantations for the year 1965). He also reported heritabilities of .56 for Norway spruce found by Mergen (1960). Bey (1973a) reported the date of leaf flushing heritabilities of .67 and .96 for two separate two-year-old progeny tests of black walnut. Nienstaedt (1974b) reported heritability of .85 for flushing in white spruce in a Wisconsin common garden.

Clinal variation

The genetic differences were often found to exhibit a clinal pattern. Hamrick and Libby (1972) found some white fir characteristics, especially those associated with growth (including flushing and growth cessation), varied clinally with relation to both altitude and latitude. Other characteristics, especially those associated with morphology of the seedlings, varied clinally with latitude, but were fairly uniform over a range of elevations at a given latitude. Kriebel and Wang (1962) found a latitudinal cline in the date of sugar maple flushing in an Ohio common garden. Morgenstern (1969a,b) found clinal variation in black spruce flushing. They found little evidence of discontinuous variation among sources.

Squillace and Silen (1962) found a rather strong east to west gradient in growth differences, including flushing, of Ponderosa pine. This gradient was related to the amount of moisture available and the annual distribution of that moisture. A moderate latitudinal cline was found in a pattern related to temperatures. A moderate altitudinal cline was also found.

Perry and Wang (1960) found a clinal pattern in the variation of the chilling requirement of red maples collected from Canada to the Everglades, with the more northern sources requiring a longer chilling period. Plants were grown in a common garden in Florida. This pattern could be related to the frost free period in the native habitat. The Everglades source did not require any winter chilling, whereas the more northern sources did.

Other experimenters have reported "ecotypic variation" in flushing patterns. Often ecotypic patterns (where ecotypic means discontinuous) are caused by the sampling methods used. If samples are taken widely or randomly spaced, the patterns found, if any, will be influenced by these sampling methods. Vaartaja (1959) stated that photoperiodic ecotypes seem to exist in trees with a wide north to south range in the Northern Hemisphere. Wright and Bull (1963) found ecotypic variation in Scots pine flushing. The ecotype barriers were pine-less areas.

### Age differences

Within a single tree, flushing differences may exist through time. As a tree grows from a seedling to a mature tree, its flushing response may change slightly. Some authors have reported that young seedlings flush earlier than mature trees of the same species. Irgens-Moller (1957, 1967) found that flushing of Douglas-fir occurred progressively later in a given plantation. Two-year-old Douglas-fir seedlings flushed about three weeks earlier than eight year old plants. Silen (1962) noted that mature Douglas-fir flushed nearly two weeks later than their seedling progeny. He attributed this difference to the warmer microclimate near to the ground. Ford and Sucoff (1961) found no significant differences in sapling hybrid poplar flushing due to height. However, at seven to nine years old, the leaves of these saplings may not have been close enough to the ground to be affected by it.

Went (1961) found a gradual shift of the optimal temperatures for many species of herbaceous plants from higher to lower levels as they became older. Kramer (1958) mentioned Sachs, who suggested that each phenological stage of growth of a plant had its own optimal temperature, e.g., vegetative growth needed higher temperatures than flowering. Wang (1960) suggested that an improvement to the heat unit approach would be changing the threshold temperature used in calculations according to the age of the plant. So possibly in addition to temperatures being warmer close to the surface of the soil, smaller seedlings, which are closer to the ground and in these warmer temperatures, respond to higher threshold temperatures. This difference might be genetically controlled to change as the tree ages. Therefore, the small seedlings might flush earlier due to warmer temperatures, but not too much earlier since their threshold is higher.

Some authors have mentioned that seedlings grow later into the fall than mature trees. Perry (1971) found that red maple seedlings grew longer than adults of the same sources. Kozlowski and Ward (1957a) reported that in many woody species, the seasonal period of height growth is much shorter in mature trees than in seedlings. However, in some species, e.g., hemlock, the growing seasons were similar for both young and old trees.

Longmann and Coutts (1974) found that seedlings and coppice shoots of Quercus robur less than four years old reflushed the most frequently during the growing season, whereas on trees over ten years old, only very vigorous shoots had two growth flushes, and the remaining shoots flushed only once. All these differences due to age seem to be selective advantages for younger trees to survive and become established.

Lewis and Lines (1973) found that flushing score trends observed in the nursery with 2+2 transplants were later seen in the same provenances three seasons after they had been planted in the forest for Picea abies. The seed sources had the same sequence of flushing at both observations (r=.89).

Terminal versus lateral shoot growth

Many authors have mentioned differences in the flushing time of terminal and lateral shoots. More cases have been cited for conifers than for angiosperms. Walters and Soos (1963) found upper and lower laterals of Douglas-fir started growth before the leaders. In western red cedar, leaders and laterals started at the same time, whereas western hemlock leaders started before the laterals. Sweet (1965) found Douglas-fir laterals began growth before the terminal buds. Nienstaedt (1974a) stated that in many conifers the laterals flushed before the terminal bud.

Different reasons for this phenomenon have been hypothesized. Ashby (1962) found that unchilled Tilia seedlings broke bud on the lower branches only. He stated that the chilling requirement may be greater for the terminal buds than for the lateral buds. Mergen (1963) studying eastern white pine hypothesized that lateral buds had a shorter dormancy requirement than terminal buds, and this was the reason the laterals flushed first. Sweet (1965) found the length of the time lag between the terminal and lateral budbursts in each provenance was strongly related to the seed source data. Those provenances with a long interval between lateral and terminal flushing (lateral first) came from mild climates that had the most chances of unexpected spring frosts.

## Frost relations

Many research workers have noted that plant growth starts before the last killing frost and stops before the first frost of autumn. Kaszkurewicz and Fogg (1967) found that for cottonwoods and sycamores growing at lower than 33°N latitude, growth initiation started after the last killing frost, but at higher latitudes, greater than 33°N, growth initiation started before the last killing frost. Growth cessation at all latitudes occurred before the first fall frost. Kozlowski and Ward (1957a,b) found that for a variety of conifer and angiosperm phenotypes in Massachusetts, growth started before all threat of frost was over;

trees completed all growth long before the first fall frost. Campbell and Sorenson (1973) found that Douglas-fir from Washington and Oregon set bud before the first fall frost.

From these reports of growth starting before the last killing frost, the differentiation between lateral and terminal budbreak could be a selective advantage to a plant. Growth could start with part of the plant, but in case a late spring frost occurred, not all of the new growth would be damaged since the terminal leader would still be dormant.

Frost resistance

The level of frost resistance in the spring was found to vary by seed sources within species as well as between species. Tryon (1971) found opposite trends for angiosperms and conifers. For most angiosperms, those species that broke bud early were more frost resistant, and those species that broke bud late were less frost resistant. In contrast, those conifers that broke bud early were less frost resistant, and those that broke bud late were more frost resistant. Little (1941) found that frost was more injurious to open grown trees of many species than in their natural forest habitat. This is probably due to the forest retaining more heat at night when temperatures are low. In the open, reradiation at night is faster and extremely cold conditions result.

In common garden tests, northern sources of a species often are more frost resistant than southern sources. This has been found in different species including mesquite

(Peacock and McMillan, 1965), balsam fir (Lester, 1970), black walnut (Bey, 1973b), and Douglas-fir (Campbell and Sorenson, 1973). Since the frost free season is generally shorter in the north, this could be a selective advantage.

Survival advantages to heat sums

Perry (1961) stated he knew of no instance where proper experimentation failed to reveal racial adaptions to the environmental factor studied. He found parallel patterns of physiological adaptions by diverse taxonomic groups. This shows that there is great variability in the gene pools and with strong selection pressures exerted by the environment, plants became adapted to their particular site. When brought together in a common garden test, progeny from different areas exhibit adaptions that have been selected for on their particular site. When these seed sources are grown on different sites, they may not grow as well or in the same rank order as at the original site. Munger and Morris (1936) reported European observations that trees from cold climates grown in warm climates burst their buds too early and were frozen by late spring frosts.

Nienstaedt (1974a) stated that the timing of spring flushing was adaptive in nature. Different characteristics were selected for by different climates. Burley (1966a) suggested that selection against early flushing did not occur in continental climates where the spring rise in temperatures occurred rapidly and late and subsequent spring temperatures rarely fell below freezing. Irgens-Moller (1957) stated that Douglas-fir plants in the flat plains had not been exposed to selection pressures similar to those of the western mountains with widely fluctuating temperatures.

Fraser (1966) reported that black spruce budbreak was usually later than white spruce on the same site. He hypothesized that this was important in allowing black spruce to grow in cold places and still avoid spring frosts. McMillan and Peacock (1964) stated that the spring foliage of mesquite was frost intolerant and therefore late initiation of bud activity developed as a mechanism to avoid spring frosts after warm conditions. Early bud bursting was a disadvantage in the northern Oklahoma range of mesquite, but was a competitive advantage in the southern Mexican portion of the range, where frosts were rare. McGee (1974) applied this argument to elevation for northern red oak. In four common gardens, at 1500, 2200, 3500, and 5500 feet in western North Carolina, he planted seeds collected at 1400, 2700, 3800, and 4600 feet. At all four plantations, the lower elevation sources flushed before the higher elevation sources. McGee thought that the higher elevation sources would have a better chance of surviving frost and cold conditions if they broke bud late, and low elevation sources had a better chance of competing with surrounding vegetation if they began growth early. However, the plantation that flushed first in 1972 was the 3500 feet of elevation garden. The maximum and minimum temperatures during April were higher there than at the lower two plantations. So possibly this is a case where the lowest elevation does not have the mildest conditions.

## Summary

In summary, the genetic component of a plant affects its reactions to the environmental conditions it grows in. The flushing process is very strongly genetically controlled, as seen by high heritability values. Those trees that have genes that are better adapted to the local environment will live to pass on their genes, whereas those trees that flush too early, and are killed by late spring frosts, or those trees that flush too late, and are overtopped by other trees will not survive. Generally, the genetic differences vary in a continuous clinal pattern over the range of the species to match the natural selection pressure in the springtime.

In some areas where late spring frosts are common, differentiation in flushing times between the lateral and terminal shoots apparently have occurred. This makes it possible for part of the plant to start growing early, but in case a late spring frost occurs, not all of the new growth is killed. The longer length of time between lateral and terminal flushing has been correlated with those area having a greater incidence of late spring frosts.

Differences within one tree (one genotype) have been noted with increasing age. Young seedlings often flush earlier than mature trees of the same seed source. Early flushing gives a selective advantage to younger seedlings in allowing them a better chance to survive and become established by getting their leaves out and photosynthesizing before they get shaded by the mature trees overhead.

Frost resistance in new foliage has been found to vary by genotype also. Generally the more northern sources are more frost resistant. This is important because, in general, the frost free season is shorter in the north.

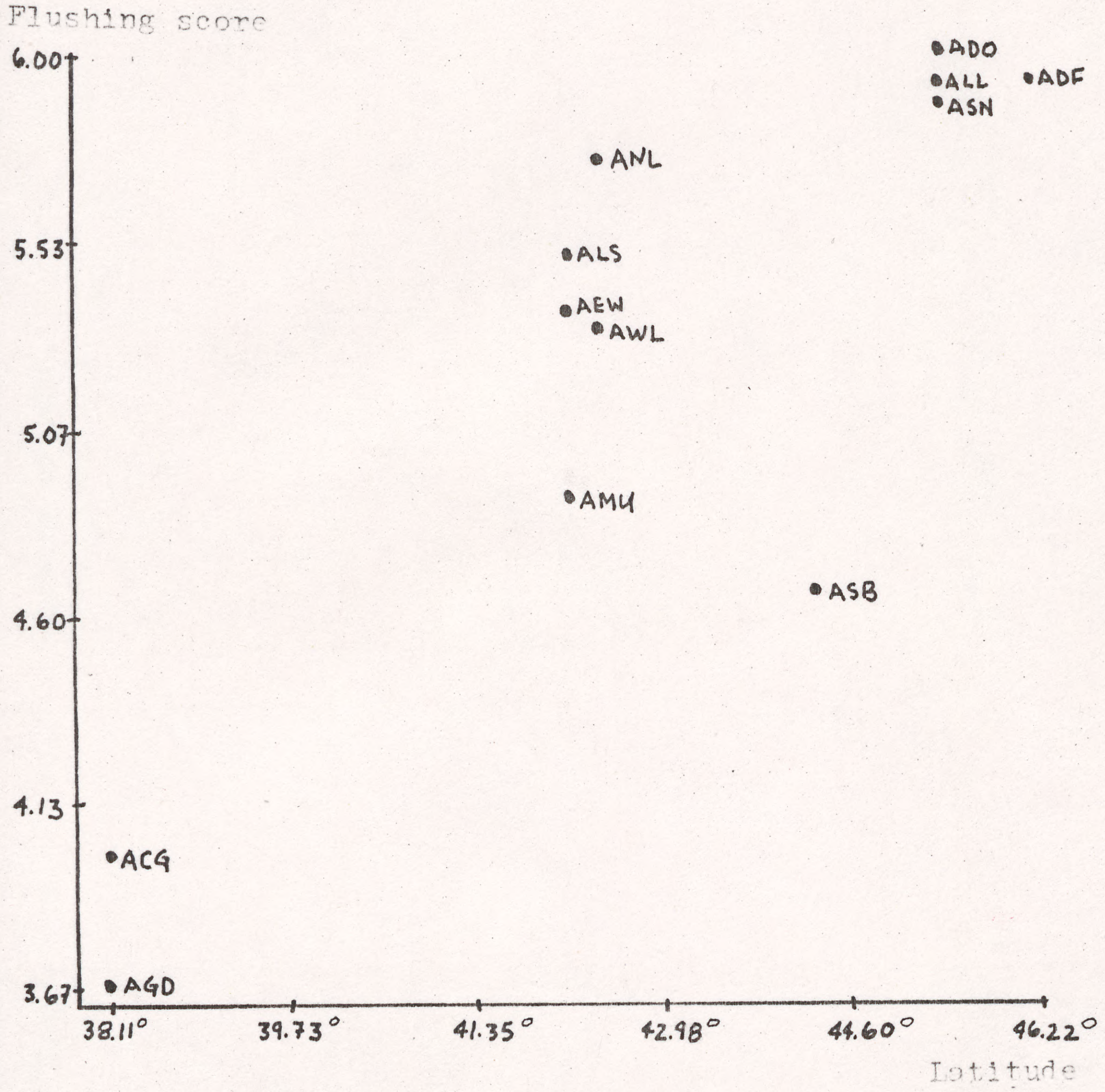
## RESULTS

### Plantation 1

The northern Michigan yellow birch sources flushed first. The average flushing score was significantly correlated to latitude ($p < .01$). The coefficient of correlation values for each of the four dates were: $r = .79$ for April 29, $r = .82$ for May 5, $r = .85$ for May 12, and $r = .71$ for May 19. The distribution of flushing values for May 12, the next to last date they were scored, is shown in Figure 1. The upper peninsula source (DF) was further advanced in flushing than all other sources except for one northern lower peninsula source (DO). The northern lower peninsula sources were more advanced than the southeastern Michigan sources, which were followed by the central Michigan source (SB). The two West Virginia sources (GD and CG) were the latest in flushing.

### Plantation 2

Yellow birch flushing was significantly related to latitude ($p < .01$); the more northern sources flushed first. On the first three scoring dates the differences were more pronounced ($r \geq .80$) than the latter two ($r = .61$ and $r = .66$) (Table 2). On the last two dates, the southern sources were almost as far advanced as the northern sources, therefore the regressions were less significant. Figure 2 shows the plot of flushing scores and latitude on April 29. The scores ranged from 1, buds at rest, to 4.2, leaves expanding.



<u>Figure 1</u>- Flushing scores for yellow birch from Michigan and West Virginia in relation to latitude of the sources for Plantation 1 on May 12, 1974.(r=0.85).

Table 2- Statistical comparisons of differences in flushing of yellow birch, sweet birch, and both together for Plantation 2 during the spring of 1974.

| | April 29 | | | May 5 | | | May 12 | | | May 19 | | | May 26 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F[1] | p[2] | r[3] | F | p | r | F | p | r | F | p | r | F | p | r |
| **Latitude** | | | | | | | | | | | | | | | |
| Yellow birch | 53.08 | .01 | .83 | 51.38 | .01 | .82 | 44.82 | .01 | .80 | 14.15 | .01 | .61 | 18.92 | .01 | .66 |
| Sweet birch | 5.68 | .03 | .57 | 3.16 | .10 | .46 | 3.30 | .09 | .46 | 2.59 | .13 | .42 | 0.36 | .56 | .17 |
| Both birches | 68.43 | .01 | .80 | 60.26 | .01 | .78 | 51.20 | .01 | .76 | 18.69 | .01 | .57 | 23.65 | .01 | .62 |
| **Adjusted latitude (1.52° per 1000 feet)** | | | | | | | | | | | | | | | |
| Yellow birch | 17.04 | .01 | .64 | 14.35 | .01 | .61 | 14.70 | .01 | .62 | 5.29 | .03 | .42 | 9.35 | .01 | .53 |
| Sweet birch | 1.19 | .30 | .30 | 0.50 | .49 | .20 | 0.72 | .41 | .24 | 0.16 | .70 | .11 | 0.04 | .84 | .06 |
| Both birches | 27.06 | .01 | .64 | 22.62 | .01 | .61 | 21.77 | .01 | .60 | 7.49 | .01 | .41 | 15.83 | .01 | .54 |
| **Adjusted latitude (1.61° per 1000 feet)** | | | | | | | | | | | | | | | |
| Yellow birch | 15.10 | .01 | .62 | 12.61 | .01 | .59 | 13.04 | .01 | .59 | 4.71 | .04 | .40 | 8.54 | .01 | .51 |
| Sweet birch | 1.01 | .34 | .28 | 0.38 | .55 | .17 | 0.58 | .46 | .21 | 0.09 | .76 | .09 | 0.03 | .86 | .05 |
| Both birches | 24.35 | .01 | .62 | 20.19 | .01 | .59 | 19.59 | .01 | .58 | 6.68 | .01 | .39 | 14.78 | .01 | .53 |
| **Elevation** | | | | | | | | | | | | | | | |
| Yellow birch | 23.64 | .01 | -.70 | 29.39 | .01 | -.74 | 22.99 | .01 | -.70 | 12.41 | .01 | -.58 | 10.08 | .01 | -.64 |
| Sweet birch | 9.62 | .01 | -.67 | 3.08 | .10 | -.45 | 2.60 | .13 | -.42 | 3.82 | .07 | -.49 | 0.42 | .52 | -.18 |
| Both birches | 25.17 | .01 | -.63 | 25.92 | .01 | -.64 | 21.26 | .01 | -.60 | 14.45 | .01 | -.52 | 8.25 | .01 | -.42 |
| **Species** | | | | | | | | | | | | | | | |
| Both birches | 8.67 | .01 | -.43 | 8.45 | .01 | -.42 | 11.04 | .01 | -.47 | 11.18 | .01 | -.47 | 26.98 | .01 | -.64 |

[1] F=F value

[2] p=significance level

[3] r=correlation coefficient

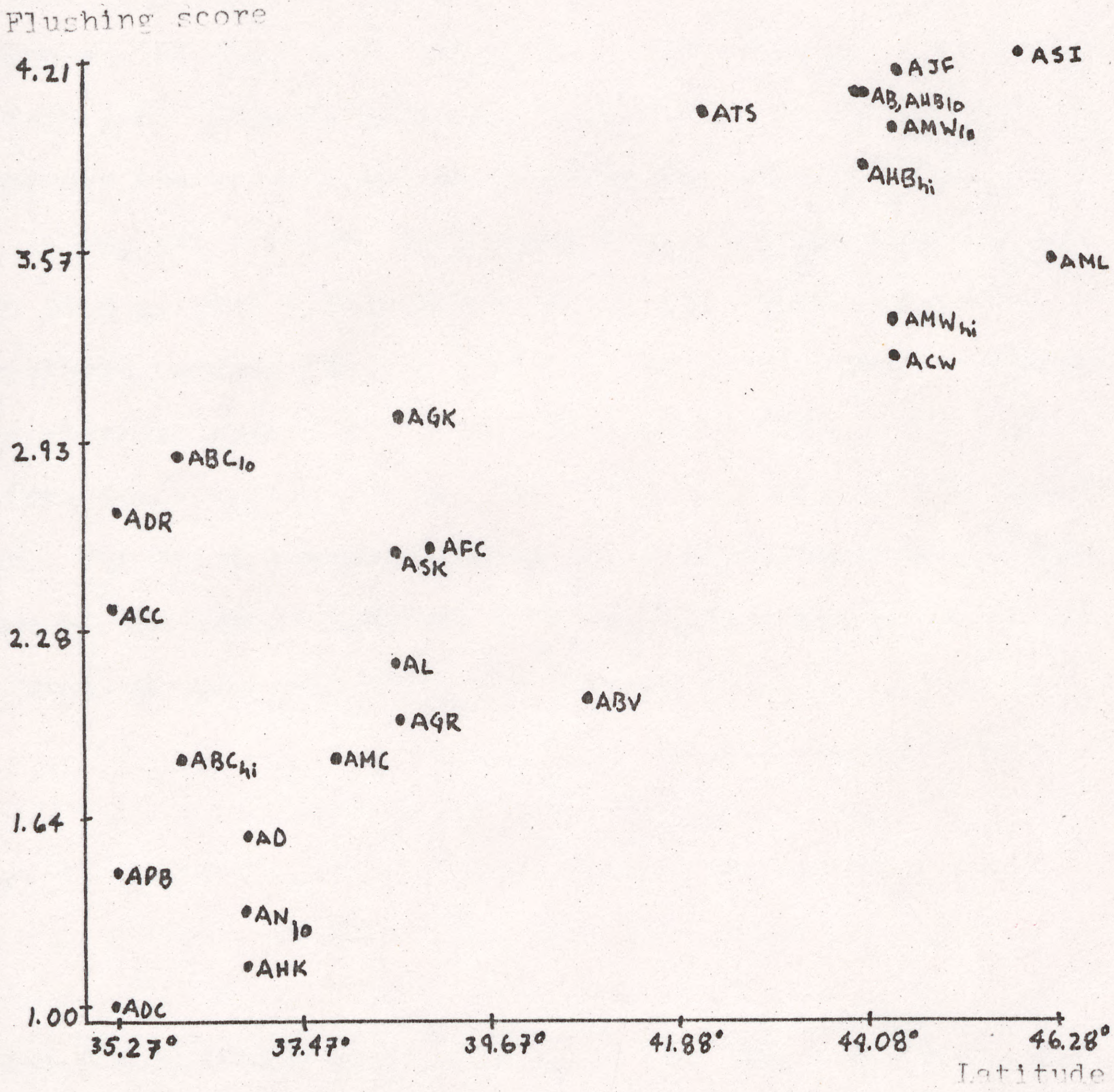


Figure 2- Flushing scores of yellow birch in relation to latitude of the sources for Plantation 2 on April 29, 1974 (r=0.83).

The upper peninsula of Michigan source (SI) was the most advanced in flushing. The northern Appalachian sources came next (JF,B,MW,HB), then the southeastern Michigan source (TS). The southern Appalachian sources followed (GK,FC,SK) with one of the lowest latitude sources (DC) not starting to flush yet. Adjusting the latitude for elevation did not improve the regressions or increase the correlations.

For sweet birch, the correlation with latitude was not as high as with yellow birch (Table 2). Generally, the northern sources flushed earlier. Figure 3 shows a northern Appalachian source (CW), the Ohio source (EV), and a high elevation Virginia source ($EV_H$) the most advanced on April 29. The least advanced source was a North Carolina one (DR), one of the lowest latitude sources. Adjusting latitude for elevation decreased the correlations.

The correlation with latitude for both yellow birch and sweet birch was less than for yellow birch alone. The regression itself, however, had higher F values than either species by itself (Table 2). Figure 4 shows the trend of northern sources being further advanced in their flushing than the southern sources on April 29. The sweet birch from the northern Appalachians (ICW) is an exception to the general trend.

There was a strong trend for the higher elevation sources to be later in their flushing than those from the lower elevations. The correlations were strongest for yellow birch ($p<.01$; $r\leq-.54$). The highest elevation source

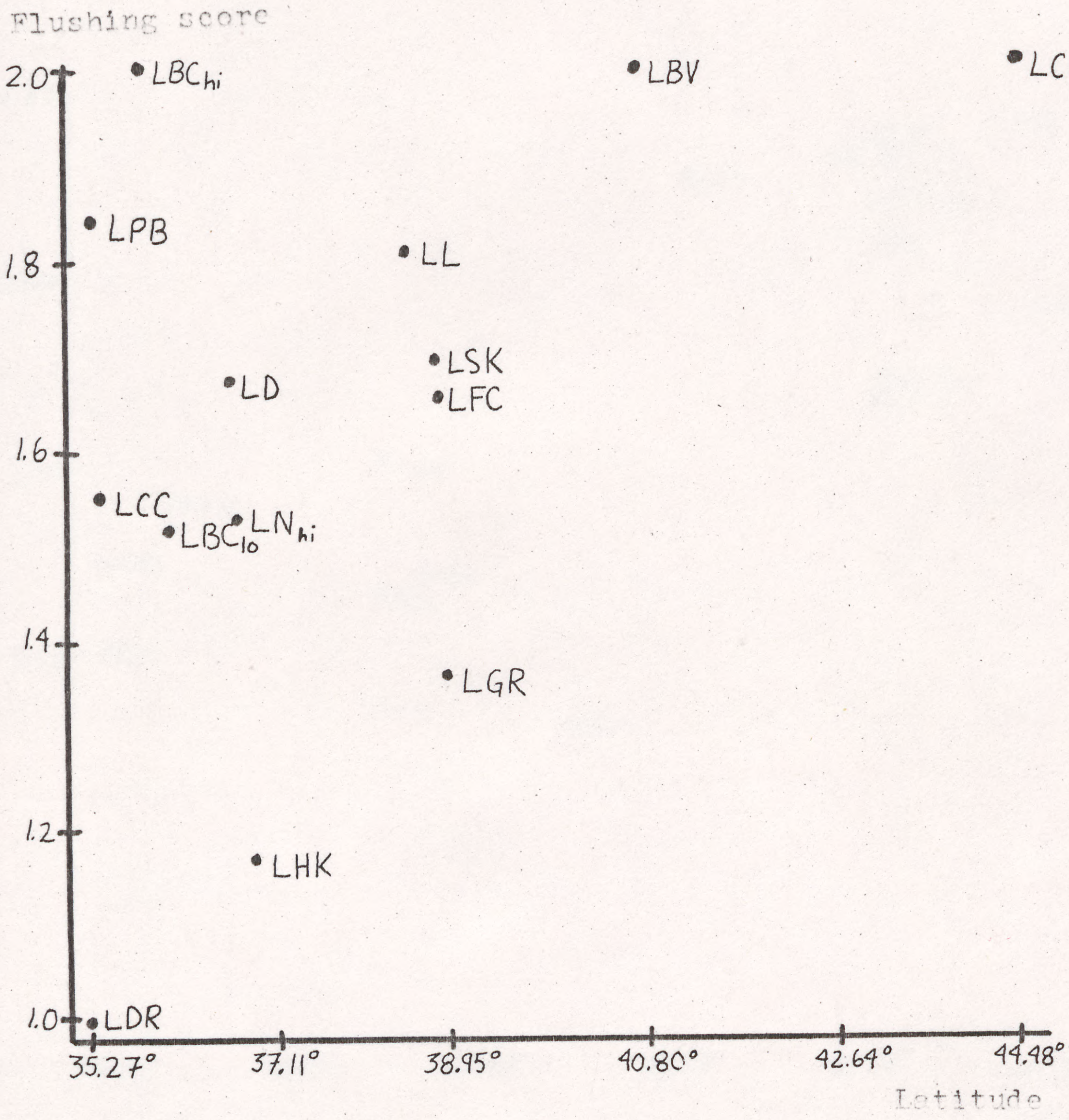


Figure 3- Flushing scores of sweet birch in relation to latitude of the sources for Plantation 2 on April 29, 1974 (r=0.57).

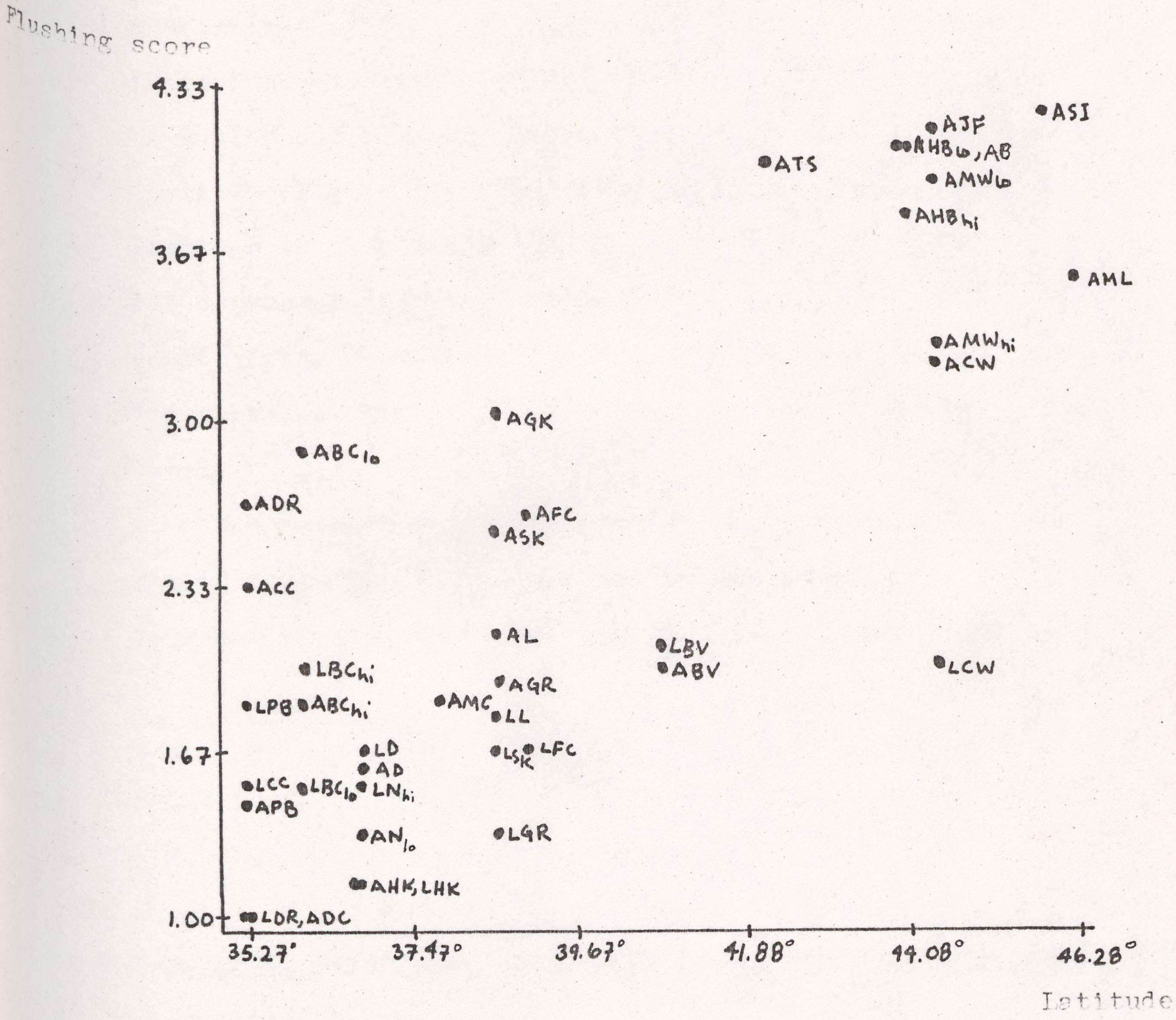


Figure 4- Flushing scores of yellow and sweet birch in relation to latitude of the sources for Plantation 2 on April 29, 1974 (r=0.80).

(DC) was the least advanced on May 5 (Figure 5) although the lowest elevation source (CW) was not the furthest advanced. The most advanced sources, from the lower elevations, were generally also from the higher latitude so that elevation is confounded with latitude. For sweet birch, the higher elevation sources were generally the least advanced also on April 29 (Figure 6). Elevation was also confounded with latitude in this case. On the earlier scoring dates there was a greater difference between sources than on the last scoring date because the scores were similar for most of the sources. The trend is not so obvious as that of yellow birch.

Taking both species together, the regression was more significant than for either species separately for the earliest scoring date, but the correlation coefficient was lower than for yellow birch alone. Figure 7 shows the higher elevational sources flushing later than the lower elevation sources on May 5. The higher elevation sources were generally from the lower latitudes, so we cannot be sure which factor had the greater effect. Both species of the Ohio source (BV) and one Vermont source (CW) are the major exceptions to the trend.

The differences between the scores of the two species (yellow birch and sweet birch) was very significant $(p<.01)$ although the correlation was not high $(r\leq-.42)$. The yellow birch were more advanced in their flushing than the sweet

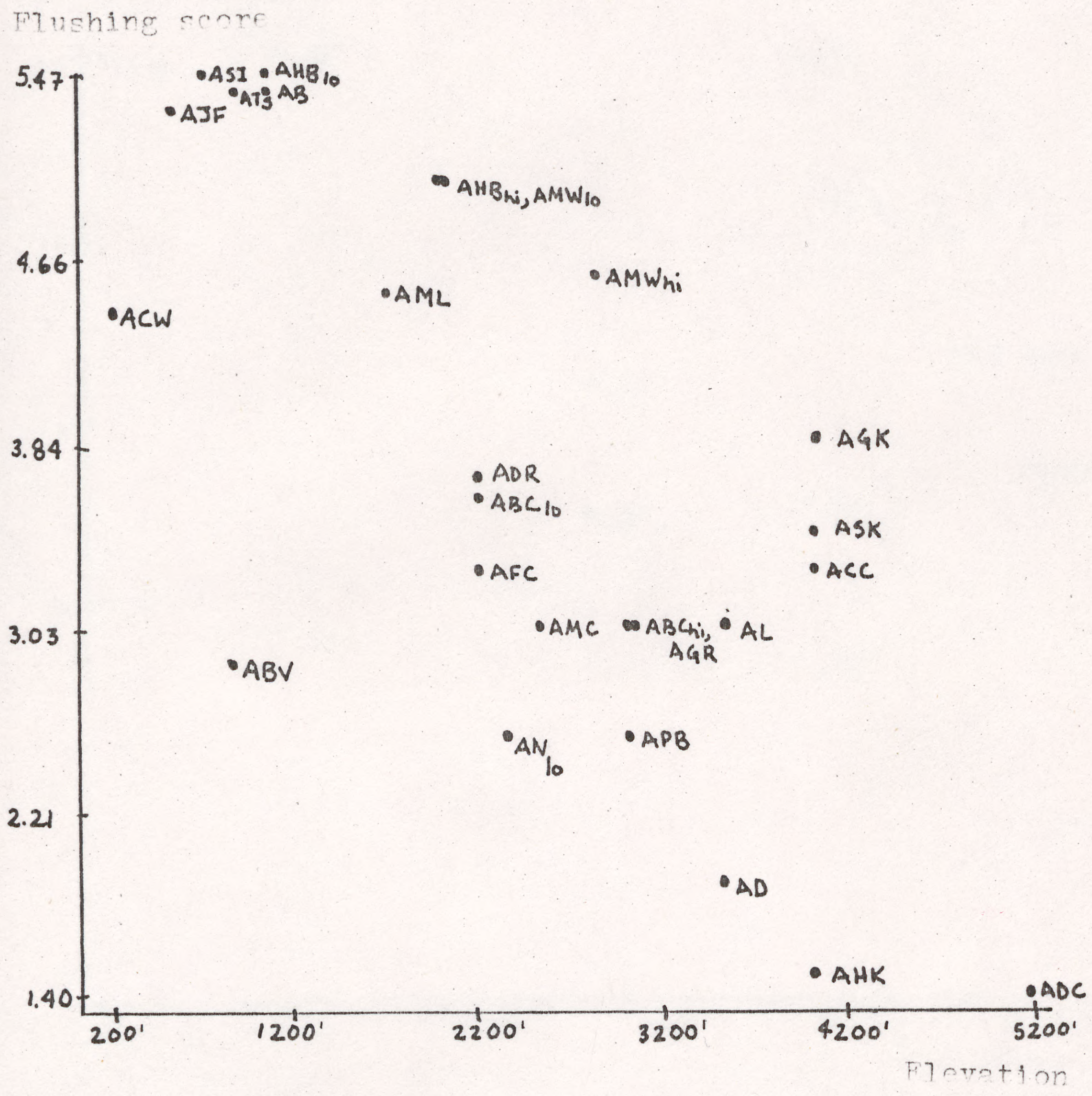


Figure 5- Flushing scores of yellow birch in relation to elevation of the sources for Plantation 2 on May 5, 1974 (r=-0.74).

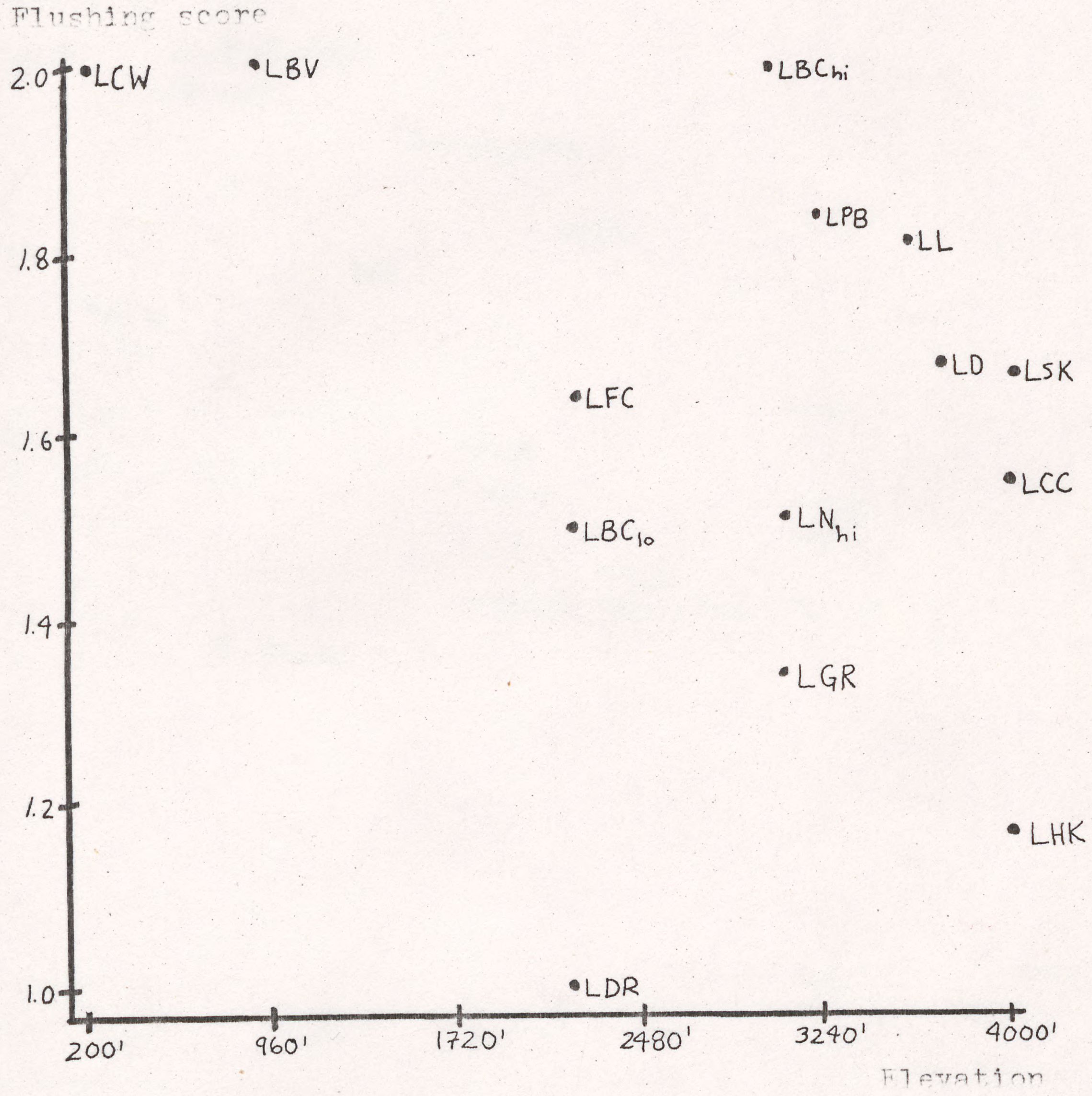


Figure 6- Flushing scores of sweet birch in relation to elevation of the sources for Plantation 2 on April 29, 1974 ($r=-0.67$).

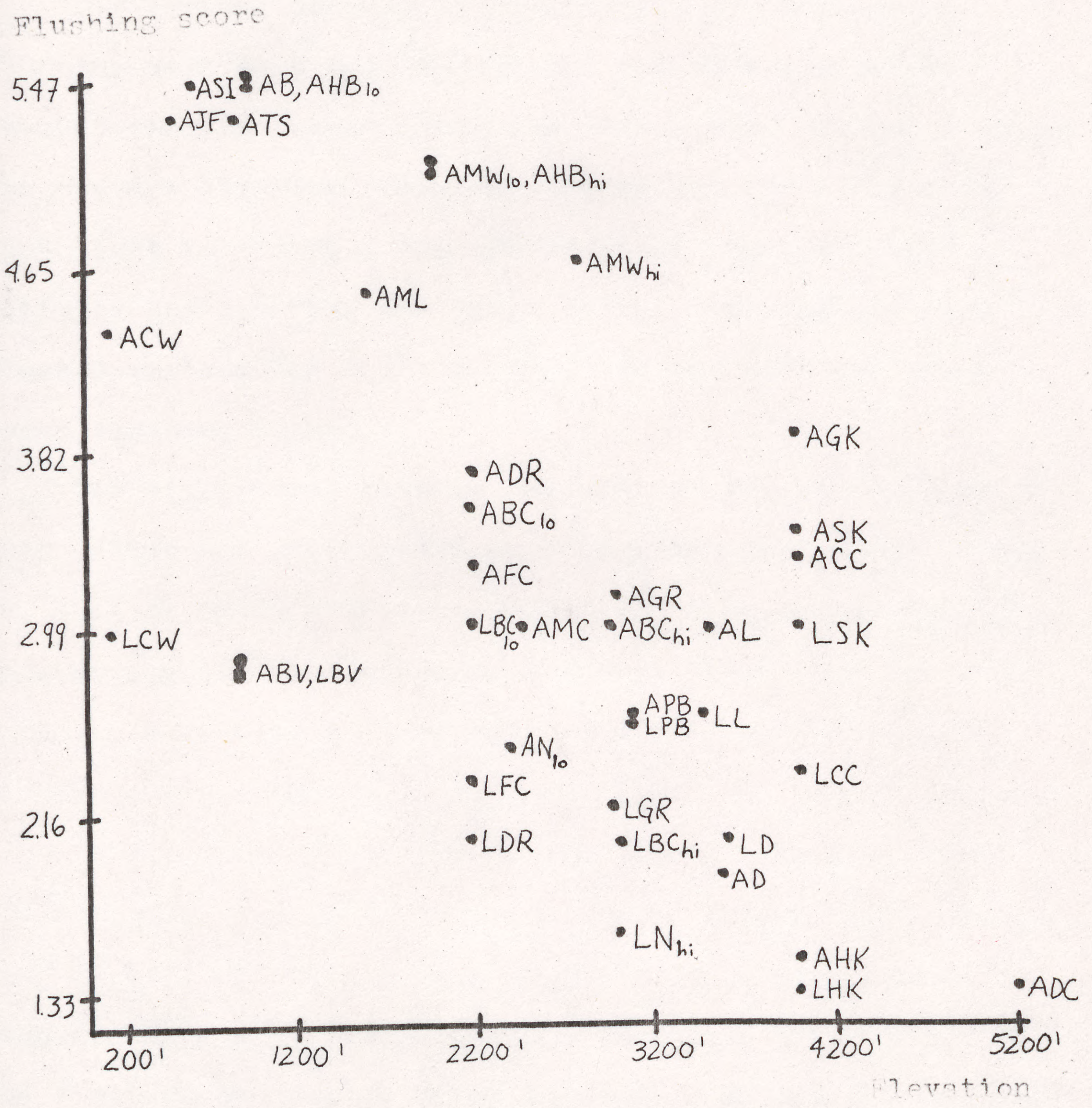


Figure 7- Flushing scores of yellow and sweet birch in relation to elevation of the sources for Plantation 2 on May 5, 1974 (r=-0.63).

birch sources at a given latitude.

## Plantation 3

Differences between light intensities in start of flushing were more significant for yellow birch ($p<.03$; $r=-.76$) than for sweet birch ($p<.10$; $r=-.29$). Figure 8 shows the average flushing score for yellow and sweet birch in each light intensity. The yellow birch began flushing activity earlier than the sweet birch. The 25% sun plot flushed earlier for both species, and the 100% sun plot began flushing later.

The differences between some of the flushing scores for both yellow and sweet birch were significant ($p<.01$) (Table 3). Yellow birch differences between light intensities were greater for the earlier scoring dates. Light intensity differences for sweet birch were more significant during the later scoring dates.

In all three light intensities the northern sources flushed first for both yellow and sweet birch. Latitude was more closely correlated with flushing score than was an adjusted latitude, except in four instances (Table 4). On the first three scoring dates latitude , adjusted 1.52° for every 1000 feet in elevation, exhibited the most significant regression for yellow birch. On the last scoring date, latitude, adjusted 1.61° for every 1000 feet in elevation, was the most significant regression for sweet birch.

Figure 9 shows the April 27 flushing scores for yellow birch sources in the three light intensities. The northern

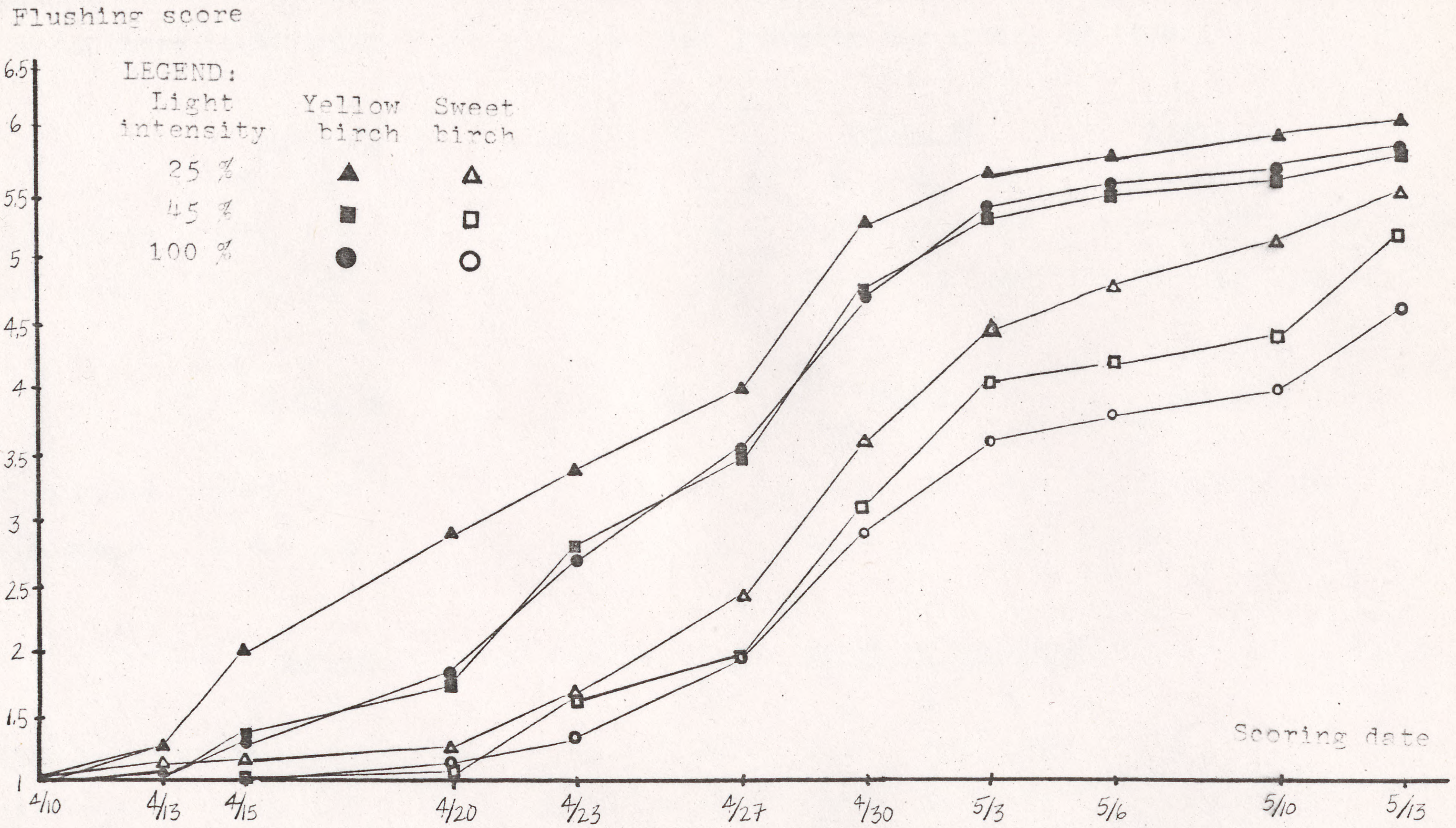


Figure 8-Flushing scores by scoring dates for each plot of yellow and sweet birch in Plantation 3 during the spring of 1974.

Table 3- Statistical comparisons of differences in flushing in yellow birch and sweet birch in three light intensities in Plantation 3 during the spring of 1974.

| | April 13 | | | April 15 | | | April 20 | | | April 23 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F[1] | p[2] | r[3] | F | p | r | F | p | r | F | p | r |
| Yellow birch | 3.79 | .04 | .32 | 6.03 | .01 | .52 | 8.94 | .01 | .58 | 1.91 | .17 | .85 |
| Sweet birch | 3.00 | .12 | .35 | 16.00 | .01 | .23 | 1.91 | .23 | .41 | 1.08 | .40 | .61 |

| | April 27 | | | April 30 | | | May 3 | | | May 6 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | p | r | F | p | r | F | p | r | F | p | r |
| Yellow birch | 1.02 | .37 | .88 | 1.24 | .31 | .89 | .63 | .54 | .88 | .45 | .64 | .85 |
| Sweet birch | 5.04 | .05 | .47 | 5.20 | .05 | .37 | 9.38 | .01 | .23 | 6.14 | .04 | .25 |

| | May 10 | | | May 13 | | | Start of flushing | | |
|---|---|---|---|---|---|---|---|---|---|
| | F | p | r | F | p | r | F | p | r |
| Yellow birch | .61 | .55 | .84 | .54 | .59 | .83 | 3.90 | .03 | -.76 |
| Sweet birch | 8.07 | .02 | .26 | 3.73 | .09 | .33 | 3.55 | .10 | -.29 |

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[1] F=F value [2] p=significance level [3] r=correlation coefficient

Table 4- Statistical comparisons of differences in yellow and sweet birch flushing related to the latitude and two adjusted latitudes over all light intensities in Plantation 3 during the spring of 1974.

| | April 13 | | | April 16-17 | | | April 20-21 | | | April 23 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F[1] | p[2] | r[3] | F | p | r | F | p | r | F | p | r |
| Latitude | | | | | | | | | | | | |
| Yellow birch | 2.91 | .13 | .52 | 6.51 | .03 | .67 | 9.04 | .02 | .73 | 66.45 | .01 | .94 |
| Sweet birch | - | - | - | - | - | - | 3.00 | .33 | .87 | 68.63$^{+14}$ | .01 | 1.00 |
| Both birches | 4.03 | .07 | .52 | 8.38 | .01 | .66 | 12.41 | .01 | .73 | 32.63 | .01 | .86 |
| Adjusted latitude (1.52° per 1000 feet) | | | | | | | | | | | | |
| Yellow birch | 4.32 | .07 | .59 | 11.39 | .01 | .77 | 14.80 | .01 | .81 | 28.81 | .01 | .88 |
| Sweet birch | - | - | - | - | - | - | .44 | .63 | .55 | 4.09 | .29 | .90 |
| Both birches | 6.30 | .03 | .60 | 15.42 | .01 | .76 | 20.41 | .01 | .81 | 32.02 | .01 | .86 |
| Adjusted latitude (1.61° per 1000 feet) | | | | | | | | | | | | |
| Yellow birch | 4.29 | .07 | .59 | 11.24 | .01 | .76 | 14.37 | .01 | .80 | 22.94 | .01 | .86 |
| Sweet birch | - | - | - | - | - | - | .36 | .66 | .52 | 3.26 | .32 | .87 |
| Both birches | 6.32 | .03 | .60 | 15.49 | .01 | .76 | 20.13 | .01 | .80 | 29.54 | .01 | .85 |

| | April 27 | | | April 30 | | | May 3 | | | May 6 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | p | r | F | p | r | F | p | r | F | p | r |
| Latitude | | | | | | | | | | | | |
| Yellow birch | 50.39 | .01 | .93 | 51.55 | .01 | .93 | 75.33 | .01 | .95 | 45.71 | .01 | .92 |
| Sweet birch | 68.63$^{+14}$ | .01 | 1.00 | 3.00 | .33 | .86 | .33 | .67 | .50 | .33 | .67 | .50 |
| Both birches | 27.65 | .01 | .84 | 27.78 | .01 | .85 | 25.42 | .01 | .84 | 21.20 | .01 | .81 |
| Adjusted latitude (1.52° per 1000 feet) | | | | | | | | | | | | |
| Yellow birch | 12.09 | .01 | .78 | 11.67 | .01 | .77 | 8.43 | .02 | .72 | 5.90 | .04 | .65 |
| Sweet birch | 4.09 | .29 | .90 | .44 | .62 | .55 | .01 | .96 | .06 | .01 | .96 | .06 |
| Both birches | 19.00 | .01 | .80 | 17.93 | .01 | .79 | 13.01 | .01 | .74 | 10.24 | .01 | .69 |
| Adjusted latitude (1.61° per 1000 feet) | | | | | | | | | | | | |
| Yellow birch | 10.52 | .01 | .75 | 10.14 | .01 | .75 | 7.21 | .03 | .69 | 5.04 | .06 | .62 |
| Sweet birch | 3.26 | .32 | .87 | .36 | .66 | .52 | .01 | .99 | .02 | .01 | .99 | .02 |
| Both birches | 17.49 | .01 | .78 | 16.46 | .01 | .77 | 11.86 | .01 | .72 | 9.34 | .01 | .68 |

| | May 10 | | | May 13 | | | May 20 | | | Start of flushing | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | p | r | F | p | r | F | p | r | F | p | r |
| Latitude | | | | | | | | | | | | |
| Yellow birch | 47.18 | .01 | .92 | 23.91 | .01 | .87 | 13.03 | .01 | .79 | 38.04 | .01 | -.91 |
| Sweet birch | 1.33 | .45 | .76 | .33 | .67 | .50 | .33 | .67 | -.50 | 12.00 | .18 | -.96 |
| Both birches | 22.67 | .01 | .82 | 16.15 | .01 | .77 | 8.78 | .01 | .66 | 26.01 | .01 | -.84 |
| Adjusted latitude (1.52° per 1000 feet) | | | | | | | | | | | | |
| Yellow birch | 5.86 | .04 | .65 | 3.69 | .09 | .56 | 5.02 | .06 | .62 | 11.65 | .01 | -.77 |
| Sweet birch | .18 | .75 | .39 | .01 | .96 | .06 | 2.25 | .37 | -.83 | 1.20 | .47 | -.74 |
| Both birches | 10.99 | .01 | .71 | 7.12 | .02 | .63 | 6.23 | .03 | .60 | 17.84 | .01 | -.79 |
| Adjusted latitude (1.61° per 1000 feet) | | | | | | | | | | | | |
| Yellow birch | 5.00 | .06 | .62 | 3.13 | .11 | .53 | 4.49 | .07 | .60 | 10.23 | .01 | -.75 |
| Sweet birch | .13 | .77 | .34 | .01 | .99 | .02 | 2.77 | .34 | -.86 | .99 | .50 | -.71 |
| Both birches | 10.02 | .01 | .69 | 6.47 | .03 | .61 | 5.87 | .03 | .59 | 16.45 | .00 | -.77 |

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[1] F=F value [2] p=significance level [3] r=correlation coefficient

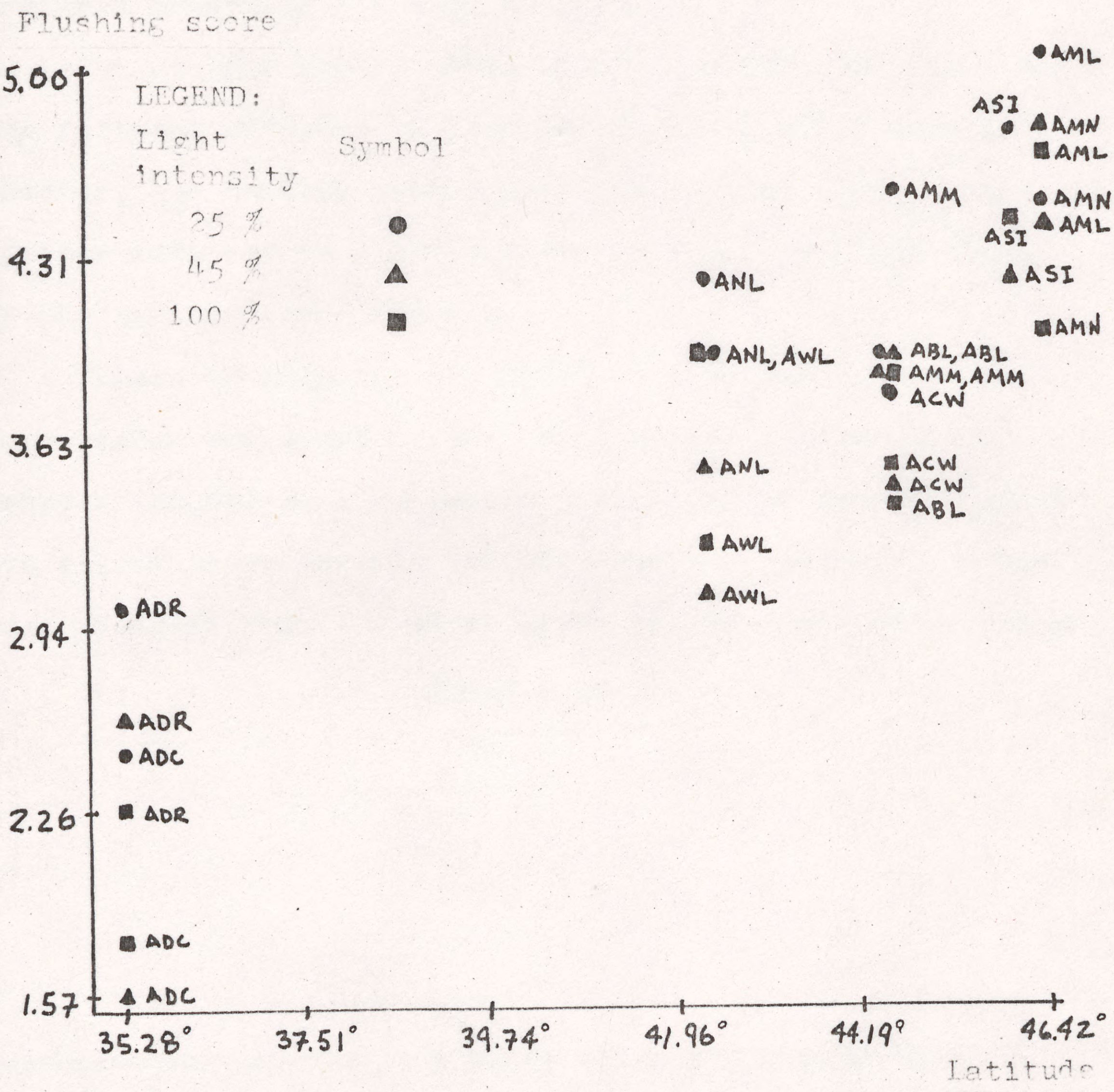

Figure 9- Flushing scores of yellow birch in relation to latitude of the sources for Plantation 3 on April 27, 1974 (r=0.93).

sources (ML,MN,SI) were the farthert advanced, and the southern sources (DC,DR) were the least advanced. The heavily shaded, 25% sun, plot was generally the furthest advanced treatment for each source.

The heavily shaded sweet birch from the north (CW) was the furthest advanced in flushing on April 27 (Figure 10), however, the heavily shaded southern sources (CC,DR) were further advanced than the 45% sun and full sunlight plots of the northern source (CW).

Figure 11 presents the April 27 flushing scores for both yellow and sweet birch. The northern yellow birch sources (ML,MN) were generally more advanced than the southern yellow birch sources (DC,DR), and the yellow birch were more advanced than the sweet birch of the same source (CW,DR).

## Plantation 4

Latitude was always highly significant ($p<.01$) for yellow birch flushing on all the scoring dates (Table 5). Strong correlations were also found between flushing and latitude, the lowest being $r=.76$ and the highest $r=.84$. The northern sources were the furthest advanced and the southern sources were the least advanced on each date. On April 20, the southern sources (DC,DR) were quite separate from the early flushing Michigan and northern Appalachian sources (Figure 12). Adjusting the latitude for elevation, using two different adjustment factors, made the correlations less significant on all dates (Table 5). The start of flushing scores showed a distinct

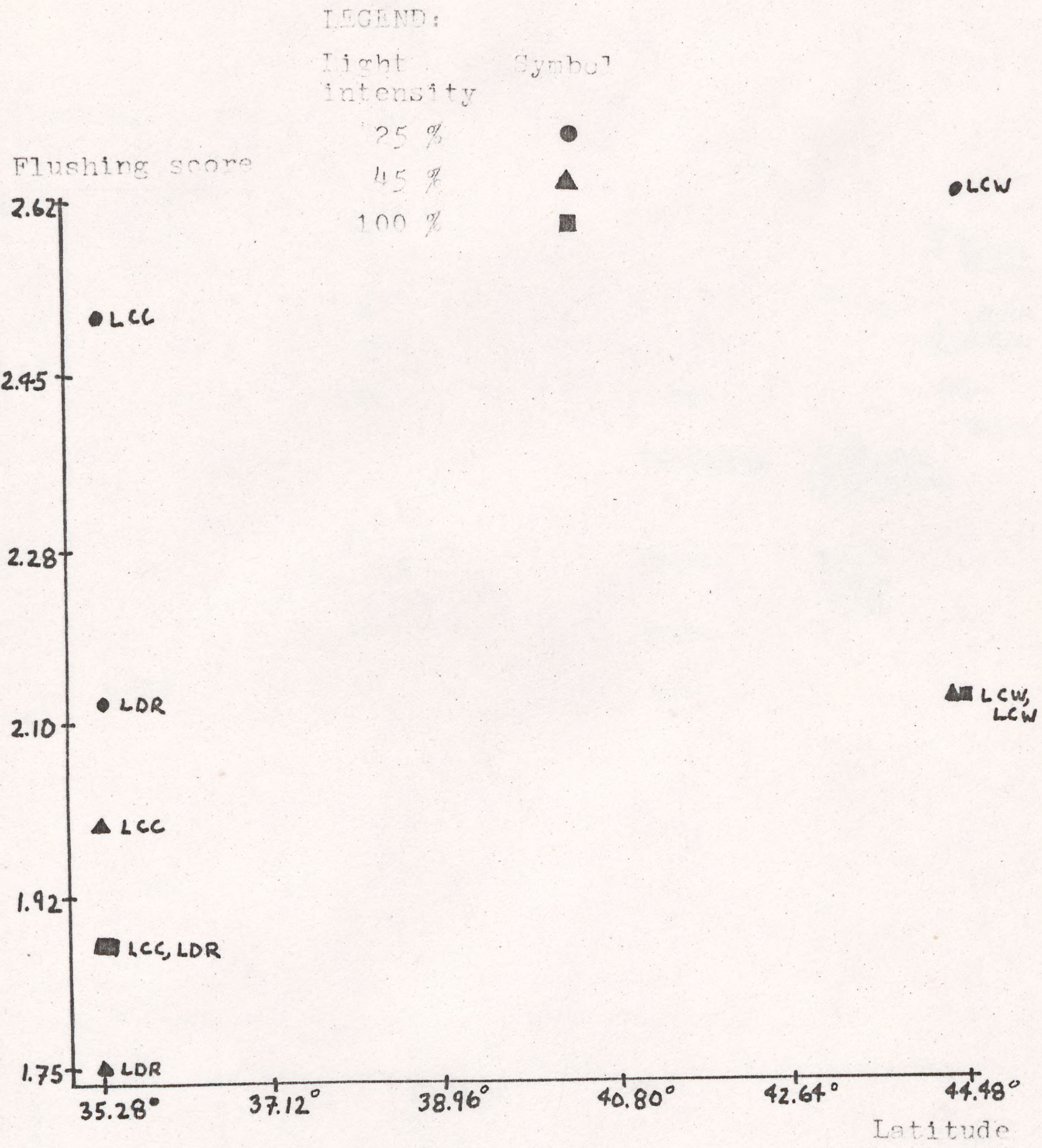

Figure 10- Flushing scores of sweet birch in relation to latitude of the sources for Plantation 3 on April 27, 1974 (r=1.00).

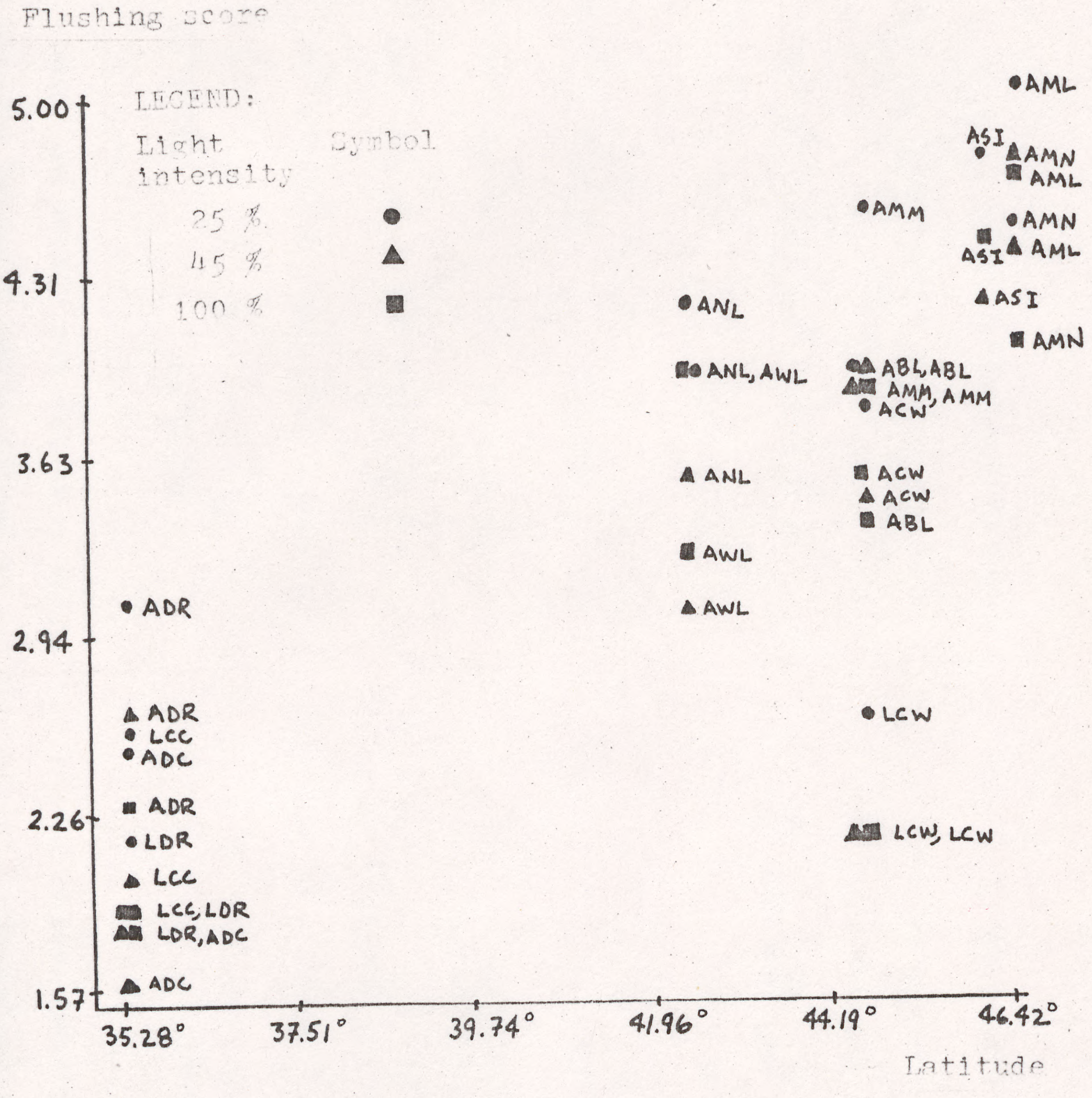

Figure 11- Flushing scores of yellow and sweet birch in relation to latitude of the sources for Plantation 3 on April 27, 1974 (r=0.84).

Table 5- Statistical comparisons of differences in yellow birch flushing related to latitude and two adjusted latitudes for Plantation 4 during the spring of 1974.

| | April 15 | | | April 20 | | | April 24 | | | April 27 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F[1] | p[2] | r[3] | F | p | r | F | p | r | F | p | r |
| Latitude | 37.62 | .01 | .76 | 40.59 | .01 | .77 | 55.78 | .01 | .82 | 59.52 | .01 | .82 |
| Adjusted latitude (1.52° per 1000 feet) | 24.65 | .01 | .68 | 23.67 | .01 | .68 | 18.48 | .01 | .63 | 20.45 | .01 | .65 |
| Adjusted latitude (1.61° per 1000 feet) | 23.26 | .01 | .67 | 22.18 | .01 | .66 | 16.81 | .01 | .61 | 18.64 | .01 | .63 |

| | April 30 | | | May 6 | | | May 13 | | | Start of flushing | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | p | r | F | p | r | F | p | r | F | p | r |
| Latitude | 73.57 | .01 | .84 | 60.49 | .01 | .81 | 30.18 | .01 | .72 | 52.37 | .01 | -.81 |
| Adjusted latitude (1.52° per 1000 feet) | 19.09 | .01 | .64 | 11.72 | .01 | .54 | 5.95 | .02 | .41 | 27.22 | .01 | -.70 |
| Adjusted latitude (1.61° per 1000 feet) | 17.24 | .01 | .62 | 10.39 | .01 | .52 | 5.15 | .03 | .39 | 25.31 | .01 | -.69 |

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[1] F=F value [2] p= significance level [3] r=correlation coefficient

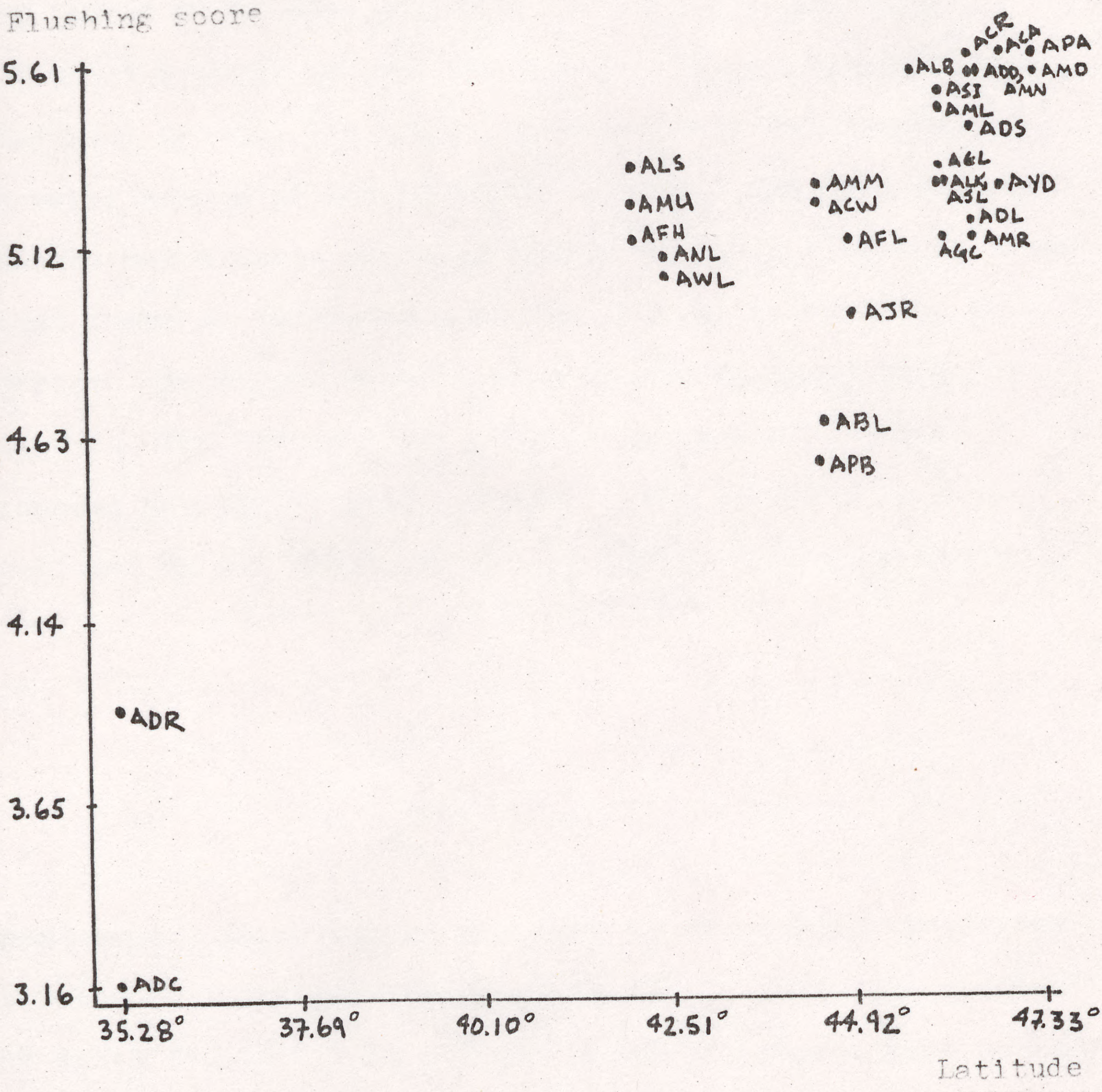


Figure 12- Flushing scores of yellow birch in relation to latitude of the sources for Plantation 4 on April 20, 1974 (r=0.77).

north to south trend, with the southern sources taking longer to start flushing (Figure 13).

In addition to latitude, the Michigan sources can also be looked at by region (Table 6). The regions with the shortest growing seasons are listed first. Generally the Superior Upland and Huron Mountains have the shortest growing season of the Michigan sources. The Keweenaw peninsula and eastern upper peninsula follow. Figure 14 shows that there is overlapping of the regions in flushing behavior. No region has flushing scores distinct from all others. The approximate order of the upper peninsula sources was the Keweenaw peninsula the furthest advanced, followed by the Huron Mountains, then the eastern upper peninsula, with the Superior Uplands the least advanced. There was overlapping of the regions on all adjacent edges.

The lower peninsula generally has a longer growing season than the upper peninsula. The northern lower peninsula has a shorter growing season than the southern lower peninsula. Three out of the four northern lower peninsula sources were less flushed than the upper peninsula sources on April 20. The southeastern Michigan sources were spread out, one source (MU) as far advanced in flushing as some Huron Mountain and Keweenaw peninsula sources. Another southeastern Michigan source (WL) was the second least flushed of the Michigan sources on April 20.

The start of flushing scores (Figure 15) were even less distinct regionally than the flushing scores on April 20.

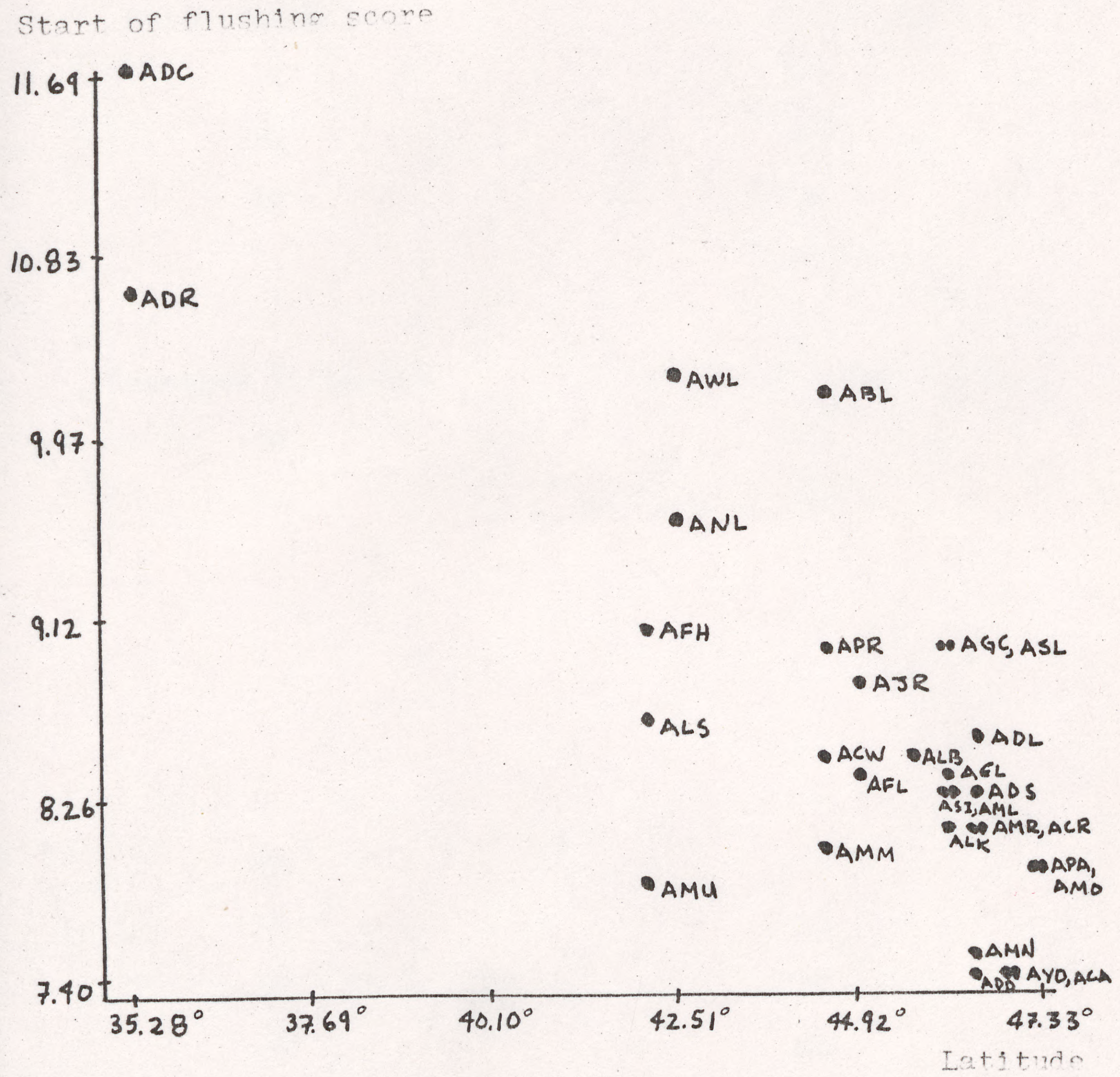


Figure 13- Start of flushing scores of yellow birch in relation to latitude of the sources for Plantation 4 during the spring of 1974 (r=-0.81).

Table 6- Michigan yellow birch seed sources from Plantation 4 listed by region.

Huron Mountains

- DD
- MR
- YD

Superior Upland

- DL
- GC
- LK
- ML
- SL

Keweenaw Peninsula

- CA
- MO
- PA

Eastern Upper Peninsula

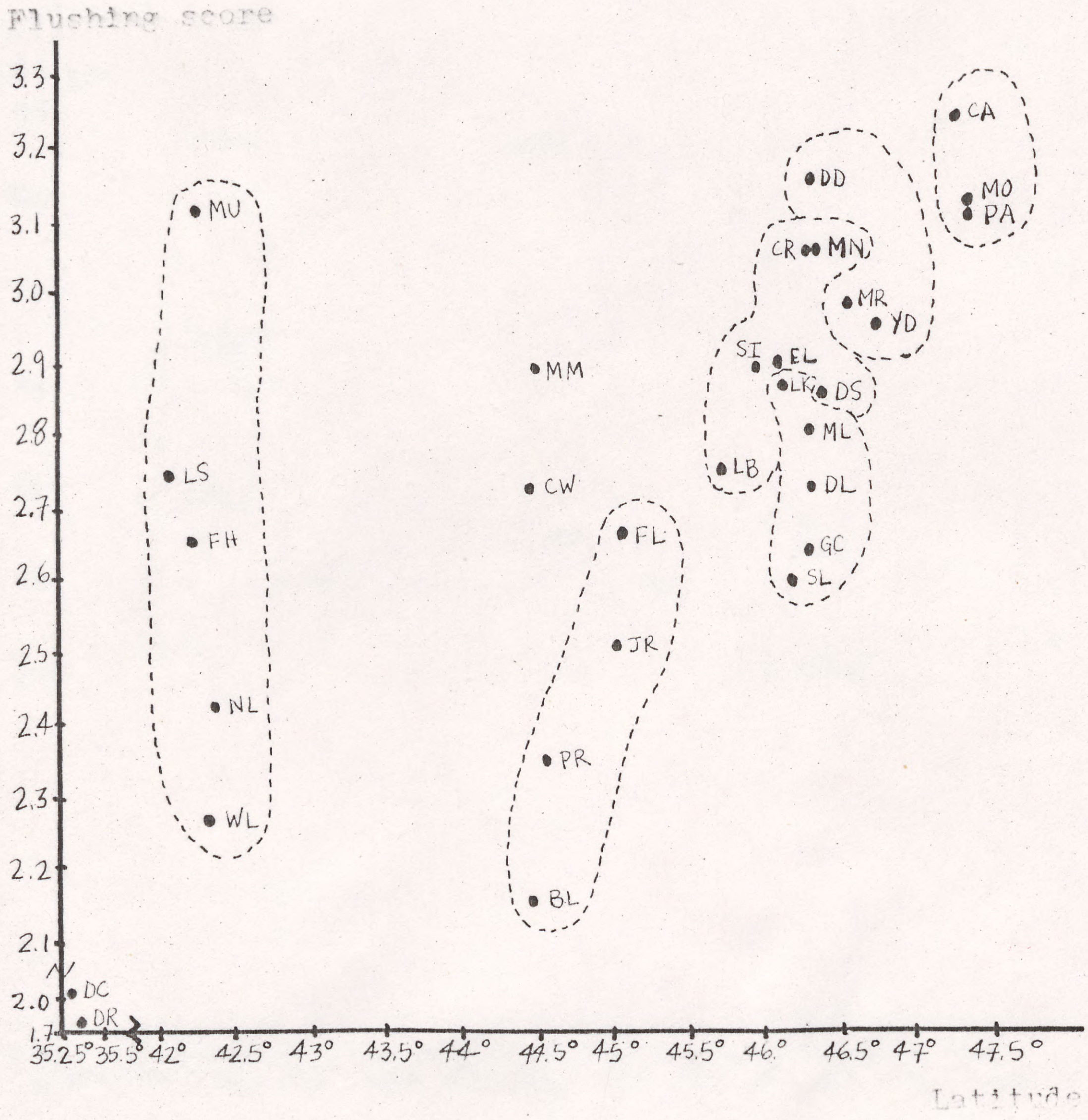
- CR
- DS
- EL
- LB
- MN
- SI

Northern Lower Peninsula

- BL
- FL
- JR
- PR

Southeastern Michigan

- FH
- LS
- MU
- NL
- WL



<u>Figure 14</u>-Flushing scores of yellow birch in relation to latitude of the sources for Plantation 4 on April 20, 1974 (r=0.77). Michigan sources are grouped by regions of seed origin.

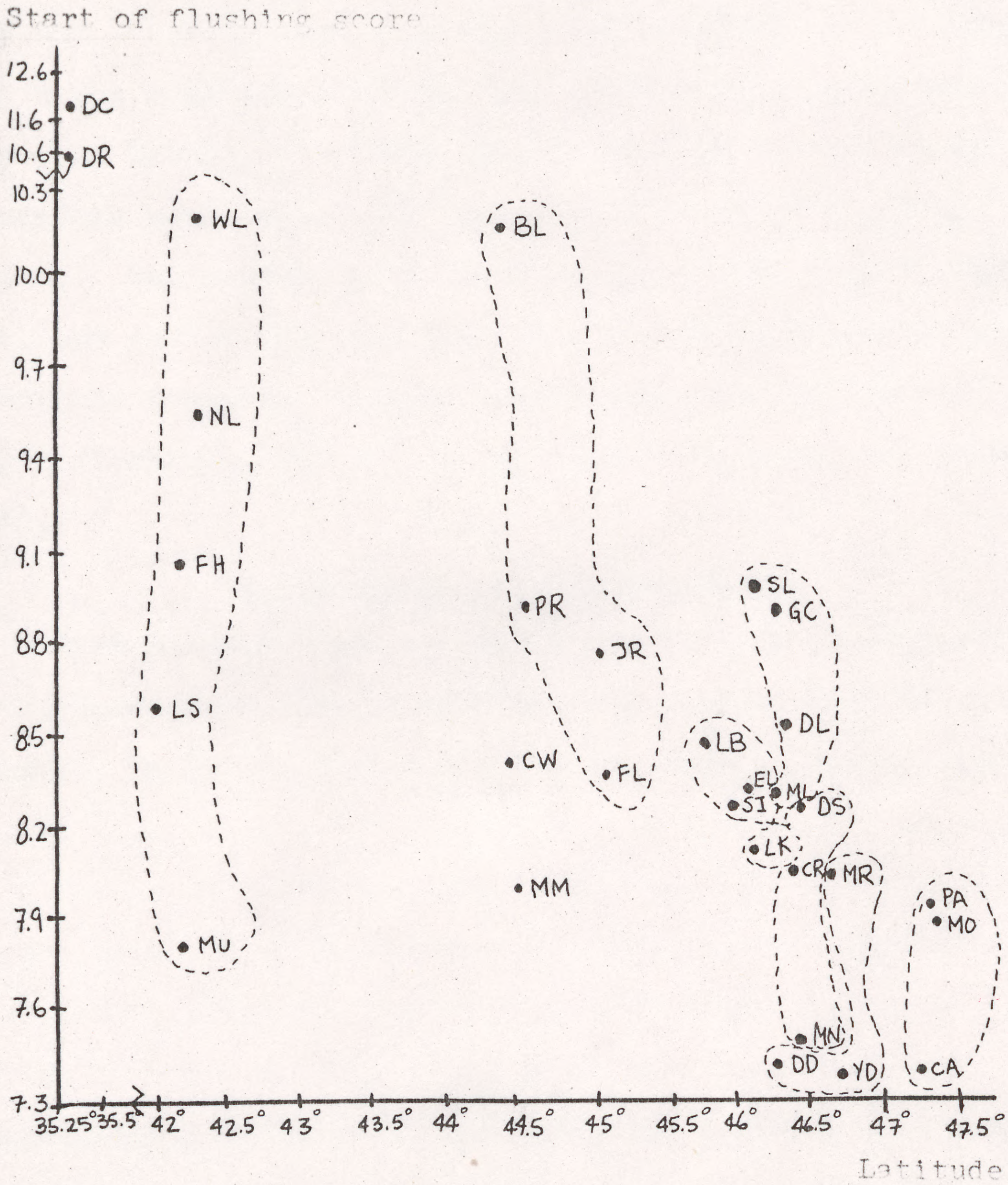


Figure 15-Start of flushing scores of yellow birch in relation to latitude of the sources for Plantation 4 during the spring of 1974 (r=-0.81). Michigan sources are grouped by regions of seed origin.

The Keweenaw peninsula and Huron Mountain sources were the earliest in flushing. Two eastern upper peninsula sources (CR,MN) started flushing as early as the Keweenaw peninsula and Huron Mountain sources. The eastern upper peninsula, Superior Upland, and three out of the four northern lower peninsula sources were similar in the start of flushing scores. The southeastern Michigan sources were quite spread out, one source (MU) starting flushing as early as the upper peninsula sources. Another source (WL) was the last to start flushing, following a northern lower peninsula source (BL).

### Yellow birch in all plantations

Both latitude ($p < .01$; $r \geq .77$) and plot ($p < .01$; $r \leq -.62$) differences were very significant for yellow birch flushing scores. There was a strong north to south gradient, with the northern sources flushing first on April 30 (Figure 16).

On the three scoring dates graphed, the two plantations at the Southern Michigan Nursery (3 and 4) were further advanced in flushing than the two at the Botanical Gardens (1 and 2) (Figure 17). Using three different threshold temperatures, 35°F, 40°F, and 45°F, the patterns of flushing were the same in all three cases. On each scoring date, the two Southern Michigan Nursery plantations had accumulated a lower number of degree-hours than the Botanical Garden plantations, yet they were farther advanced in flushing. If this experiment were to be continued over a number of years, one could determine which of the three thresholds was the

### Plantation 1

| | |
|---|---|
| AGD | 1 |
| ACG | 2 |
| ALS | 3 |
| AEW | 4 |
| AMU | 5 |
| AWL | 6 |
| ANL | 7 |
| ASB | 8 |
| ALL | 9 |
| ADO | 10 |
| ASN | 11 |
| ADF | 12 |

### Plantation 2

| | |
|---|---|
| APB | 13 |
| ACC | 14 |
| ADR | 15 |
| ADC | 16 |
| ABC$_{hi}$ | 17 |
| ABC$_{lo}$ | 18 |
| AHK | 19 |
| AD | 20 |
| AN$_{lo}$ | 21 |
| AMC | 22 |
| AL | 23 |
| ASK | 24 |
| AGR | 25 |
| AGK | 26 |
| AFC | 27 |
| ABV | 28 |
| ATS | 29 |
| AHB$_{lo}$ | 30 |
| AHB$_{hi}$ | 31 |
| AB | 32 |
| AMW$_{lo}$ | 33 |
| AMW$_{hi}$ | 34 |
| AJF | 35 |
| ACW | 36 |
| ASI | 37 |
| AML | 38 |

### Plantation 3

| | |
|---|---|
| ADR | 39 |
| ADC | 40 |
| AWL | 41 |
| ANL | 42 |
| ABL | 43 |
| ACW | 44 |
| AMM | 45 |
| ASI | 46 |
| AML | 47 |
| AMN | 48 |

### Plantation 4

| | |
|---|---|
| ADR | 49 |
| ADC | 50 |
| ALS | 51 |
| AFH | 52 |
| AMU | 53 |
| AWL | 54 |
| ANL | 55 |
| ABL | 56 |
| ACW | 57 |
| AMM | 58 |
| APR | 59 |
| AJR | 60 |
| AFL | 61 |
| ALB | 62 |
| ASI | 63 |
| AEL | 64 |
| ALK | 65 |
| ASL | 66 |
| AGC | 67 |
| AML | 68 |
| ADL | 69 |
| ADD | 70 |
| ACR | 71 |
| AMN | 72 |
| ADS | 73 |
| AMR | 74 |
| AYD | 75 |
| ACA | 76 |
| AMO | 77 |
| APA | 78 |

### Legend to Figure 16

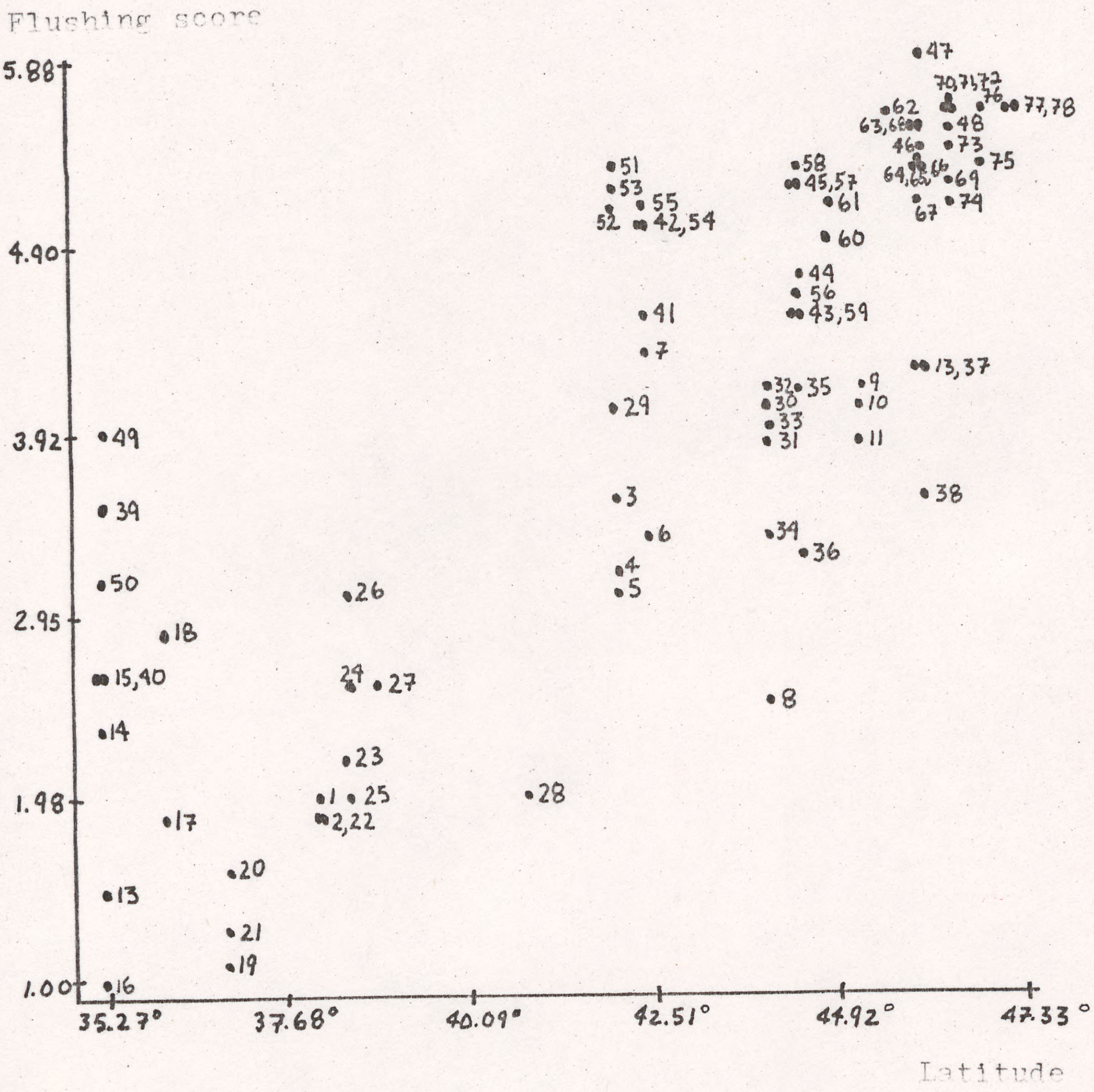


Figure 16- Flushing scores of yellow birch in relation to latitude of the sources for all plantations (only the 100% sun plot in Plantation 3) on April 30, 1974 (r=0.81).

| Plantation | Average latitude of sources | Symbol |
|---|---|---|
| 1 | 42.82°N | ● |
| 2 | 39.96°N | ◆ |
| 3 | 42.74°N | ■ |
| 4 | 44.63°N | ▲ |

| Threshold | Symbol |
|---|---|
| 35° | ▬ ▬ ▬ ▬ |
| 40° | —— |
| 45° | …… |

Legend to Figure 17

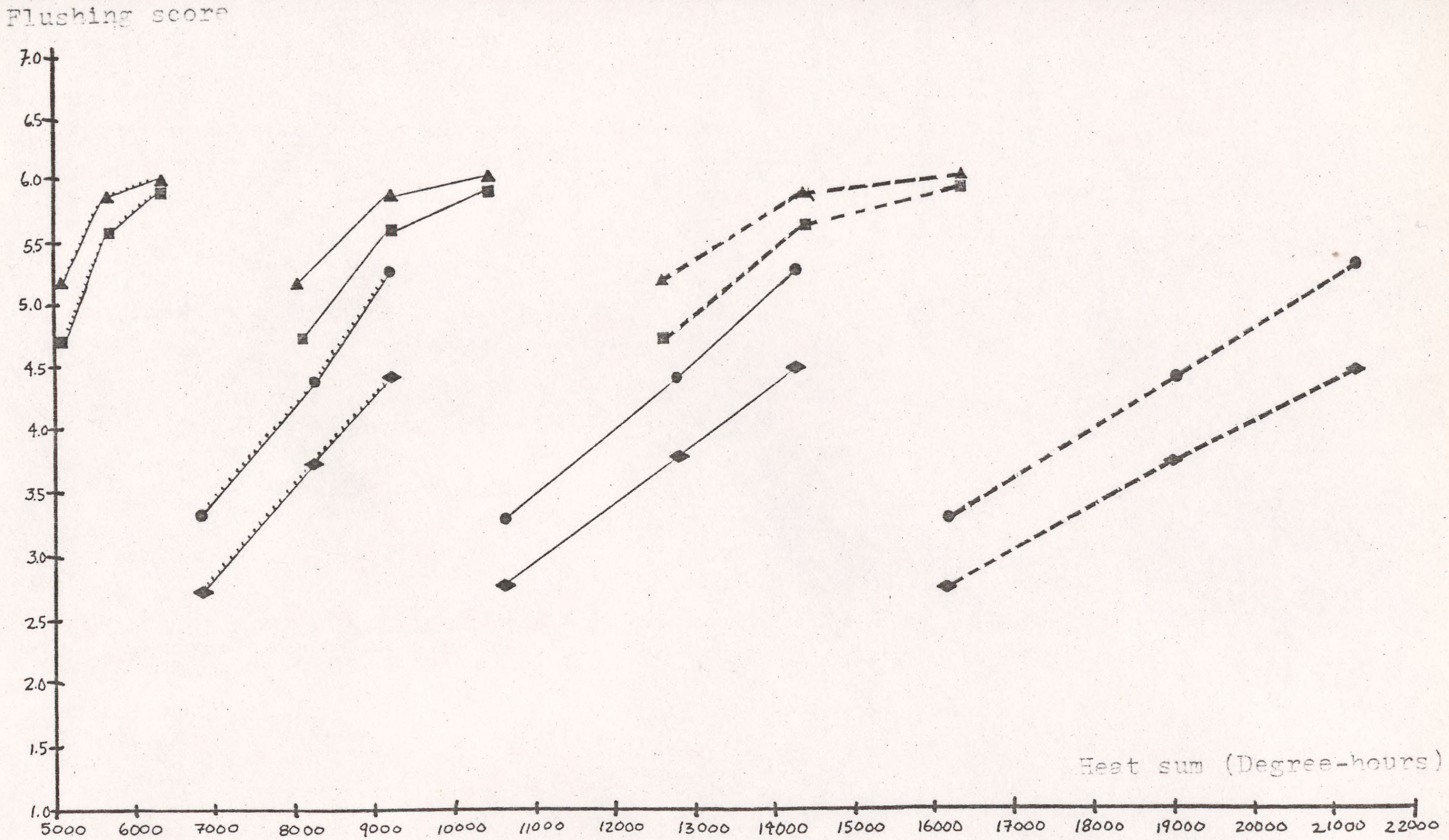


Figure 17-Heat sums associated with flushing scores for each plantation, with three thresholds during the spring of 1974.

critical temperature in inducing flushing. The threshold which best explained the flushing differences found among the sources would be the critical value. Using data from one year, the general pattern can be noted, but it is not possible to determine which threshold is the most correct.

The mean latitude of the sources of each plantation was calculated to see if this might have any effect on the heat summations. Sources in Plantations 1 and 3 had nearly identical mean latitudes, therefore, the north to south effects could not have caused Plantation 3 to be further advanced at similar heat summations. Possibly the age differences played a part here, the younger Plantation 3 yellow birches flushing before the older Plantation 1 yellow birches. Since the two younger plantations were grown at the State Nursery and the two older plantations at the Botanical Gardens, one cannot be sure whether age or site was the more important factor. Plantations 1 and 2 are nearly the same age, yet the curves are spaced far apart from each other in the heat summation graph, Plantation 1 being farther advanced in flushing on all three dates. The mean latitude of yellow birch sources in Plantation 1 was 42.82°N, compared to 39.96°N for those of Plantation 2. The more northern sources in Plantation 1 probably accounted for the flushing scores being more advanced at the same heat summation compared to Plantation 2.

Table 7 shows comparisons of the temperature at the ground and at three feet above the ground (air temperature)

Table 7- Comparisons of average temperatures at ground level and at three feet above the ground at Southern Michigan State Nursery, Brighton, Michigan during the spring, 1974. Values are averaged from three readings per date.

| Date | Air Temperature (3' above ground) | Ground Temperature (1 cm. above ground) | Conditions |
|---|---|---|---|
| April 27 | 22.86°C/73.16°F | 23.60°C/74.56°F | Sunny |
| April 30 | 19.66°C/67.4°F | 19.41°C/66.95°F | Partly sunny |
| May 3 | 12.23°C/54.03°F | 12.62°C/54.73°F | Sunny |
| May 6 | 9.75°C/49.55°F | 9.16°C/48.5°F | Cloudy |
| May 10 | 21.0°C/69.8°F | 17.77°C/64.0°F | Overcast |
| May 13 | 10.7°C/51.26°F | 12.75°C/54.95°F | Sunny |
| May 20 | 22.22°C/72.0°F | 20.5°C/68.9°F | Overcast |

at the Southern Michigan Nursery. The results show that on sunny days the ground temperature is higher than the air temperature. On overcast days the ground temperature is cooler than the air temperature. On cloudy days the air temperature is slightly higher than the ground temperature.

## DISCUSSION

Many of the important points discussed in the literature review are illustrated in the results of the field studies of yellow birch flushing. It has been noticed as early as 1820 by Vilmorin that in a common garden different seed sources of the same species flush at different times (Langlet, 1970). Since that time, many other workers have also noticed this phenomenon. In the plantations observed in this study, different seed sources of both yellow and sweet birch flushed at varying times. These differences are genetically controlled. Many workers have found high heritability values for flushing (Wilcox and Farmer, 1967; Wilcox, 1970; Bey, 1973a; Nienstaedt, 1974b). In this study, leaf flushing scores for seedlings of the same species from the same seed source were usually very similar.

The differences in flushing times frequently vary in recognizable patterns. Very often environmental pressures on the genetic selection causes the pattern. Such characteristics as times of killing frosts and perennial droughts affect selection by killing or weakening trees that are not adapted to that particular growing place. Many times the variation in flushing times has a clinal pattern (Kriebel, 1957; Perry and Wang, 1960; Kriebel and Wang, 1962; Squillace and Silen, 1962; Morgenstern, 1969a,b; Hamrick and Libby, 1972). One of the strongest patterns is a latitudinal cline. Many studies have reported a latitudinal cline with the northern sources flushing earlier than the southern sources (Kriebel, 1957; Clausen and Garrett, 1969; Wright, 1970; Sharik, 1970; Hart, 1974). Some other studies have shown the reverse trend, with the southern sources flushing earlier than the northern sources (Ching and Bever, 1960; Sluder, 1960, 1963; McMillan and Peacock, 1964; Nienstaedt, 1974a). In this study, both yellow and sweet birch flushing scores showed significant correlations to latitude in all four plantations. The yellow birch flushing scores from all four plantations taken together were also significantly correlated to latitude. In all these cases, the more northern sources flushed earlier than the southern sources.

Another clinal pattern that has been observed in flushing is an elevational cline (Lamb, 1915; Munger and Morris, 1936; Irgens-Moller, 1957, 1967; Lines, 1970). In some common garden studies, the higher elevation sources flushed earlier, parallel to the northern latitudinal sources flushing earlier. Other sources showed the lower or medium elevation sources flushing earlier. In this study, the elevational effects on Plantation 2, the plantation with the greatest range of elevations, were significant, but the correlations were not as strong as for latitude. For both yellow and sweet birch, the lower elevation sources flushed earlier than the higher elevation sources.

In this study, there was a confounding of elevation with latitude. The sources that flushed earliest were generally from the lower elevations and the higher latitudes. The later flushing sources were from the higher elevations and the lower latitudes. Adjusting latitude for elevation, using two different adjustment factors, did not improve the regressions, except in four instances in Plantation 3. It is therefore not possible to determine whether the latitude or elevation or the interactions of the two factors had the greatest effect. Perhaps a different adjustment factor could compensate better for elevation at different latitudes.

The difference in the length of the growing season affects the order of seed source flushing (Sluder, 1960; Mergen, 1963; McMillan and Peacock, 1964; Smithberg and Weiser, 1968). The latitudinal gradient is based on the length of the growing season, since generally the more northern sources have a shorter growing season. On an elevational gradient, the higher elevations usually have the shorter growing period. By looking at the length of the growing season for each seed source, microsite differences that are often overlooked in the more general latitudinal or elevational approach can be seen. In Plantation 4, the length of the growing season in six regions of Michigan did not correspond closely with the flushing scores. Perhaps if a close study was made of the length of the growing season at each individual seed source, the relationship would be stronger.

Some authors have reported differences in flushing of seedlings from the same seed source at different ages, with the younger seedlings flushing earlier than mature trees (Irgens-Moller, 1957, 1967; Silen, 1962). In this study, the younger seedlings (Plantations 3 and 4) flushed earlier than the older saplings (Plantations 1 and 2) on the same dates and with similar heat summations. It was not certain whether this was caused by warmer temperatures closer to the ground, or whether the threshold temperature changed with age. The results of the temperature measurements at ground level and three feet above the ground were variable, changing with the amount of sun and clouds during the time the measurements were taken. However, during the growing season, there are more sunny days than overcast days, so one can conclude that the ground temperature would be warmer than the air temperature more often than the reverse during the time leaves were flushing.

There were some important points in the literature review that were not directly illustrated by the results of the field study. Temperature as expressed by a heat summation appears to be the trigger to flushing in the spring (Smithberg and Weiser, 1968). We can tell from the variability in the flushing date from year to year that the trigger to flushing is not constant in yearly cycles, as photoperiod is. The flushing observations in this study only covered one year, so it shows no direct evidence on yearly variability.

A period of low temperatures during the winter before flushing can occur is another important point mentioned in the literature review (Coville, 1920; Daubenmire, 1949; Wareing, 1956; Naylor, 1961). Without a minimum amount of chilling flushing was either retarded or abnormal if it occurred at all. Clinal variation in the amount of chilling needed before flushing could occur was found to vary by some workers. Since all the plants in this study spent the winter outside during a typical Michigan winter, the chilling requirement was met for all the sources. No conclusions about the patterns of chilling requirements were drawn.

Some workers have mentioned a lapse of time between the flushing of the lateral branches and the terminal branches (Mergen, 1963; Walters and Soos, 1963; Sweet, 1965). None of this behavior appeared with any of the yellow or sweet birch. The Japanese white birch in Plantation 1, however, did show this trait in some of the smaller seedlings, the lateral branches flushing before the terminal bud.

## SUMMARY AND CONCLUSIONS

The phenomenon of leaf flushing in the spring is not completely understood. When seeds of a species are collected from many parts of its range and grown together in a common garden, variation in the time of leaf flushing is observed. Often, patterns to the differences in flushing time are observed. Various environmental factors have been cited as causing the differences in flushing times: temperature, photoperiod, and winter chilling are among the most cited factors.

The general objective of this paper was to study the phenomenon of flushing in woody plants and determine what mechanisms affect and control it. The specific components of latitude and altitude of the populations, age of seedlings, and heat summations during the spring were studied. The flushing of species of the genus *Betula*, particularly yellow birch (*Betula alleghaniensis* Britton), in common gardens was related to environmental and genetic factors.

One of the approaches to this problem was an extensive literature review on the topic of flushing in woody plants. Areas investigated included historical aspects and early thoughts, recent studies of dormancy and winter chilling, heat summations, patterns of flushing associated with environmental factors, and genetic variation in flushing. A second approach to the problem was a field study of flushing of yellow and sweet birch (*Betula lenta* L.) in Michigan common gardens during the spring of 1974. Four plantations were observed. Two were located at the University of Michigan Matthaei Botanical Gardens in Ann Arbor, and two were located at the Southern Michigan State Forest Nursery near Brighton, Michigan. Seeds for the plantations were procured from the northern and southern Appalachian Mountains from both high and low elevations, and in the upper and lower peninsulas of Michigan. The plantations were established in different years, so four ages (from two to six years from seed) were represented. During the spring the seedlings were scored as to flushing stage every three days for the two younger plantations, and once a week for the older two plantations. The air and ground temperatures were taken each scoring date. Heat summations were calculated for each plantation site using temperatures from the U.S. Environmental Data Service (1974) using the duration summation method developed by Lindsey and Newman (1956).

Statistical analyses were conducted using the MIDAS statistical computer program of the University of Michigan. Yellow birch flushing scores were regressed on latitude of the source in each plantation; for one plantation they were regressed on elevation of the source as well. Sweet birch scores were also analyzed in the same manner for two plantations. Regressions of flushing scores on latitude adjusted for elevation were computed for two plantations. Correlation coefficients were calculated for each regression. The yellow birch flushing scores from all four plantations were analyzed together using multiple regression to test the effects of latitude and plantation upon flushing scores.

One of the major trends found in both the literature review and the field results was a difference in flushing behavior by species and by seed source within species. Strong genetic control of the time of flushing was apparent. A latitudinal cline with the northern sources flushing significantly earlier than the more southern sources in the common garden was observed. In the literature, depending on the species and the place of the test, either the northern or the southern sources flushed earlier. In most cases, the sources with the short growing seasons flushed earliest. This was confirmed for yellow birch and sweet birch in this study.

Elevational patterns were not clear because latitude and elevation were confounded. The higher elevation sources came from lower latitudes, and vice versa. However, in the Southern Appalachian Mountains where both high and lower elevations were represented, the higher elevation sources generally flushed earlier than the lower sources.

Differences in flushing behavior due to age have been reported, and in this study the younger seedlings flushed earlier. However, due to plantation layouts, with the two younger plantations at a different less protected site than the two older plantations, the results were not clearly due to age alone.

Some major points found in the literature review were not specifically tested in the field study. The most recent experiments show that temperature, which may be expressed as a heat sum, is the trigger to leaf flushing. Although some early papers reported photoperiod as a cause, most of the evidence today supports heat summations. If photoperiod alone were the trigger to flushing, leaves would flush on the same day each year, since photoperiod is constant from year to year. However, this was not found to be the case with various species in nature. In unusual cases, photoperiod might act as a "second line" trigger.

A minimum of cold during the winter is necessary for normal flushing in the spring. Without the minimum of winter chilling, flushing is abnormal if it occurs at all. Northern populations, for example, when grown in southern plantations may flush abnormally late because their chilling requirement has not been satisfied. The Michigan winter in Ann Arbor apparently fulfilled the chilling requirement for all sources.

There was no one conclusion that emerged from this study. However, the field results emphasize the importance of genetic control in flushing in the spring as shown by the marked latitudinal cline in the time of flushing in the common garden. The consensus from experiments in the literature review is that once winter chilling requirements are satisfied leaf flushing in the spring is directly related to temperature as expressed by heat summation. The amount of winter chilling and the number of degree-hours necessary are geneticaaly controlled, and vary from species to species and source to source.

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# APPENDIX A

## Seed source data

### Species code

A= *Betula alleghaniensis*, Yellow birch

B= *Betula pumila*, Bog birch

H= *B. alleghaniensis* X *B. papyrifera*, Hybrid birch

L= *Betula lenta*, Sweet birch

M= putative polyploid derivative of *Betula Xpurpusii*

P= *Betula papyrifera* and *Betula platyphella*, White birch and Japanese white birch

Q= *B. alleghaniensis* X the putative polyploid derivative of *B. Xpurpusii*, Walsh hybrid birch

| CODE | SITE LANDMARK | COUNTY | STATE | LATITUDE | ELEVATION | PLANTATION | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | 1 | 2 | 3 | 4 |
| B | Bartlett | Caroll | N. H. | 44.05 | 1000 | | A[1] | | |
| $BC_{lo}$ | Burns Creek | Wise | Va. | 35.93 | 2200 | | A,L | | |
| $BC_{hi}$ | Burns Creek | Wise | Va. | 35.90 | 3000 | | A,L | | |
| BL | Bear Lake | Manistee | Mi. | 44.47 | 750 | | | A | A |
| BV | Beaver Creek | Columbiana | Ohio | 40.73 | 900 | | A,L | | |
| CA | Calumet | Houghton | Mi. | 47.25 | 1100 | | | | A |
| CC | Courthouse Creek | Transylvania | N. C. | 35.28 | 4000 | | A,L | L | |
| CG | Cranberry Glades | Pocahontas | W. Va. | 38.12 | 3300 | A | | | |
| CR | Creighton | Schoolcraft | Mi. | 46.38 | 850 | | | | A |
| CW | Centennial Woods | Chittendon | Vt. | 44.48 | 200 | | A,L | A,L | A |
| D | Doubles | Harlan | Ky. | 36.90 | 3600 | | A,L | | |
| DC | Devil's Courthouse | Transylvania | N. C. | 35.30 | 5200 | | A | A | A |
| DF | Duke's Experimental Forest | Marquette | Mi. | 46.22 | 1075 | A | | | |
| DL | Deadman Lake | Ontonogan | Mi. | 46.33 | 1570 | | | H | A,H |

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[1] The letter listed under each plantation represents the species of that source planted.

| CODE | SITE LANDMARK | COUNTY | STATE | LATITUDE | ELEVATION | PLANTATION 1 | 2 | 3 | 4 |
|---|---|---|---|---|---|---|---|---|---|
| DO | Douglas Lake | Cheboygan | Mi. | 45.37 | 730 | A | | | |
| DR | Davidson River | Transylvania | N. C. | 35.28 | 2200 | | A,L | A,L | A |
| DS | Deadman's Lake | Luce | Mi. | 46.43 | 900 | | | | A |
| DW | Davis Woods | Washtenaw | Mi. | 42.23 | 920 | B | | | |
| EL | East Lake | Mackinac | Mi. | 46.10 | 850 | | | | A |
| EW | Erwin's Woods | Washtenaw | Mi. | 42.14 | 950 | A | | | |
| FC | Files Creek | Randolf | W. Va. | 38.78 | 2200 | | A,L | | |
| FH | Fox Hills | Washtenaw | Mi. | 42.21 | 940 | | | | A |
| FL | Flott Lake | Otsego | Mi. | 45.07 | 1350 | | | | A |
| GC | Gibbs City | Iron | Mi. | 46.28 | 1520 | | | | A |
| GD | Gauley Ranger District | Pocahantas | W. Va. | 38.11 | 2900 | A | | | |
| GK | Gaudineer Knob | Pocohantas | W. Va. | 38.62 | 4000 | | A | | |
| GR | Greenbriar River | Pocohantas | W. Va. | 38.48 | 3000 | | A,I | | |
| $HB_{lo}$ | Hubbard Brook | Grafton | N. H. | 43.93 | 1000 | | A | | |
| $HB_{hi}$ | Hubbard Brook | Grafton | N. H. | 43.95 | 2000 | | A | | |

| CODE | SITE LANDMARK | COUNTY | STATE | LATITUDE | ELEVATION | PLANTATION |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | 1 | 2 | 3 | 4 |
| HK | High Knob | Wise | Va. | 36.88 | 4000 |  | A,L |  |  |
| J | James Lake | Iron | Mi. | 46.11 | 1750 |  |  |  | H |
| JF | Jerico Forest | Chittendon | Vt. | 44.45 | 600 |  | A |  |  |
| JR | Jordan River | Antrim | Mi. | 45.02 | 900 |  |  |  | A |
| KY | Kyoto | ----- | JAPAN | 35.02 | 380 | P |  |  |  |
| L | Linwood | Pocohantas | W. Va. | 38.42 | 3500 |  | A,L |  |  |
| LB | Little Bay DeNoc | Delta | Mi. | 45.73 | 620 |  |  |  | A |
| LK | Lake 17 | Iron | Mi. | 46.12 | 1700 |  |  |  | A |
| LL | Lark's Lake | Emmett | Mi. | 45.33 | 720 | A |  |  |  |
| LS | Liberty Swamp | Washtenaw | Mi. | 42.07 | 950 | A,B |  |  | A |
| M | Marquette | Marquette | Mi. | 46.31 | 1020 |  |  |  | H |
| MC | Meadow Creek | Greenbriar | W. Va. | 37.97 | 2500 |  | A,L |  |  |
| MI | Winslow Lake | Iron | Mi. | 46.30 | 1575 |  | P |  |  |
| ML | Mallard Lake | Iron | Mi. | 46.28 | 1700 |  | A | A | A |
| MM | Mount Mansfield | Lamoille | Vt. | 44.52 | 2800 |  |  | A | A |
| MN | McNearny Lake | Chippewa | Mi. | 46.42 | 1050 |  |  | A | A |

| CODE | SITE LANDMARK | COUNTY | STATE | LATITUDE | ELEVATION | PLANTATION |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | 1 | 2 | 3 | 4 |
| MO | Mohawk | Keweenaw | Mi. | 47.33 | 1100 |  |  |  | A |
| MR | McCormick | Marquette | Mi. | 46.63 | 1800 |  |  |  | A |
| MU | Mud Lake | Washtenaw | Mi. | 42.25 | 880 | A |  |  | A |
| $MW_{lo}$ | Mount Washington | Coos | N. H. | 44.28 | 2000 |  | A |  |  |
| $MW_{hi}$ | Mount Washington | Coos | N. H. | 44.28 | 2800 |  | A |  |  |
| $N_{lo}$ | Norton | Wise | Va. | 36.92 | 2400 |  | A |  |  |
| $N_{hi}$ | Norton | Wise | Va. | 36.92 | 3000 |  | L |  |  |
| NL | North Lake | Washtenaw | Mi. | 42.36 | 950 | A |  | A | A |
| PA | Point Abbaye | Baraga | Mi. | 47.33 | 1100 |  |  |  | A |
| PB | Panther Branch | Transylvania | N. C. | 35.27 | 3100 |  | A,L |  |  |
| PR | Platte River | Benzie | Mi. | 44.58 | 700 |  |  |  | A |
| PV | Pleasant View Swamp | Emmett | Mi. | 45.33 | 720 | B |  |  |  |
| SB | Shetron's Birch | Crawford | Mi. | 44.31 | 1200 | A |  |  |  |
| SI | Saint Ignace | Mackinac | Mi. | 45.93 | 650 |  | A | A | A |
| SK | Smoke Camp Knob | Pocahantas | W. Va. | 38.55 | 4000 |  | A,L |  |  |
| SL | Sunset Lake | Iron | Mi. | 46.18 | 1620 |  |  |  | A |

| CODE | SITE LANDMARK | COUNTY | STATE | LATITUDE | ELEVATION | PLANTATION | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | 1 | 2 | 3 | 4 |
| SN | St. Nichols Church | Emmett | Mi. | 45.37 | 720 | A | | | |
| TS | Third Sister Lake | Washtenaw | Mi. | 42.16 | 910 | M | A | | |
| WL | Walsh Lake | Washtenaw | Mi. | 42.35 | 965 | A,B,<br>H,Q | | A | A |
| YD | Yellow Dog | Marquette | Mi. | 46.73 | 1440 | | | | A |
| UK | Higgins Lake | Crawford | Mi. | 44.31 | 1200 | | | P | |

# APPENDIX B

## Average flushing score raw data

# PLANTATION 1

## FLUSHING SCORES 1974

| CODE[1] | 4/29 | 5/5 | 5/12 | 5/19 |
|---|---|---|---|---|
| ACG | 1.8 | 3.0 | 4.0 | 5.8 |
| ADF | 4.2 | 5.5 | 5.9 | 6.4 |
| ADO | 4.0 | 5.0 | 6.0 | 6.0 |
| BDW | 4.7 | 5.0 | 5.0 | 5.5 |
| AEW | 3.2 | 4.3 | 5.3 | 6.1 |
| AGD | 2.0 | 2.7 | 3.7 | 5.0 |
| PKY | 3.8 | 4.4 | 5.0 | 5.8 |
| ALL | 4.1 | 5.3 | 5.9 | 6.2 |
| ALS | 3.5 | 4.6 | 5.5 | 6.1 |
| BLS | 4.4 | 4.9 | 5.7 | 6.0 |
| AMU | 3.0 | 4.0 | 4.9 | 5.9 |
| ANL | 4.3 | 5.2 | 5.7 | 6.4 |
| BPV | 5.0 | 5.2 | 6.0 | 6.0 |
| ASB | 2.5 | 3.5 | 4.7 | 5.8 |
| ASN | 3.8 | 5.0 | 5.9 | 6.4 |
| MTS | 3.4 | 4.6 | 5.7 | 5.7 |
| AWL | 3.3 | 4.4 | 5.3 | 6.0 |
| BWL | 4.4 | 4.8 | 5.2 | 5.8 |
| HWL | 3.8 | 5.2 | 5.8 | 6.2 |
| QWL | 3.9 | 5.3 | 5.8 | 6.1 |

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[1] The first letter of the code indicates the species, the last two letters indicate the seed source (Appendix A).

## PLANTATION 2

## FLUSHING SCORES 1974

| CODE | 4/29 | 5/5 | 5/12 | 5/19 | 5/26 |
|---|---|---|---|---|---|
| AB | 4.1 | 5.4 | 5.8 | 6.4 | 6.8 |
| $ABC_{lo}$ | 2.9 | 3.6 | 4.5 | 5.8 | 6.4 |
| $ABC_{hi}$ | 1.9 | 3.0 | 4.0 | 5.4 | 6.3 |
| $LBC_{lo}$ | 1.5 | 3.0 | 4.0 | 6.0 | 6.0 |
| $LBC_{hi}$ | 2.0 | 2.0 | 2.0 | 3.5 | 6.0 |
| ABV | 2.0 | 2.9 | 3.5 | 5.1 | 6.4 |
| LBV | 2.1 | 2.8 | 3.6 | 5.5 | 6.0 |
| ACC | 2.3 | 3.3 | 4.1 | 5.8 | 6.9 |
| LCC | 1.5 | 2.3 | 2.6 | 4.5 | 6.1 |
| ACW | 3.2 | 4.4 | 5.1 | 6.0 | 6.7 |
| LCW | 2.0 | 3.0 | 4.0 | 6.0 | 6.0 |
| AD | 1.6 | 1.9 | 2.6 | 4.3 | 6.1 |
| LD | 1.7 | 2.0 | 2.0 | 3.0 | 6.0 |
| ADC | 1.0 | 1.4 | 2.2 | 4.0 | 6.0 |
| ADR | 2.7 | 3.7 | 4.3 | 6.0 | 7.0 |
| LDR | 1.0 | 2.0 | 2.8 | 4.8 | 6.0 |
| AFC | 2.6 | 3.3 | 4.1 | 6.0 | 6.4 |
| LFC | 1.6 | 2.2 | 2.8 | 4.6 | 6.0 |
| AGK | 3.0 | 3.8 | 4.8 | 5.8 | 6.3 |
| AGR | 1.9 | 3.1 | 4.1 | 6.0 | 6.3 |
| LGR | 1.3 | 2.2 | 2.8 | 4.7 | 6.0 |
| $AHB_{lo}$ | 4.1 | 5.5 | 5.8 | 6.2 | 6.7 |
| $AHB_{hi}$ | 3.8 | 5.0 | 5.8 | 6.3 | 6.9 |
| AHK | 1.1 | 1.4 | 2.2 | 4.1 | 6.0 |

Plantation 2 (continued)

| CODE | 4/29 | 5/5 | 5/12 | 5/19 | 5/26 |
|---|---|---|---|---|---|
| LHK | 1.2 | 1.3 | 1.8 | 3.5 | 6.0 |
| AJF | 4.2 | 5.3 | 6.0 | 6.0 | 6.8 |
| AL | 2.1 | 3.0 | 3.9 | 5.7 | 6.4 |
| LL | 1.8 | 2.6 | 3.4 | 4.8 | 6.0 |
| AMC | 1.8 | 3.0 | 3.9 | 5.8 | 6.4 |
| AML | 3.5 | 4.5 | 5.2 | 5.9 | 6.8 |
| $AMW_{lo}$ | 3.9 | 5.0 | 5.9 | 6.5 | 6.9 |
| $AMW_{hi}$ | 3.3 | 4.6 | 5.3 | 6.1 | 6.8 |
| AN | 1.3 | 2.5 | 3.2 | 5.2 | 6.2 |
| LN | 1.5 | 1.7 | 2.3 | 3.8 | 6.0 |
| APB | 1.5 | 2.5 | 3.1 | 5.0 | 6.0 |
| LPB | 1.8 | 2.6 | 3.4 | 5.4 | 6.0 |
| ASI | 4.2 | 5.5 | 6.0 | 6.4 | 6.9 |
| ASK | 2.5 | 3.5 | 4.3 | 5.9 | 6.6 |
| LSK | 1.7 | 3.0 | 4.3 | 6.0 | 6.0 |
| ATS | 4.0 | 5.4 | 5.9 | 6.0 | 6.5 |

# PLANTATION 3

## FLUSHING SCORES 1974

| CODE | LIGHT % | 4/10 | 4/13 | 4/16-17 | 4/20-21 | 4/23 | 4/27 |
|---|---|---|---|---|---|---|---|
| ABL | 100 | 1.0 | 1.1 | 1.2 | 1.8 | 2.8 | 3.4 |
| | 45 | 1.0 | 1.0 | 1.2 | 1.6 | 3.1 | 3.9 |
| | 20 | 1.0 | 1.0 | 1.5 | 2.9 | 3.8 | 3.9 |
| LCC | 100 | 1.0 | 1.0 | 1.0 | 1.0 | 1.2 | 1.9 |
| | 45 | 1.0 | 1.0 | 1.0 | 1.1 | 1.8 | 2.0 |
| | 20 | 1.0 | 1.1 | 1.1 | 1.2 | 1.8 | 2.5 |
| ACW | 100 | 1.0 | 1.0 | 1.0 | 1.2 | 2.6 | 3.5 |
| | 45 | 1.0 | 1.0 | 1.1 | 1.9 | 2.4 | 3.4 |
| | 20 | 1.0 | 1.2 | 1.8 | 2.2 | 3.2 | 3.8 |
| LCW | 100 | 1.0 | 1.0 | 1.0 | 1.2 | 1.5 | 2.1 |
| | 45 | 1.0 | 1.0 | 1.0 | 1.0 | 1.9 | 2.1 |
| | 20 | 1.0 | 1.2 | 1.2 | 1.5 | 2.0 | 2.6 |
| ADC | 100 | 1.0 | 1.0 | 1.0 | 1.0 | 1.1 | 1.8 |
| | 45 | 1.0 | 1.0 | 1.0 | 1.0 | 1.4 | 1.6 |
| | 20 | 1.0 | 1.0 | 1.1 | 1.4 | 1.6 | 2.4 |
| HDL | 100 | 1.0 | 1.1 | 1.4 | 2.0 | 2.5 | 3.1 |
| | 45 | 1.0 | 1.2 | 1.5 | 1.6 | 2.6 | 3.2 |
| | 20 | 1.0 | 1.1 | 2.0 | 2.6 | 3.6 | 4.6 |
| ADR | 100 | 1.0 | 1.0 | 1.1 | 1.1 | 1.2 | 2.2 |
| | 45 | 1.0 | 1.1 | 1.1 | 1.4 | 1.9 | 2.6 |
| | 20 | 1.0 | 1.1 | 1.5 | 2.0 | 2.5 | 3.0 |
| LDR | 100 | 1.0 | 1.0 | 1.0 | 1.1 | 1.2 | 1.9 |
| | 45 | 1.0 | 1.0 | 1.0 | 1.1 | 1.2 | 1.8 |
| | 20 | 1.0 | 1.0 | 1.1 | 1.1 | 1.2 | 2.1 |

Plantation 3 (continued)

| CODE | LIGHT % | 4/30 | 5/3 | 5/6 | 5/10 | 5/13 | 5/20 |
|---|---|---|---|---|---|---|---|
| ABL | 100 | 4.5 | 5.8 | 5.9 | 5.9 | 6.1 | 6.4 |
| | 45 | 5.1 | 5.8 | 5.9 | 6.0 | 6.0 | --- |
| | 20 | 5.5 | 5.9 | 5.9 | 5.9 | 6.0 | --- |
| LCC | 100 | 2.6 | 3.2 | 3.4 | 3.5 | 4.0 | 5.5 |
| | 45 | 2.8 | 3.9 | 3.9 | 3.9 | 4.6 | --- |
| | 20 | 3.8 | 4.5 | 4.9 | 5.1 | 5.5 | --- |
| ACW | 100 | 4.8 | 5.6 | 5.7 | 6.0 | 6.0 | 6.5 |
| | 45 | 4.7 | 5.4 | 5.7 | 5.9 | 6.0 | --- |
| | 20 | 5.1 | 5.6 | 6.0 | 6.0 | 6.0 | --- |
| LCW | 100 | 3.1 | 3.8 | 4.0 | 4.2 | 4.9 | 5.5 |
| | 45 | 3.2 | 4.0 | 4.2 | 4.5 | 5.2 | --- |
| | 20 | 3.8 | 4.6 | 5.0 | 5.2 | 5.9 | --- |
| ADC | 100 | 2.6 | 3.4 | 3.8 | 4.0 | 4.6 | 5.5 |
| | 45 | 2.6 | 3.4 | 3.6 | 3.9 | 4.7 | --- |
| | 20 | 3.4 | 4.4 | 4.6 | 5.0 | 5.3 | --- |
| HDL | 100 | 4.6 | 5.4 | 5.6 | 5.8 | 6.0 | 6.2 |
| | 45 | 4.5 | 5.0 | 5.4 | 5.6 | 5.9 | --- |
| | 20 | 5.9 | 6.0 | 6.0 | 6.0 | 6.3 | --- |
| ADR | 100 | 3.5 | 4.1 | 4.5 | 4.8 | 5.5 | 6.2 |
| | 45 | 3.4 | 4.4 | 4.8 | 5.0 | 5.4 | --- |
| | 20 | 4.1 | 5.1 | 5.5 | 5.6 | 5.9 | --- |
| LDR | 100 | 2.9 | 3.8 | 4.0 | 4.0 | 4.9 | 6.0 |
| | 45 | 3.2 | 4.1 | 4.5 | 4.8 | 5.5 | --- |
| | 20 | 3.2 | 4.1 | 4.4 | 4.9 | 5.2 | --- |

Plantation 3 (continued)

| CODE | LIGHT % | Start of flushing |
|---|---|---|
| ABL | 100 | 9.5 |
| | 45 | 10.1 |
| | 20 | 8.1 |
| LCC | 100 | 16.2 |
| | 45 | 13.6 |
| | 20 | 13.0 |
| ACW | 100 | 11.9 |
| | 45 | 10.9 |
| | 20 | 6.9 |
| LCW | 100 | 15.4 |
| | 45 | 14.5 |
| | 20 | 12.8 |
| ADC | 100 | 18.8 |
| | 45 | 16.3 |
| | 20 | 12.7 |
| HDL | 100 | 8.4 |
| | 45 | 8.8 |
| | 20 | 6.0 |
| ADR | 100 | 14.9 |
| | 45 | 12.9 |
| | 20 | 9.6 |
| LDR | 100 | 16.0 |
| | 45 | 16.1 |
| | 20 | 15.0 |

Plantation 3 (continued)

| CODE | LIGHT % | 4/10 | 4/13 | 4/16-17 | 4/20-21 | 4/23 | 4/27 |
|---|---|---|---|---|---|---|---|
| PMI | 100 | 1.0 | 1.4 | 1.6 | 2.0 | 2.4 | 3.0 |
| | 45 | 1.0 | 1.1 | 1.5 | 2.0 | 2.8 | 3.8 |
| | 20 | 1.0 | 1.9 | 2.6 | 3.2 | 3.8 | 4.0 |
| AML | 100 | 1.0 | 1.2 | 2.0 | 3.0 | 3.8 | 4.6 |
| | 45 | 1.0 | 1.1 | 2.4 | 2.9 | 3.6 | 4.4 |
| | 20 | 1.0 | 1.6 | 3.0 | 3.9 | 4.0 | 5.0 |
| AMM | 100 | 1.0 | 1.2 | 1.6 | 2.5 | 3.4 | 3.8 |
| | 45 | 1.0 | 1.3 | 1.7 | 1.7 | 3.3 | 3.9 |
| | 20 | 1.0 | 1.1 | 2.2 | 3.5 | 3.9 | 4.5 |
| AMN | 100 | 1.0 | 1.0 | 1.7 | 2.1 | 3.5 | 4.0 |
| | 45 | 1.0 | 1.1 | 1.4 | 2.4 | 4.0 | 4.8 |
| | 20 | 1.0 | 1.3 | 2.6 | 3.6 | 4.0 | 4.4 |
| ANL | 100 | 1.0 | 1.0 | 1.2 | 2.1 | 3.0 | 3.9 |
| | 45 | 1.0 | 1.0 | 1.5 | 1.9 | 3.1 | 3.5 |
| | 20 | 1.0 | 1.0 | 1.7 | 2.7 | 3.3 | 4.1 |
| ASI | 100 | 1.0 | 1.4 | 1.8 | 2.1 | 3.2 | 4.4 |
| | 45 | 1.0 | 1.0 | 1.1 | 1.4 | 2.7 | 4.1 |
| | 20 | 1.0 | 1.9 | 3.0 | 3.6 | 4.0 | 4.8 |
| PUK | 100 | 1.0 | 1.5 | 1.8 | 1.9 | 2.6 | 3.6 |
| | 45 | 1.0 | 1.5 | 1.9 | 2.2 | 3.0 | 4.0 |
| | 20 | 1.0 | 1.5 | 1.8 | 1.9 | 2.8 | 3.5 |
| AWL | 100 | 1.0 | 1.0 | 1.1 | 1.4 | 2.2 | 3.2 |
| | 45 | 1.0 | 1.0 | 1.1 | 1.3 | 2.4 | 3.0 |
| | 20 | 1.0 | 1.8 | 1.9 | 3.1 | 3.4 | 3.9 |

Plantation 3 (continued)

| CODE | LIGHT % | 4/30 | 5/3 | 5/6 | 5/10 | 5/13 | 5/20 |
|---|---|---|---|---|---|---|---|
| PMI | 100 | 4.0 | 4.9 | 5.2 | 5.4 | 5.6 | 6.0 |
| | 45 | 5.1 | 5.6 | 5.9 | 6.0 | 6.2 | --- |
| | 20 | 5.8 | 6.0 | 6.0 | 6.0 | 6.0 | --- |
| AML | 100 | 5.9 | 6.0 | 6.0 | 6.1 | 6.2 | 6.9 |
| | 45 | 5.5 | 5.8 | 5.9 | 6.0 | 6.1 | --- |
| | 20 | 5.9 | 6.0 | 6.0 | 6.4 | 6.4 | --- |
| AMM | 100 | 5.2 | 5.9 | 5.9 | 6.0 | 6.1 | 6.8 |
| | 45 | 5.0 | 5.9 | 5.9 | 5.9 | 6.1 | --- |
| | 20 | 6.0 | 6.0 | 6.0 | 6.1 | 6.1 | --- |
| AMN | 100 | 5.5 | 6.0 | 6.0 | 6.0 | 6.0 | 6.8 |
| | 45 | 6.0 | 6.0 | 6.0 | 6.0 | 6.0 | --- |
| | 20 | 6.0 | 6.0 | 6.0 | 6.0 | 6.1 | --- |
| ANL | 100 | 5.0 | 5.8 | 6.0 | 6.0 | 6.0 | 6.0 |
| | 45 | 5.0 | 5.8 | 6.0 | 6.0 | 6.0 | --- |
| | 20 | 5.4 | 6.0 | 6.0 | 6.0 | 6.0 | --- |
| ASI | 100 | 5.4 | 5.8 | 6.0 | 6.0 | 6.1 | 6.9 |
| | 45 | 5.3 | 5.7 | 6.0 | 6.0 | 6.0 | --- |
| | 20 | 5.8 | 6.0 | 6.0 | 6.0 | 6.4 | --- |
| PUK | 100 | 5.2 | 5.6 | 5.8 | 5.9 | 6.0 | 6.2 |
| | 45 | 5.8 | 5.9 | 6.0 | 6.0 | 6.1 | --- |
| | 20 | 4.9 | 5.4 | 5.5 | 5.5 | 5.6 | --- |
| AWL | 100 | 4.5 | 5.6 | 5.9 | 5.9 | 6.0 | 6.8 |
| | 45 | 4.3 | 5.3 | 5.6 | 5.8 | 6.0 | --- |
| | 20 | 5.4 | 5.9 | 6.0 | 6.0 | 6.0 | --- |

Plantation 3 (continued)

| CODE | LIGHT % | Start of flushing |
|---|---|---|
| PMI | 100 | 6.8 |
| | 45 | 7.6 |
| | 20 | 3.8 |
| AML | 100 | 6.0 |
| | 45 | 5.4 |
| | 20 | 4.1 |
| AMM | 100 | 7.7 |
| | 45 | 7.9 |
| | 20 | 5.9 |
| AMN | 100 | 7.7 |
| | 45 | 8.5 |
| | 20 | 5.1 |
| ANL | 100 | 9.0 |
| | 45 | 9.2 |
| | 20 | 7.0 |
| ASI | 100 | 7.8 |
| | 45 | 10.9 |
| | 20 | 3.5 |
| PUK | 100 | 6.4 |
| | 45 | 5.9 |
| | 20 | 7.0 |
| AWL | 100 | 11.6 |
| | 45 | 11.7 |
| | 20 | 6.2 |

## PLANTATION 4

## FLUSHING SCORES 1974

| CODE | 4/16-17 | 4/20-21 | 4/24 | 4/27 | 4/30 | 5/3 |
|---|---|---|---|---|---|---|
| ABL | 1.4 | 2.2 | 2.9 | 3.3 | 4.6 | 5.5 |
| ACA | 2.2 | 3.2 | 3.7 | 4.3 | 5.6 | 6.0 |
| ACR | 2.0 | 3.0 | 3.6 | 4.3 | 5.6 | 6.0 |
| ACW | 1.8 | 2.7 | 3.5 | 4.0 | 5.2 | 5.8 |
| ADC | 1.2 | 1.7 | 2.2 | 2.4 | 3.2 | 3.8 |
| ADD | 2.2 | 3.2 | 3.7 | 4.2 | 5.6 | 5.9 |
| ADL | 1.9 | 2.7 | 3.5 | 4.1 | 5.2 | 5.9 |
| HDL | 2.1 | 3.0 | 3.5 | 4.2 | 5.6 | 5.9 |
| ADR | 1.3 | 2.0 | 2.6 | 2.8 | 3.9 | 4.8 |
| ADS | 1.8 | 2.8 | 3.6 | 4.2 | 5.4 | 5.8 |
| AEL | 1.9 | 2.9 | 3.6 | 4.0 | 5.3 | 5.9 |
| AFH | 1.6 | 2.7 | 3.4 | 3.9 | 5.1 | 5.8 |
| AFL | 1.7 | 2.7 | 3.3 | 3.8 | 5.1 | 5.8 |
| AGC | 1.7 | 2.6 | 3.5 | 3.9 | 5.1 | 5.8 |
| HJ | 1.6 | 2.6 | 3.6 | 4.0 | 5.6 | 6.0 |
| AJR | 1.7 | 2.5 | 3.2 | 3.6 | 4.9 | 5.6 |
| ALB | 1.9 | 2.7 | 3.6 | 4.2 | 5.5 | 5.9 |
| ALK | 1.9 | 2.8 | 3.6 | 4.0 | 5.3 | 5.9 |
| ALS | 1.8 | 2.7 | 3.6 | 4.1 | 5.3 | 5.9 |
| HM | 1.9 | 2.9 | 3.8 | 4.4 | 5.8 | 6.0 |
| AML | 1.8 | 2.8 | 3.5 | 4.0 | 5.4 | 6.0 |
| AMM | 1.8 | 2.9 | 3.5 | 4.1 | 5.3 | 5.8 |
| AMN | 2.2 | 3.0 | 3.8 | 4.3 | 5.6 | 6.0 |
| AMO | 2.1 | 3.1 | 3.7 | 4.3 | 5.6 | 5.8 |

Plantation 4 (continued)

| CODE | 5/6 | 5/13 | Start of flushing |
|---|---|---|---|
| ABL | 5.8 | 6.0 | 10.2 |
| ACA | 6.0 | 6.0 | 7.4 |
| ACR | 6.0 | 6.0 | 8.0 |
| ACW | 5.8 | 6.0 | 8.4 |
| ADC | 4.3 | 5.2 | 11.7 |
| ADD | 6.0 | 6.0 | 7.4 |
| ADL | 6.0 | 6.0 | 8.5 |
| HDL | 6.0 | 6.1 | 6.9 |
| ADR | 5.2 | 5.8 | 10.6 |
| ADS | 5.9 | 6.0 | 8.3 |
| AEL | 6.0 | 6.0 | 8.3 |
| AFH | 6.0 | 6.0 | 9.1 |
| AFL | 5.9 | 6.0 | 8.4 |
| AGC | 5.9 | 6.0 | 8.9 |
| HJ | 6.0 | 6.1 | 8.9 |
| AJR | 5.8 | 6.0 | 8.8 |
| ALB | 5.9 | 5.9 | 8.5 |
| ALK | 6.0 | 6.0 | 8.1 |
| ALS | 5.9 | 6.0 | 8.6 |
| HM | 6.0 | 6.1 | 8.4 |
| AML | 6.0 | 6.0 | 8.3 |
| AMM | 5.9 | 6.0 | 8.0 |
| AMN | 6.0 | 6.1 | 7.5 |
| AMO | 5.0 | 5.9 | 7.9 |
| AMR | 5.8 | 5.9 | 8.1 |

Plantation 4 (continued)

| CODE | 4/16-17 | 4/20-21 | 4/24 | 4/27 | 4/30 | 5/3 |
|---|---|---|---|---|---|---|
| AMR | 2.0 | 3.0 | 3.5 | 4.1 | 5.1 | 5.7 |
| AMU | 2.0 | 3.1 | 3.7 | 4.3 | 5.2 | 5.8 |
| ANL | 1.6 | 2.4 | 3.3 | 3.8 | 5.1 | 5.7 |
| APA | 2.1 | 3.1 | 3.6 | 4.3 | 5.6 | 5.8 |
| APR | 1.7 | 2.3 | 3.2 | 3.5 | 4.5 | 5.2 |
| ASI | 2.0 | 2.9 | 3.6 | 4.2 | 5.5 | 6.0 |
| ASL | 1.6 | 2.6 | 3.4 | 4.0 | 5.3 | 5.9 |
| AWL | 1.4 | 2.2 | 3.2 | 3.8 | 5.0 | 5.8 |
| AYD | 2.1 | 3.0 | 3.6 | 4.2 | 5.2 | 5.9 |

Plantation 4 (continued)

| CODE | 5/6 | 5/13 | Start of flushing |
|---|---|---|---|
| AMU | 5.8 | 5.9 | 7.8 |
| ANL | 5.9 | 6.0 | 9.6 |
| APA | 5.9 | 6.0 | 7.9 |
| APR | 5.6 | 5.9 | 8.9 |
| ASI | 6.0 | 6.0 | 8.3 |
| ASL | 5.9 | 6.0 | 9.0 |
| AWL | 5.9 | 6.0 | 10.2 |
| AYD | 6.0 | 6.0 | 7.4 |