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AN ABSTRACT OF THE THESIS OF

CATHERINE A. ASKREN   for the degree of   MASTER OF SCIENCE

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Title: EVALUATION OF THE OSCILLOSCOPE TECHNIQUE FOR DETECTION OF

DORMANCY AND SURVIVAL POTENTIAL OF CONIFEROUS SEEDLINGS

Abstract approved: _____
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Oscilloscope display of modification of a square wave signal
passed through stem tissue was evaluated as a means of detecting
depth of dormancy and survival potential of coniferous seedlings.
Trace form did not change during release from deep dormancy in Douglas-
fir. This release was judged by observing speed of flushing of lateral
and terminal buds in a favorable long-day environment. In contrast,
increased apical activity in the pine was signaled by trace change. In
both Douglas-fir and ponderosa pine approaching spring bud-swell was
well indicated by peaking of trace form. Half of the seedlings sampled
from fall through spring had been subjected to moisture stress during
the previous summer to hasten the onset of dormancy. Fall trace forms
of the stressed pine indicated this change. Moisture stress did not
change dormancy patterns in the fir.

Date of cambial growth cessation in the fir and pine was deter-
mined using Wolter's cambial scarring technique. Diameter growth
ceased during the period in which trace form changed greatly. Cam-
bial growth cessation has been linked to cold acclimation; this and
other evidence suggest that the oscilloscope technique could be used
to detect frost hardiness.

The second part of this research was a direct test of the ability
of the oscilloscope technique to detect survival potential of Douglas-

fir seedlings lifted on six dates from October 11 through March 24, and planted after zero, four, or eight weeks of cold storage. On a site with moderate moisture stress, trace form at time of lifting indicated potential survival of stored Douglas-fir seedlings. Survival of mid-October and late March lifted seedlings was low. These seedlings had peaked traces when lifted. Seedlings from the middle lifting dates had nearly square traces; survival of these seedlings was excellent. Growth performance of November lifted seedlings with square traces was poor, however. On a more severe site, these seedlings may not have survived. A square trace form at time of lifting is not, therefore, necessarily a guarantee of survival.

Correlation of trace form after storage with survival and growth parameters was poor. Trace character is apparently not capable of detecting vigor per se but only seasonally related physiological factors.

EVALUATION OF THE OSCILLOSCOPE TECHNIQUE FOR
DETECTION OF DORMANCY AND SURVIVAL POTENTIAL
OF CONIFEROUS SEEDLINGS

by

Catherine Anita Askren

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EVALUATION OF THE OSCILLOSCOPE TECHNIQUE FOR DETECTION OF DORMANCY AND SURVIVAL POTENTIAL OF CONIFEROUS SEEDLINGS

INTRODUCTION

It is common knowledge among those concerned with regeneration of western conifers that success in planting varies with the time of year seedlings are lifted from the nursery bed (Cleary et al., 1978). Lifting of western coniferous stock in early fall, and particularly lifting followed by cold storage, can result in poor survival. It is recognized that physiological changes occur in the seedling in the summer and fall which eventually culminate in the seedling being fit for planting. This fitness for planting cannot be detected by simple visual inspection. Seedlings in this state are often referred to as "dormant".

The date of entry into dormancy for a species varies from year to year and from location to location. Intra- as well as interspecies variation may be considerable. Initiation of dormancy is the result of interactions among photoperiod, air and soil temperatures, availability of nutrients, and availability of water. The nurseryman may affect timing of dormancy initiation, intentionally or not, by manipulation of irrigation and fertilization schedules.

Clearly it is not possible to state that a given species will enter dormancy by a given date each and every year. As a result it is recommended practice to plant seedlings well within what might be a favorable period. Planting operations may begin later than necessary. Short planting seasons make planting operations much more difficult. A simple mithod for detecting entry into dormancy would be of great value to regeneration efforts as well as being a research tool with many applications.

Three Forest Service researchers, Ferguson, Ryker, and Ballard, have proposed an oscilloscope technique for detecting physiological fitness of planting stock (Ferguson et al., 1975). They noted that a square wave electrical signal will pass through stem tissue essentially unchanged in form, although decreased in amplitude, at the time

of the year when seedlings are generally believed to be "dormant". No attempt was made by these researchers to actually pinpoint the growth status of the seedlings by growth room or other tests. Furthermore, no research was presented which indicated that the oscilloscope technique could actually predict survival of lifted planting stock.

The principal objective of my investigation was to evaluate the oscilloscope technique as a method for detecting: 1) depth of dormancy, and 2) survival potential. "Dormancy" was defined and divided into phases using physiological response criteria. Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) and ponderosa pine (Pinus ponderosa Laws.) were chosen for the study due to their dominant roles in forest nursery production in the Pacific Northwest.

The investigation was divided into two independent parts. In Part I seasonal changes in trace form were compared with seasonal changes in shoot growth status. One-half of the seedlings sampled on each of the seven dates had been subjected to drought stress the summer before sampling. The purpose of this stress was to hasten the onset of dormancy. The ability of the oscilloscope technique to detect this change was evaluated. The study was limited to consideration of activity of apical and lateral meristems. It is questionable if roots are subject to any dormancy control other than the absence or presence of favorable growth conditions (Lavender et al., 1970).

Part II of this study was a direct attempt to correlate trace character at time of lifting and at time of planting with survival through the following summer. Seedlings were lifted from October, 1976, through March, 1977, and were stored for zero, four or eight weeks. Survival was tallied in September, 1977. Despite water stress, mortality was low, and additional measures of growing ability were thought necessary. Those used in this evaluation were speed of flushing, length of growing season, height growth, and needle elongation.

LITERATURE REVIEW

Dormancy Phases and Survival Potential

Apical Dormancy Cycle

Dormancy is defined here, in accordance with Samish (1954), as
the absence of growth, without regard to the cause of such absence.
Growth refers only to an irreversible increase in volume of a cell,
tissue or organ; and is distinct from development, those processes
contributing to changes in plant function with time. Although stem
elongation in coniferous species commonly has ceased by the first
week of July, development within the apical bud may actually accelerate
at that time. Marked increases in meristematic activity over those
occurring during spring burst have been observed in Douglas-fir
(Sterling, 1946; Owens and Molder, 1973) and ponderosa pine (Sacher,
1954). The meristem produces a succession of leaf primordia which
remain within the bud scales until the following spring.

Initiation of apical dormancy during July and August is prob-
ably the result of interactions between photoperiod, soil and air temp-
eratures, availability of nurtients, and availability of moisture
(Perry, 1971). Early dormancy can be induced in Douglas-fir by short
photoperiods, low night temperatures, and dry soils (Lavender, Ching,
and Hermann, 1968). Endogenous rhythms may also play an important
role in dormancy induction (Weiser, 1970).

Dormancy is a continuous phenomenon, grading gradually from a
period in which growth cessation is easily reversed by making the
environment more favorable to growth into a period where growth will
not occur in response to favorabe conditions (Vegis, 1964). Growth
will only recommence in response to environmental signals different
from those normally associated with spring growth. Specifically,
numerous studies have shown that woody species native to temperate
zones require a period of winter chilling to break dormancy and resume
normal shoot growth (Romberger, 1963; Wareing, 1969). Once this period
of chilling has been received the seedling will once again grow in

response to warm temperature and adequate precipitation. However, if these condition do not prevail at the time of completion of chilling requirements, the seedling remains dormant.

Wareing (1969) gives the length of the chilling requirement for many species as 260-1000 hours at 0-5°C. These are uninterrupted hours of chilling. Trees subjected to fluctuating outdoor temperatures may require considerably longer exposure to low temperatures to break rest than would be required if low temperatures were constant (Bennett, 1950; Nienstaedt, 1967). Most of the chilling requirement of trees in the northern temperate zone may be met by the end of December. Additional exposure to cold in January and February will accelerate renewal of growth when trees are transferred to a warm greenhouse (Perry, 1971).

The chilling requirement of ponderosa pine has not been reported in the literature. Wommack (1964) found that 1300 to 2000 hours of temperatures constantly between 3 and 6°C were necessary to satisfy the chilling requirements of Douglas-fir. Van den Driessche (1975), in British Columbia, reported that under fluctuating temperature conditions outdoors, 2,500 to 3,000 hours below 4.4°C were necessary to fulfill Douglas-fir's chilling requirement.

Depth of Apical Dormancy

Although apical dormancy is best viewed as a continuous phenomenon, dividing it into phases allows one to relate these phases to other phenomena, such as physiological fitness for planting. A first division is to divide dormancy into periods in the summer and early spring when growth is stopped because of unfavorable external conditions, and into a period in the fall and winter when an environmental signal such as chilling is required for normal growth to resume. Samish (1954) calls the fall and winter period rest and the other periods quiesence. Rest in turn is divided according to depth into preliminary, middle, and after rest. During preliminary rest the dormant bud will no longer grow in response to favorable conditions but can be "forced" by subjection to heat, wounding, or similar

stimuli. During middle rest only the most drastic treatments will stimulate response. Growth response is more easily stimulated during after-rest.

Samish states that preliminary and after-rest periods have much in common. In contrast, Smith and Kefford (1964) prefer to divide dormancy into phases which emphasize the differences between development of and release from deep dormancy. Dormancy is divided into three phases separated by three transitions. The transitions are:

1. Dormancy development leading to the dormant steady state or deep dormancy.

2. Release from the dormant steady state leading to the post dormant state and spring bud-burst.

3. Initiation of spring burst leading to a spring growth phase.

Whether one uses the classification of Samish or of Smith and Kefford, some measure of depth of rest is helpful. Depth of rest can be judged in part by the amount of the chilling requirement which remains unfulfilled. This has been judged by observing the number of days required for a seedling to flush in a favorable environment. Campbell and Sugano (1975) emphasize that the chilling requirement determined in this manner can be considerably modified by the temperature and photoperiod of the test environment. In some, but not in all, coniferous species, long photoperiods can substitute in part for the chilling requirement. This has been demonstrated for Douglas-fir (Lavender and Hermann, 1970; Roberts et al., 1974; Van den Driessche, 1975).

Depth of rest has also been judged by comparing flushing activity in a favorable environment of the terminal bud, laterals on the terminal shoot, and laterals on the remainder of the seedling. Nigond (1966) found that breaking of dormancy in grape vines corresponded with disappearance of flushing speed differences between basal and terminal buds. Such a pattern was noted by Roberts et al. (1974) in Douglas-fir.

Cambial Growth Cessation

Cambial growth in coniferous species generally continues after
terminal shoot elongation stops. Emmingham (1977) compared cambial and
leader growth of Douglas-fir saplings in four western Oregon environ-
ments and found that leader growth stopped in August long before cam-
bial growth which continued into October. There is considerable de-
bate over whether the lateral cambia of coniferous species have a chil-
ling requirement. Little and Bonga (1974) found that chilling in-
creased cambial activity of cuttings of Abies balsamea collected in the
field between September and December but not of seedlings collected
later. This effect was manifested whether or not buds were present.
They concluded that the cambium of balsam fir has an autumnal rest
period. Lavender et al.(1970), Worrall (1971), and Timmis and Worrall
(1974), however, found that chilling of buds alone was sufficient to
break rest of the cambium of Douglas-fir, and concluded that the cam-
bium does not have its own rest.

Physiological Fitness for Planting

Studies of survival, root-regeneration potential, root exposure
tolerance, and frost hardiness together provide circumstantial evid-
ence that fitness for planting increases as the seedling has its chil-
ling requirement fulfilled and leaves deep dormancy. The most perinent
of these studies are summarized below.

Stone and Schubert (1959) lifted ponderosa pine seedlings every
fifteen days from September 15 through December 1, and replanted them
in a greenhouse after zero, one, two, and three months of cold stor-
age. Seedling survival after storage improved after each two week
delay in lifting until November 1. After this date, there was no sig-
nificant improvement. Reduction in survival with storage was most
evident when the pine was lifted before October 15. When seedlings
were lifted before November 1, root regeneration following cold stor-
age was significantly reduced by each month of additional storage.
Root regeneration potential is an important survival factor; one of the
major causes of failure immediately after planting is dessication.

Stone et al. (1962) found that Douglas-fir also exhibited a marked seasonal periodicity in root-regeneration potential. Root-regeneration potential was low during the summer, rose abruptly in September, was high during the winter months, and dropped off sharply in April when new top growth began.

Winjum (1963) lifted Douglas-fir seedlings from October through April. Seedlings planted immediately showed little difference in survival due to lifting date. Storage for four weeks resulted in significantly lowered survival of stock lifted in October, April, and May.

Lavender (1964) reported that Douglas-fir seedlings were adversely affected by lifting prior to December or after buds began to swell in the spring, particularly when such lifting was followed by cold storage. Seedlings lifted prior to December showed a poor ability to regenerate roots when placed in a favorable environment. Bud-burst and growth of shoots of a separate sample placed under favorable long days was poor during this pre-December period. This observation indicates that the period of poor survival and root regeneration for Douglas-fir may correspond with its period of middle rest or dormant steady state. Lavender proposed that the disruption of seedling physiology caused by lifting at this time was due to aberration of the balance of growth promoting and growth inhibiting hormones in the seedling. Detailed studies of the regulation of growth potential of Douglas-fir seedlings during dormancy later supported this hypothesis (Lavender and Hermann, 1970).

Further research by Lavender and Wareing (1972) confirmed the deleterious effects of fall lifting and storage of Douglas-fir. These studies demonstrated that increased resistance to stress conditions after December was dependent upon exposure to short days and chilling for several weeks. These authors concluded that chilling can considerably increase both root growth and root regeneration capacity as well as overcome bud dormancy. Hermann (1967) found a distinct increase between early November and late January in tolerance of Douglas-fir seedlings to root exposure. This increase was accentuated when seedlings were stored.

Van den Driessche (1977) reported that no provenances of Douglas-fir tested survived storage well in a non-hardy condition. However, a large portion of the variation in survival could not be accounted for by hardiness differences alone.

Roberts et al. (1974) demonstrated that rooting ability of Douglas-fir cuttings was inversely related to intensity of bud dormancy. During September and October rooting treatments of any type had very limited success. Response of cuttings to auxin treatment rises greatly in November before sufficient chilling has been received for normal bud break under short days. In December bud break begins under short days and cutting success without auxin also begins to increase.

Electrical Detection of Changes in Shoot Physiology

Plant Tissue As An Electrical Circuit

Since the early recognition of the value of electrophysiological measurements in medicine, the electrical characteristics of both animal and plant tissues have been examined in some detail. The picture which has emerged, however, is not well integrated and is far from complete.

When a direct current is passed through a cell, the resting potential of the cell takes on a new value. The ratio of the amount of change in potential to the amount of current applied is known as resistance. The inverse of resistance, conductance, is a measure of ion permeability.

Living cell membranes have high resistances (Hayden et al., 1969). Membranes act as capacitors, however, and alternating current may bypass these high resistances. Membranes are not perfect capacitors; some current may flow directly across their surfaces (Williams et al., 1964).

The resistance a capacitor offers to current flow, called reactance, decreases with increasing frequency. Reactance also decreases as capacitance, or ability to store charge, increases. The capacitances of most animal and plant membranes examined to date are about

the same per unit area, 1-2 microfarad cm.$^{-2}$ (Cole, 1970).

The combined effect of resistance and reactance in opposing alternating current flow in plant tissue is referred to as impedance. Reduction of impedance of plant tissue upon exposure to killing agents has frequently been observed. Osterhout (1922) attributed a drop in low frequency impedance of tissue in water of high electrolyte content to changes in cell membranes. The permeability of the membrane was believed to have increased with injury. Luyet (1932) also observed that impedance of plant tissue decreased upon injury. He further noted that the decrease was much greater at lower frequencies than at higher frequencies. Rothschild (1946) considered this differential frequency response to be indicative of injury changing membrane resistance. At low frequencies, the capacitance of the living cell membrane limits current flow; cytoplasmic resistance is relatively unimportant. At high frequency capacitance of the membrane no longer severely limits conductivity and the effect of cytoplasmic resistance becomes paramount. When the tissue is killed, membrane impedance to ion flow drops drastically, while cytoplasmic resistance is relatively unchanged. As a result, high and low frequency responses become more similar. Rothschild's research was with animal tissue. His theories can be extended to plant tissue if cell walls have the characteristics of cytoplasm. Cell walls have been attributed a resistance greater than that of the cytoplasm, but still considerably less than that of membranes (Hayden et al., 1969).

De Plater and Greenham (1959) proposed use of differential frequency response to determine injury and death in plant tissue. The ratio of the parallel resistance component of impedance at low frequency (1 khz) to that at high frequency (1 Mhz), called the resistance ratio, was comparatively high in healthy tissue. In some cases this ratio increased with initial injury, but it always decreased with further injury to give a value of approximately one at death.

Working from estimates of specific impedance of vacuoles, intracell wall fluid, and cell membranes, Fensom (1966) concluded that resistances measured at very low frequencies (60-100 hz) are normally due to resistances of cell wall fluids. At higher frequencies, the

contribution of membranes to resistance is highly variable, and the
path of current can no longer be easily ascertained. Resistance due
to cell wall fluids depends upon the concentration, mobility, and
charge of ions in these fluids. Hayden et al. (1969) also concluded
that it is changes in cell wall fluids that are detected when low
frequency currents are used. On the assumption that cells in a tissue
are like many small capacitors-resistors in parallel, they presented
a simple model of the electric circuit of plant tissue. These authors
were able to explain the frequency responses of alfalfa and potato
tissues on the basis of this model. Other researchers (Glerum and
Krenciglowa, 1970; Evert, 1973) have pointed out that this simple
model cannot adequately represent the observed impedance frequency
relationships of the more highly differentiated stems of woody plants.

Despite inability to interpret the exact character of electrical
properties being measured in plant tissue, it is clear that these
measurements can give an indication of the vitality of that tissue.
Ratios of response at two frequencies would be expected to give the
most promising results. Use of ratios allows for greater investigation
of circuit character and minimizes the effect of extraneous variables,
such as diameter. Greenham and Daday (1957), Glerum (1970), Evert and
Weiser (1971), Evert (1973), and Timmis (1976) have successfully used
impedance ratios to detect damage due to boiling and freezing.

In electronics, the response of a circuit to a wide range of
frequencies is often indirectly tested by observing modification of a
square wave voltage signal passed through the circuit. A circuit
reacts to a square wave as if it were alternating not only at the
applied or fundamental frequency but also at the frequencies of all
harmonics of the fundamental frequency. Voltage is displayed as a
function of time on the screen of an oscilloscope. Higher frequency
responses appear close to the leading edge of the wave trace. Zaerr
(1972) showed that modification of the appearance of the leading
edge could be used to detect killing of needle tissue of Douglas-fir,
pine, and other woody species by freezing, steaming, or treatment with
an herbicide. A trace from healthy tissue had a decidedly spiked
leading edge. A trace passed through dead tissue had a very rounded

leading edge. Under certain conditions partially injured tissue could be detected by a trace with a character between that from living and dead tissue. Zaerr's technique is commonly referred to as the "oscilloscope technique".

Electrical Detection of Seasonal Changes in Shoot Physiology

Development of a quick accurate system for evaluating frost hardiness has been the major thrust of research concerning electrical detection of seasonal changes in woody shoot physiology. Woody species become dormant at approximately the same time of the year that frost hardiness begins to develop (Perry, 1971). For this reason, the assumption is often made that dormancy and frost hardiness are causally connected, specifically that a tissue most be dormant to become frost hardy. Evidence to the contrary has been presented by Irving and Lanphear (1967) for box elder (Acer negundo) and viburnum (Viburnum plicatum) and by Timmis and Worrall (1975) for Douglas-fir. In any case, one would expect that an electrical method which could detect frost hardiness development might do so in part by detecting physiological changes attributable to dormancy development.

Wilner has conducted a series of investigations in which a probe with two electrodes is inserted into the stem of a tree in situ. Resistance of apple stem tissue to direct current increased as the growing season advanced from summer into fall. Resistance measurements on three varieties of apples appeared to reflect the hardiness ratings of the varieties (Wilner, 1964, 1967). During the winter, the resistance of detached shoots or of shoots with frozen roots was lower than that of normally grown shoots. This suggested that the measurement may have use as a viability test (Wilner, 1967). Wilner and Brach (1974) reported that resistance of roots and ratios of shoot to root resistance were correlated with hardiness differences among rose species. These relationships did not hold in the spring when the roots were dehardened and growing.

Weaver et al.(1968) assessed winter-hardiness in peach cultivars using impedance (1 khz). They found impedance to be closely

related to established levels of hardiness for the cultivars. However, a significant relationship was also found between hardiness and stem diameter. Svejda (1970) discounted Weaver's results because they were confounded by these diameter differences. Svejda could not find any relationship between impedance and winter-hardiness in rose cultivars tested. Magnitude of impedance appeared to characterize certain plant genotypes, however.

Noting that diameter, electrolyte concentration and other variables appear to influence resistance measurements, Evert and Weiser (1971) used a ratio of conductance (more properly termed admittance) at two frequencies in their acclimation study. They found that a ratio of admittance at 50 hz to that at 100 khz could be used to predict cold hardiness of stem sections of dogwood (Cornus stolonifera) during the first stages of cold acclimation. After the dogwood was exposed to nonlethal frost, hardiness increased rapidly, and the relationship between hardiness and admittance ratio no longer held. These authors interpret this breakdown as indicative of significant physiological alterations being induced in stem tissue by ice crystalization.

Van den Driessche has used both conductivity of stem diffusate and impedance of stems in situ to assess frost hardiness in Douglas-fir seedlings. In early investigations both conductivity of diffusate and impedance of stems to a 4.5 khz square wave were well correlated with the hardiness of the fir (Van den Driessche, 1969). In an attempt to minimize confounding effects of stem diameter, later hardiness tests were conducted using a ratio of impedance at 1 khz to impedance at 1 Mhz (Van den Driessche, 1973). Postfreezing measurements of this ratio adequately paralleled seasonal changes in frost hardiness. The ratio peaked in January as did frost hardiness. Correlation between this impedance ratio and environmental temperatures provided further circumstantial evidence that the ratio detects hardiness. Pre-freezing measurements, although they generally showed a positive relationship between impedance and hardiness, did not predict survival of individual plants with the accuracy of post-freezing measurements.

Van den Driessche (1976) has advocated use of impedance measurements to determine lifting date. He bases this recommendation on the belief that, for all practical purposes, frost hardiness, root growth capacity, and root exposure tolerance are all positively correlated in Douglas-fir.

Glerum (1973a) noted that annual trends in impedance for seven coniferous species were similar to those in frost hardiness. A high impedance was associated with a high degree of hardiness, and a low impedance with a low degree of hardiness. Impedance increased gradually in the fall as did frost resistance; in the spring impedance decreased rapidly as did frost hardiness. Larch had a more gradual impedance trend than spruce; this was consistent with its more gradual frost hardiness trend. Glerum expressed doubt that impedance measurements could be used to compare frost hardiness of different species or even of strains within a species. Ratios have potential only for comparing seasonal trends in hardiness in one species with those in another.

Polozhentsev and Zolotov (1970) investigated seasonal changes in impedance of bast tissues of forty year old pine trees. They found that impedance (1 khz and 10 khz) was lowest upon emergence of trees from dormancy at the end of March and increased gradually until the end of August. As dormancy is entered, this rise in impedance steepens. The criteria used for judging entry and exit from dormancy were not given, and it is possible that these events were inferred from time of the year alone. Trees which were artificially traumitized (pruning, root girdling, etc.) had lower maximum impedance than healthy trees. This was attributed to these trees being less able to prepare themselves for winter.

In investigating the possibility that electrical potentials could be used to detect the presence or absence of female flower buds of slash pine (Pinus elliottii) prior to their emergence, Asher (1964) noted that these potentials were significantly related to the geographic distribution of the pine. He hypothesized that higher potentials from trees in the center of the range may have indicated higher metabolic activity among these trees. Trees from this range had been

shown to grow faster in early youth. Although not offered as an hypothesis by Asher, it is possible that differences related to growing season and dormancy were what was detected.

Dykstra (1974) noted positive correlation between impedance and survival and between impedance and root regeneration potential of lodgepole pine. All increased the later the lifting from mid-August through mid-November. Dykstra did not test these relationships statistically, however. Also all seedlings were placed in storage when lifted and left there until May. Storage was therefore greater for the earlier lifted seedlings. Relating Dykstra's results to lifting date alone is not possible.

Ferguson et al. (1975) proposed using the oscilloscope technique of Zaerr (1972) to detect dormancy in seedling shoots. They observed seasonal changes in square wave form which appeared to coincide with periods of dormancy and periods of activity. At the time of the year when seedlings are generally believed to be dormant, the square wave was observed to pass through stem tissue essentially unchanged in form although decreased in amplitude. If the seedling was actively growing, the trace peaked on the leading edge. No attempt was made in this study to actually pinpoint the span of dormancy by growth room or other tests. What is presented is no more than a calendar trend and a hypothesis to explain that trend. Recently, the Missoula Equipment Development Center of the Forest Service, USDA (1977) concluded from analyzing frequency sweeps from 50 hz to 20 khz that a ratio of voltages at 500 hz and 10 khz gives basically the same information as the oscilloscope technique used by Ferguson et al.

MATERIALS AND METHODS

Part I: Investigation of Relationship Between Oscilloscope Trace
Characteristics and Depth of Dormancy

Experimental Material

Three-year-old potted Douglas-fir (seed source near Roseburg,
Oregon, 270-1.5) and two-year-old potted ponderosa pine (seed source
near Klamath Falls, Oregon, 702-5.0) were used in this experiment.
These seedlings had been transpanted to their pots more than five
months before measurements began. This assured that transplant shock
did not confound experimental results. Seedlings with either poor
or exceptionally good growth, and seedlings that flushed late in the
spring of 1976 were not chosen for the investigation.

The seedlings were placed in a lath house at Corvallis, Oregon,
in mid-June, 1976. At that time populations of both the fir and the
pine were split into stressed and non-stressed moisture regimes. The
stressed seedlings were watered a small, measured amount whenever their
pre-dawn plant water potential reached -20 atm. The fir reached -20
atm. on July 9, July 23, August 2, August 25, and September 4; and
were at -14 atm. when stress was terminated on September 14. The
stressed pine reached a -20 atm. on July 14, August 5, August 26, and
September 15. Stress was terminated September 16. The non-stressed
fir and pine treatments were maintained at greater than -5 atm. pre-
dawn water potential until August. In August pre-dawn potential was
allowed to fall to -7 to -11 atm. before the seedlings were watered.
Thus the treatments were not very dry versus very wet. They were
rather a dry treatment and an intermediate treatment. This intermed-
iate treatment is that recommended for forest nursery practice
(Lavender and Cleary, 1974).

Determination of Cambial Growth Cessation

The cambial scarring technique of Wolter (1968) was used to
determine presence or absence of cambial activity. Forty each of the

moisture stressed and non-stressed fir and thirty-six each of the stressed and non-stressed pine formed the samples. From August 30, 1976, to December 12, 1976, the cambium of each of these seedlings was minutely injured by inserting a small (size 00) insect mounting pin horizontally through the bark and into the cambial zone. Every seedling was pricked bi-weekly on the lower part of the stem. The samples were divided so that in any one week, one-half of the trees in each sample were scarred.

If the cambium was active, the injury given by pin insertion caused aberrant cells to form; these cells were permanently retained as a mark within the annual ring. A record was obtained of cambial activity without deleterious effects on the seedlings. This record was examined in February. The Douglas-fir seedlings were examined by making a smooth cut across the stem about one mm. from each pin, and then observing the cut surface through a Ziess WL microscope with epi-illumination. For ponderosa pine a thin cross section was made about one mm. from the pin. This section was stained with safranin 0 and fast green dyes and observed under the microscope. The cambium of the fir and pine was considered active if any wound tissue was present or if any phloem cells showed any other marked change due to pin insertion. One-way analysis of variance was used to determine if there were significant differences in mean date of cambial growth cessation between moisture regimes of each species.

Determination of Depth of Apical Dormancy

Speed of flushing in a favorable environment was used as the means of judging depth of dormancy. Sixteen stressed and sixteen non-stressed fir were sampled on August 26, October 10, November 14, December 29, February 12, March 18, and April 20. Nineteen stressed and nineteen non-stressed pine were sampled on July 18, September 2, October 24, December 1, January 28, March 16, and April 14. The seedlings were placed in a controlled environment chamber where long days (18 hours) were maintained. Illumination of 8600 lx. at the level of the fir terminal bud and 6500 lx. at the level of the pine terminal

bud was provided by a combination of warm white florescent tubes and incandesent bulbs. Maximum light period temperature was 27°C and the dark period minimum was 20°C.

Observations on the fir were of flushing of the terminal and lateral buds. Laterals were classified by position. It was noted whether they were on the leader of lower on the seedling. Observation of laterals terminated after eight weeks unless none had flushed. If none had flushed, the laterals were observed until one of each kind flushed or for fourteen weeks, whichever was the shorter time period. The lateral flushing activity of the fir was summarized in two ways:

1. Mean time required for the first lateral on the leader and the first lateral below the leader to flush were calculated for each moisture regime sample on each date.

2. Total number of buds greater than 3 mm. in length on each seedling was tallied. For each seedling the percentages of total buds flushed at 0, 1, 2, 3, 4, 5, 6, 7, and 8 weeks in the growth chamber were calculated.

Fir terminal bud activity was observed for fourteen weeks. If the terminal bud had not flushed in fourteen weeks, it was, for statistical purposes, given a flushing speed of fifteen weeks. This was the case with five of the thirty-two fir seedlings sampled August 26; on the other dates all of the seedlings flushed within fifteen weeks. Mean number of weeks to terminal flushing was determined for each date/ moisture regime combination. These data were analyzed for date and moisture regime differences using a two-way analysis of variance and ranked LSD tests.

Diameter of the terminal shoot at the point of insertion of the electrode connected to the oscilloscope input was recorded for each seedling. The possibility of a linear relationship between terminal shoot diameter and flushing speed was investigated.

Means for speed of flushing of lateral buds on the leader, lateral buds below the leader, and the terminal bud were compared using paired T-tests. The goal of this comparison was to determine if the position effect described by Nigond (1966) could be detected.

Pine terminal bud observations were made and analyzed in the same

manner as fir terminal bud observations. No observations were recorded for pine laterals. Elongation of needles on the terminal shoot in the growth room was recorded.

Terminal bud burst in the spring of 1977 in the natural lath house environment was tallied for samples of twenty stressed and twenty non-stressed fir and twenty stressed and twenty non-stressed pine. With each species, a one-way analysis of variance was used to determine if mean date of flushing for seedlings in the two moisture regimes differed.

Oscilloscope Measurement Technique

Before a seedling was used in the depth of dormancy tests on any date, its electrical impedance properties were measured using Zaerr's oscilloscope technique (Zaerr, 1972). The measuring circuit contained the following: a signal generating device, the square wave generator; a signal meauring and recording device, the oscilloscope; and the source of the signal recorded, the electrode probe with plant tissue. This circuit is illustrated schematically in Figure 1.

The electrode probe was constructed of four stainless steel surgical needles approximately 0.6mm. in diameter below their tapering points. These were embedded in a straight line in a plastic block. Spacing between needles was one cm. This electrode is similar to that described by Ferguson et al. (1975). The only difference is that the needles are at a spacing of one rather than 0.66 cm. One cm. spacing was used based on research of Glerum and Zazula (1973) who found that contact resistance due to electrode polarization was minimal if electrodes were spaced at least one cm. apart.

The electrode probe was inserted through stem tissue in situ in the manner shown in Figure 1. The electrodes were pushed through the center of the stem until the tapering ends of the needles were just exposed on the other side of the stem. A separate investigation with pine indicated that positioning of the twig on the electrode could slightly affect trace form. For this reason consistency in positioning was considered important.
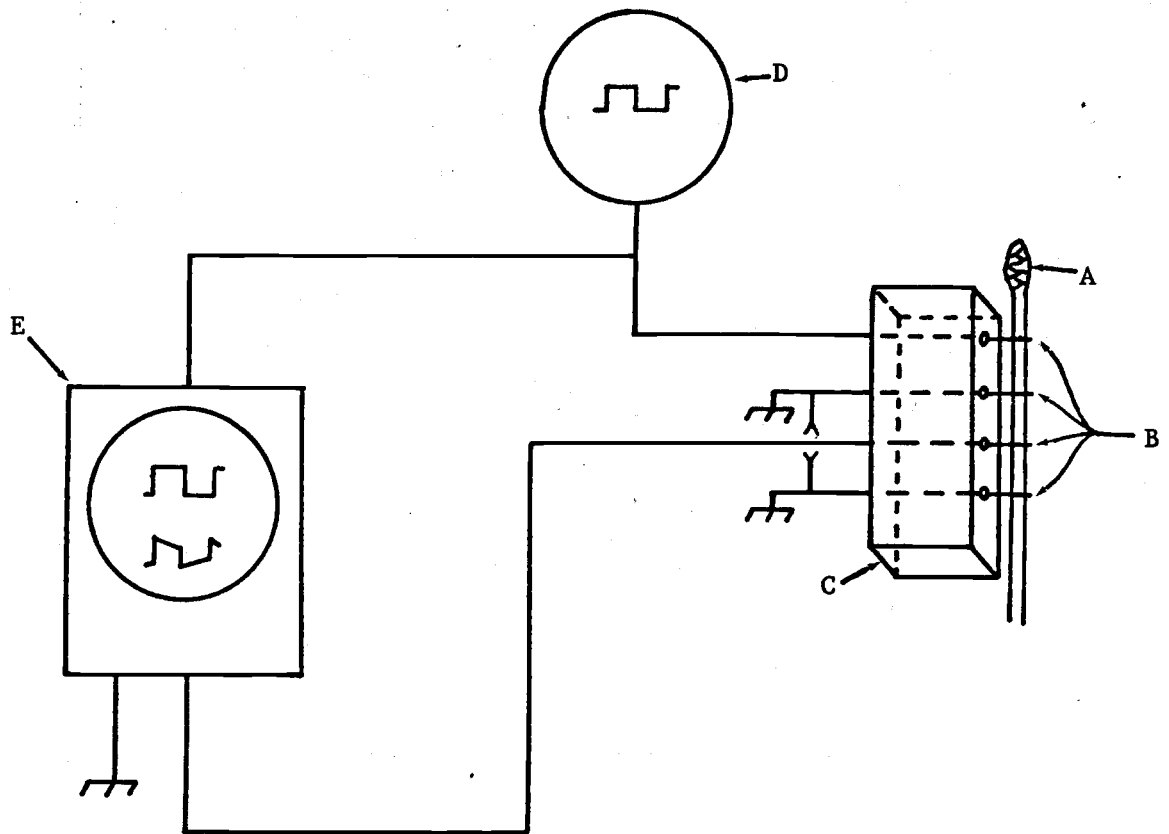
Figure 1. Schematic diagram of measuring circuit: A, terminal shoot
of seedling; B, stainless steel electrode pins; C, plastic
block; D, square wave generator; E, dual trace oscilloscope.

A Wavetek Model 30 generator supplied a 4.5 V square wave signal with a frequency of 850 hz to the first electrode of the probe. The output signal from the probe was measured by a Tektronix model 564 storage oscilloscope. This oscilloscope had a dual trace amplifier which allowed both the square wave input directly from the generator and the modified signal from the electrode to be displayed (Fig. 2a). Both of these signals were photographed for every seedling probed. It was thus possible to confirm that the input signal and oscilloscope amplification were the same in every case. The storage capacity of the display mode made it possible to photograph the electrode signal as it appeared within one minute after application of the square wave to the stem tissue. A Tektronix polaroid camera specifically designed for photographing oscilloscope displays was used for all photos (Fig. 2b).

The seedlings were allowed to come to room temperature (26°C) before measurements began. Investigations of Hayden (1968) and Glerum (1969) show that temperature can have a significant effect on impedance readings.

Glerum and Krenciglowa (1970) and Evert (1973) have shown that stem diameter also can markedly affect impedance readings. This diameter dependence is due not only to amount of tissue on the electrode but also to different sized stems containing different proportions of bark and xylem tissue. The possibility of diameter confounding results in this study was dealt with in two ways. First, the seedlings used were selected to be as uniform in size as possible. Second, diameter at the point of insertion of the electrode connected to the oscilloscope imput was recorded for each seedling and used as a covariable in statistical analysis whenever this appeared necessary.

Analysis of Trace Characteristics

The oscilloscope technique has been proposed as a simple visual means for the nurseryman to detect dormancy. It is evaluated herein as such. Measurements on the traces had to be both easily understood and objective. Measurements of "heights" at points along the trace at various distances from the leading edge proved most suitable. These
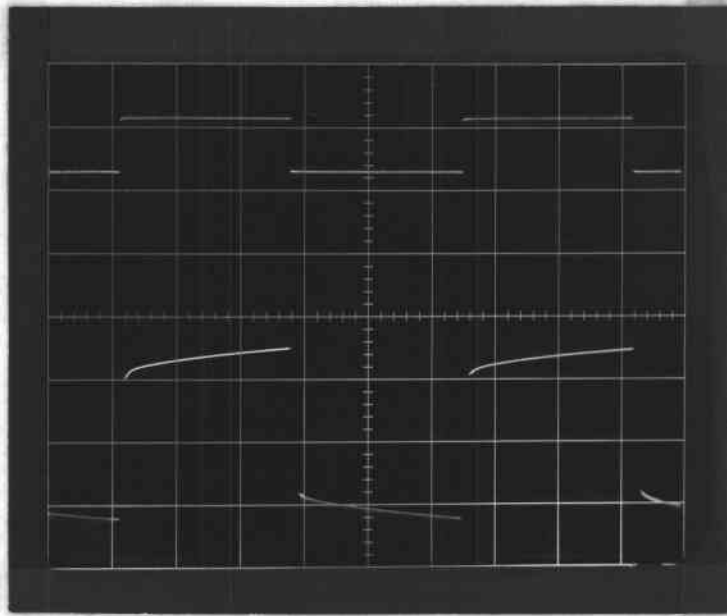
a.   Dual trace storage display.
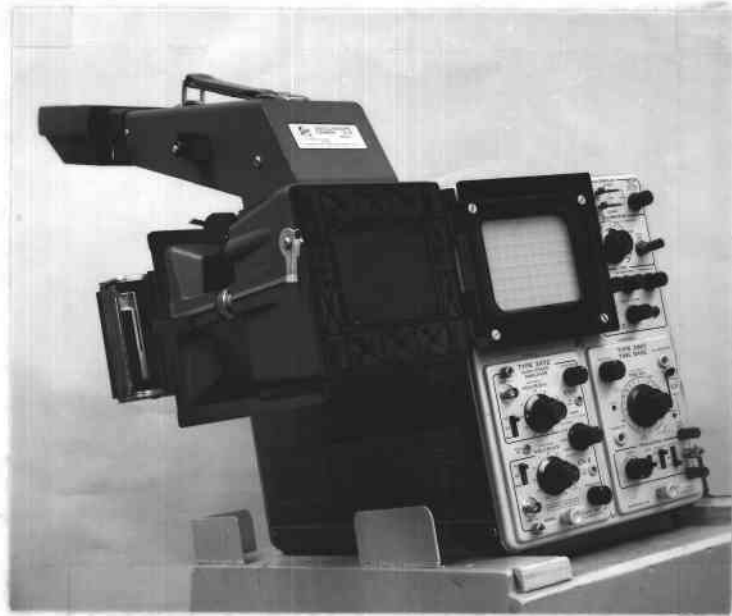
b.   Camera mounted on oscilloscope.

Figure 2.   Oscilloscope used.

are in effect voltage measurements taken a specific amount of time after the signal changes direction.

The number of voltage measurements which must be taken on a trace depends upon the number of points at which slope of the trace form changes magnitude significantly and/or changes direction. For both the fir and the pine three voltage measurements sufficed to characterize a trace (Fig. 3). These measurements were:

1. For the fir and the pine: the greatest voltage in the first 0.039 msec. of the trace. This will be referred to as high frequency voltage or HFV.

2. For the fir: the voltage after a time interval of 0.170 msec. For the pine: the voltage after 0.118 msec. This will be referred to as mid frequency voltage or MFV.

3. For the fir and the pine: the voltage at the trailing edge of the trace (at 0.588 msec.). This will be referred to as low frequency voltage or LFV.

Measurements on the photos were made using an illuminated magnifier and a caliper calibrated in hundredths of a mm. Precision of measurement was to within 0.0012 V.

The three voltage measurements were used in two ways:

1. On the basis of differences between HFV and MFV, MFV and LFV, and HFV and LFV, each trace was placed in a form class. The classes and how they were determined are indicated in Table 1. Typical Douglas-fir traces from each class are illustrated in Figure 4. The distribution of traces in these classes on each date was tabulated.

2. Ratios of HFV to MFV, MFV to LFV, and HFV to LFV were calculated for each seedling. A two-way analysis of variance was used to determine if there were significant differences in ratio means among dates and between moisture regimes. Differences between HFV and MFV, MFV and LFV, and HFV and LFV were examined to see if these presented different trends than the ratios. Trends in HFV, MFV, and LFV alone were also reviewed.
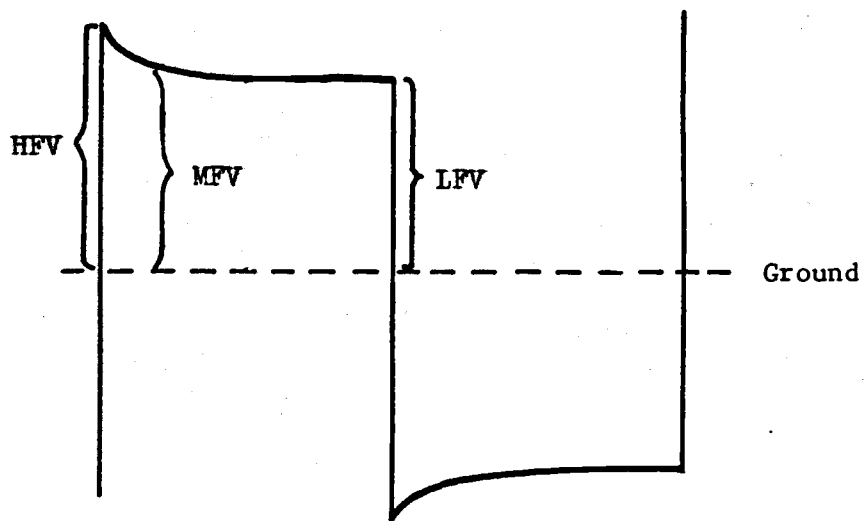
Figure 3.   Measurement of voltages at three points (HFV, MFV, LFV)
            on the oscilloscope trace.

CLASS		CRITERIA
II	HFV > MFV	HFV − MFV ≥ 0.0036 V
	MFV > LFV	MFV − LFV ≥ 0.0036 V
II	HFV > MFV	HFV − MFV ≥ 0.0036 V
	MFV = LFV	MFV − LFV > −0.0036 V and < 0.0036 V
III	HFV > MFV	HFV − MFV ≥ 0.0036 V
	MFV < LFV	MFV − LFV ≤ −0.0036 V
IV	HFV = MFV	HFV − MFV > −0.0036 V and < 0.0036 V
	MFV = LFV	MFV − LFV > −0.0036 V and < 0.0036 V
	HFV > LFV	HFV − LFV ≥ 0.0036 V
V	HFV = MFV	HFV − MFV > −0.0036 V and < 0.0036 V
	MFV = LFV	MFV − LFV > −0.0036 V and < 0.0036 V
	HFV = LFV	HFV − LFV > −0.0036 V and < 0.0036 V
VI	HFV = MFV	HFV − MFV > −0.0036 V and < 0.0036 V
	MFV = LFV	MFV − LFV > −0.0036 V and < 0.0036 V
	HFV < LFV	HFV − LFV ≤ −0.0036 V
VII	HFV = MFV	HFV − MFV > −0.0036 V and < 0.0036 V
	MFV < LFV	MFV − LFV ≤ −0.0036 V
VIII	HFV < MFV	HFV − MFV ≤ −0.0036 V
	MFV = LFV	MFV − LFV > −0.0036 V and < 0.0036 V
IX	HFV < MFV	HFV − MFV ≤ −0.0036 V
	MFV < LFV	MFV − LFV ≤ −0.0036 V

Table 1. Trace form classes. Class boundaries were set up to take into
account precision error. The maximum error in precision which
could occur with a difference measurement was 0.0036 V. If
such an error should occur, the seedling would still fall into
one of the squarer classes.

I   II   III   · IV   V   VI   VII   IX
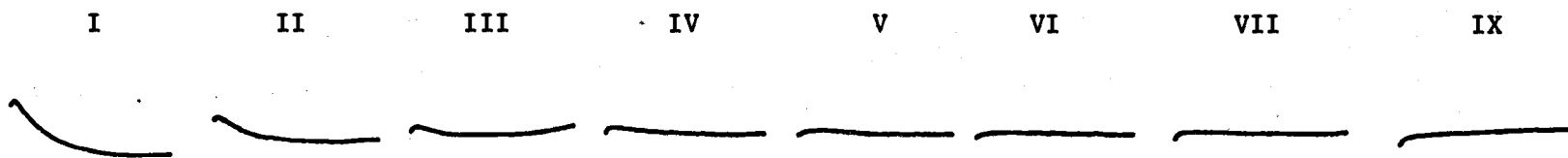
Figure 4.   Typical Douglas-fir trace from each trace form class.   There were no Douglas-fir in class VIII.

Testing for Correlation of Trace Characteristics and Depth of Dormancy

Regression analyses of trace and apical dormancy data proved un-
suitable. Over the period of observation, trace form peaked, dipped,
and peaked again, while speed of bud-burst in the growth room contin-
uously increased. These data were compared graphically. It was noted
whether or not significant changes in trace character corresponded with
significant changes in dormancy development, and whether or not trace
character changed greatly during the period in which cambial growth
ceased.

Testing for Correlation of Trace Characteristics and Temperature

Temperature was recorded on a Foxboro seven day thermograph
placed among the seedlings in the lath house. Mean maximum temp-
erature, mean minimum temperature, and hours below 4.5°C were deter-
mined for the two weeks previous to every sampling date after, but
not including, September 2. Voltage ratios and amplitudes for each
sampling date were regressed in turn on these temperature variables.

Observation and Analysis of Needle Traces

Trace form of a needle from the terminal shoot was also recorded
for every sample tree. A frequency of 100 hz. and a smaller electrode
probe were used for these measurements. Examination of photos revealed
no pronounced seasonal trends, and these traces were not analyzed in-
tensively. Unless stated otherwise, trace form referred to in this
thesis is that of stem tissue.

Part II: Investigation of Relationship Between Oscilloscope Trace
Characteristics and Seedling Survival Potential

Experimental Material

Two-year-old (2-0) Douglas-fir seedlings were lifted from one
uniform bed of a private nursery near Brownsville, Oregon. Seed source
was 471-2.5 (Willamette Valley, Ore.). Watering and fertilization

practices used with these seedlings were as recommended by Lavender
and Cleary (1974) for coniferous seedling production. Seedlings
lifted were between four and six mm. in diameter at ground level and
twenty to thirty cms. in height. Seedlings with either exceptionally
poor or exceptionally good root systems were not used.

Lifting Methodology

One hundred and eight seedlings were lifted on each of six
dates: October 11, November 10, and December 8, 1976; January 4,
February 8, and March 24, 1977. A pressure chamber apparatus was used
to determine the plant water potential of six seedlings in the bed on
each date. These seedlings were not lifted. This measurement was
done during the warmest part of the lifting period.

Storage Methodology

One-third of the seedlings lifted on each date were placed in
cold storage (3°C) overnight before planting; one-third were stored for
four weeks; and one-third were stored for eight weeks. Before placing
the seedlings in polyethylene bags, their tops were dried and their
roots wrapped in wet paper toweling. The seedlings appeared in good
condition when removed from storage.

Oscilloscope Measurement Technique

Twenty-four of the thirty-six seedlings in each of the eighteen
lifting/storage treatments were used for trace measurements on the day
of planting. The remaining seedlings were used for pre-dawn measure-
ments of plant water potential during the summer. Traces were recorded
after the seedlings were removed form the cold storage room and allowed
to equilibrate to room temperature (21°C). Trace form of the seedlings
stored overnight only was taken as trace form at time of lifting for
all three storage treatments on a given lifting date. It is doubtful
that this measurement differed much from one actually taken during
lifting. This methodology allowed complete control over environmental
variables during measurement. Measurement technique and trace analysis

were the same as used for Douglas-fir in Part I.

Planting Procedure and Design

The seedlings were planted in cold frames at Corvallis, Oregon. A randomized block design was used. Treatments were planted as rows of nine trees within the blocks. It was recognized that the cold frames would provide a more favorable moisture regime than that normally encountered in the field. Therefore, in an attempt to make the water stress encountered comparable to that in the field, the cold frames were covered with plastic whenever it rained after April 15. The seedlings received no rain or irrigation after this date, with the exception of the March 24 lifted/stored four weeks and March 24 lifted/stored eight weeks treatments which were watered when planted. Development of water stress was monitored by measurement of pre-dawn moisture stress.

Measurement of Growth and Survival Parameters

Growing season

Bud-burst of sample seedlings was tallied every three days. The date of flushing of the terminal bud and of the first lateral bud was recorded for every seedling. A bud was considered flushed when some green was visible through the scales. Set of terminal buds was tallied every four days. A bud was considered set when scale formation could be detected. Growing season for each seedling was determined by subtracting days to terminal bud-burst from days to bud-set. Analysis of variance was used to determine if there were significant differences among lifting dates and among storage treatments in the speed of flushing of the first lateral bud, speed of flushing of the terminal bud, and length of the growing season. The interaction of lifting date and storage was also tested in the analysis of variance.

Height-growth ratio

All treatments were lifted from the cold frames on September 15,

1977. At this time two measurements were made on each seedling:

No. 1. The length of the seedling from the cotyledon scar
to the node marking the end of the 1976 season's
growth.

No. 2. The length of the seedling from the node marking
the end of growth in 1976 to the tip of the terminal
bud (i.e. 1977's growth).

The ratio of measurement no. 1 to measurement no. 2 was recorded for
each seedling. An analysis of variance in this height-growth ratio
was carried out as with the growing season data.

Needle length

The length of four needles from the center of the terminal shoot
was recorded on September 12. These lengths were averaged and sub-
jected to analysis of variance.

Survival

The percentage of seedlings surviving and the percentage of
seedlings surviving undamaged were calculated for each block of each
lifting/storage treatment. A seedling was considered damaged if more
than two-thirds of its terminal shoot was dry and discolored. This
type of damage occurred during the winter months. A seedling was con-
sidered dead when greater than three-fourths of its foliage, including
the terminal shoot, was dry and discolored. The seedlings were sorted
by storage treatment, and an analysis of variance by lifting date was
performed on each storage set separately. This was dictated by the
lack of variance in the zero and four week storage treatments.

Correlation of Trace Characteristics With Growth and Survival

Both trace character at time of lifting and trace character at
time of planting were tested as indicators of potential seedling growth
and survival.

Correlation of trace form at time of planting with growth and survival

Correlations between ratios of HFV to MFV, MFV to LFV, and HFV to

LFV at time of planting and growth and survival were investigated. HFV, MFV, and LFV alone also were regressed on the response variables. Those trace variables which made the greatest contribution to reduction of residual variablity were determined. There were eighteen points per regression, the eighteen treatment means. Regressions which employed the individual data points, rather than means were also carried out to ascertain the degree of within sample variability.

The possibility that sorting in the trace form classes used in Part I would help predict placement in growth and survival classes was also examined. Strength of relationship was tested with chi square and gamma statistics. The value of gamma can be looked at as the probability of correctly guessing the ordering of a pair of cases on one variable once the ordering on the other variable is known (Nie et al., 1975).

Correlation of trace form at time of lifting with growth and survival

Regression analysis of trace characteristics at time of lifting with growth and survival parameters was carried out as with trace characteristics at time of planting. Use of classes did not promise to yield more information, and it was not employed.

RESULTS OF PART I

INVESTIGATION OF RELATIONSHIP BETWEEN OSCILLOSCOPE TRACE CHARACTERISTICS AND DEPTH OF DORMANCY

Results for Douglas-fir

Cambial Growth Cessation

The mean date of cambial growth cessation for Douglas-fir was October 31 (95 percent confidence interval: October 28 to November 3). Mean dates of cambial growth cessation for the two moisture regime treatments were not significantly different.

Growth Room Response of Terminal Bud

Weeks to terminal bud burst in the favorable growth chamber environment for Douglas-fir brought in on the seven sampling dates are presented in Figure 5. The August 26 sample took an average of eleven weeks to burst their terminal buds. Time to bud burst declined significantly between August 26 and October 10. The response of the October 10 and November 14 seedlings was statistically the same. A second significant decline in weeks to flushing occurred between November 14 and December 29. This was followed again by a period in which time to bud-burst decreased very slowly. Weeks to bud-burst fell significantly and relatively sharply between March 18 and April 20. Eighty percent of the seedlings brought into the growth room on April 20 already had swollen buds.

An analysis of variance of weeks to terminal bud-burst by sampling date and by moisture regime indicated differences between dates were highly significant (F prob. = .001), while differences between stress and non-stress moisture regimes were nonsignificant (F prob. = .684). Differences were biologically insignificant as well; mean weeks to terminal flushing never differed by more than two-tenths of a week between the two treatments on any date. Interaction of date and moisture regime was nonsignificant (F prob. = .458).
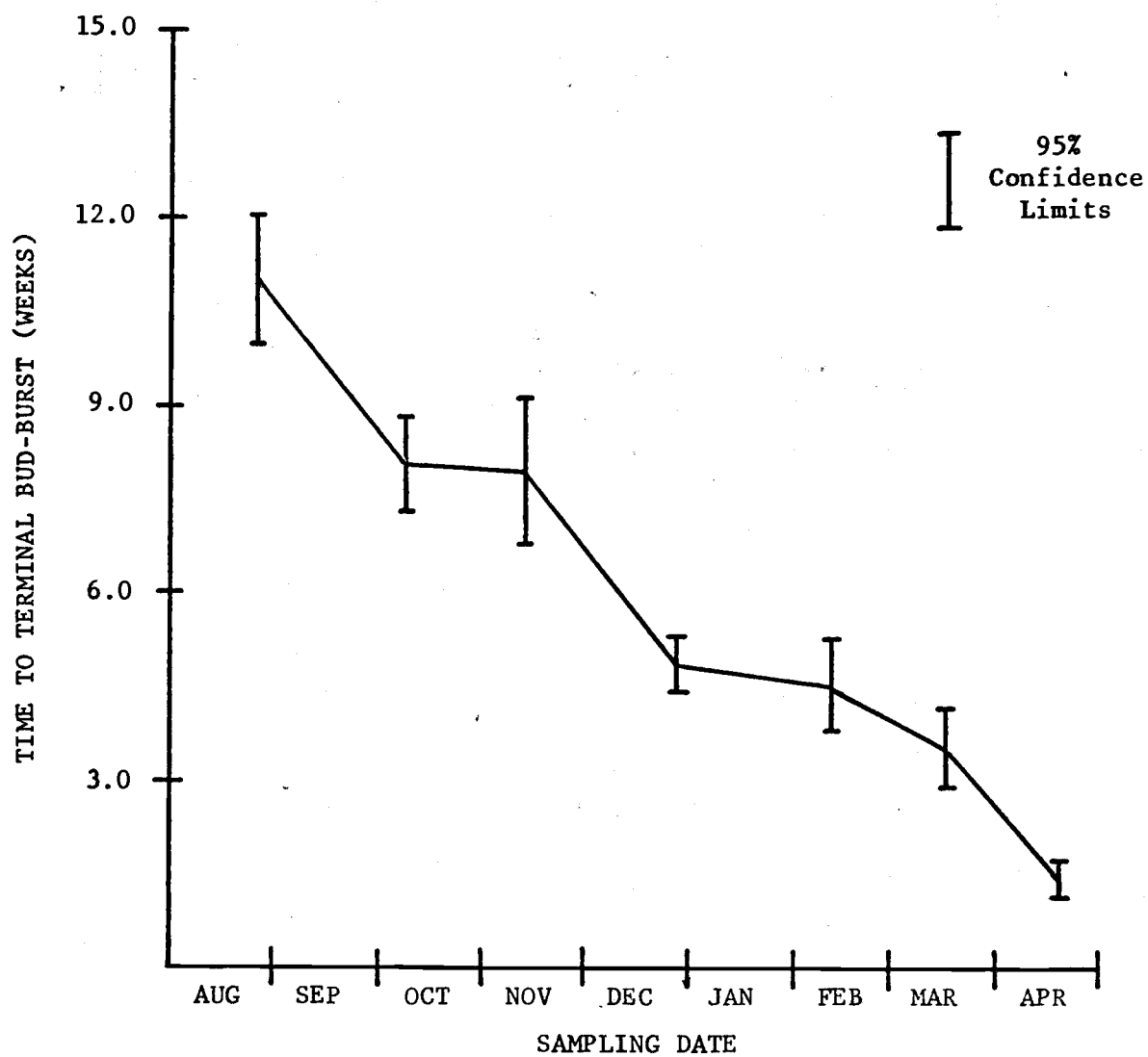
Figure 5. Time required for flushing of terminal bud of Douglas-fir seedlings brought into favorable long-day environment.

Further Observations on Stressed Versus Non-stressed Seedlings

Stressed Douglas-fir seedlings did not reach a pre-dawn water potential of -20 atm. until July 9. By this time bud-set in the lath house was completed, and no differences in this activity could be noted between stressed and non-stressed seedlings. There was little difference in second flushing behavior between stressed and non-stressed seedlings. A tally of second flushing on July 14 showed seven percent of the stressed seedlings second flushing versus nine percent of the non-stressed seedlings. In August second flushing did not occur in either treatment. Difference in bud-burst timing between stressed and non-stressed seedlings in the lath house in the spring of 1977 was not significant.

Growth Room Response of Lateral Buds

The first laterals to flush on the leader and below the leader demonstrated bud-burst trends similar to those for the terminal bud (Fig. 6). These lateral buds consistently flushed sooner than the terminal bud; the differences between the laterals and the terminal bud on all dates were statistically significant. Differences between buds in the three position, however, decreased greatly between November 14 and December 29.

Speed of flushing of all lateral buds on every seedling in a sample, expressed as mean percentage flushed by a given week, again indicated large increases in activity between August 26 and October 10 and between November 14 and December 29 (Fig. 7).

Seasonal Changes in Oscilloscope Trace Characteristics

Definite seasonal changes in trace form were found. The distribution of seedlings in trace form classes reveals a succession from traces which peaked on the leading edge on August 26 and October 10 to traces which became square or rounded by December 29 (Fig. 8). Traces began to peak again on February 12. By March 18 almost all traces peaked, and by April 20 the distribution in classes was almost identical to that of August 26.
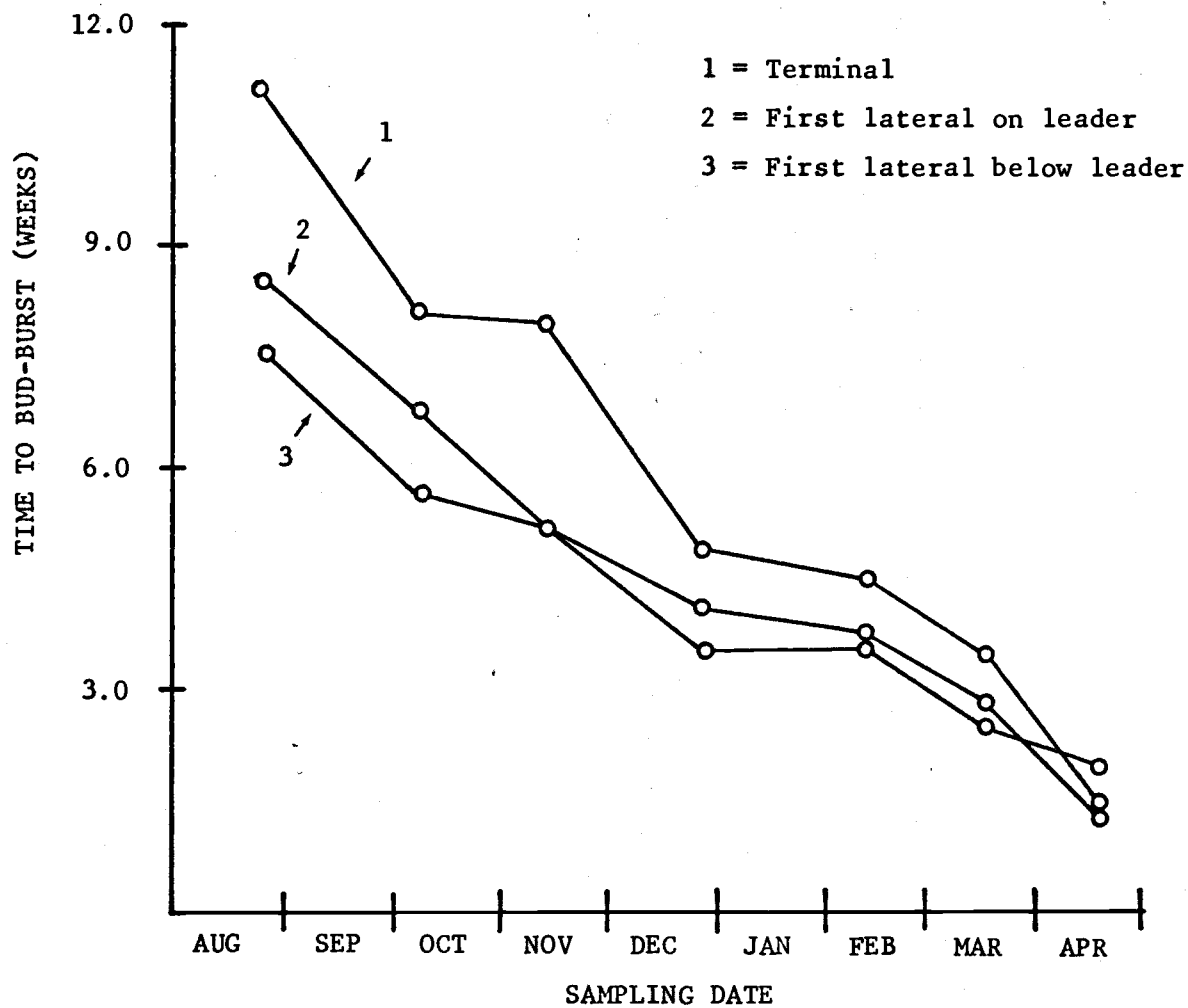
Figure 6. Time required for flushing of terminal and lateral buds of Douglas-fir seedlings brought into favorable long-day environment.
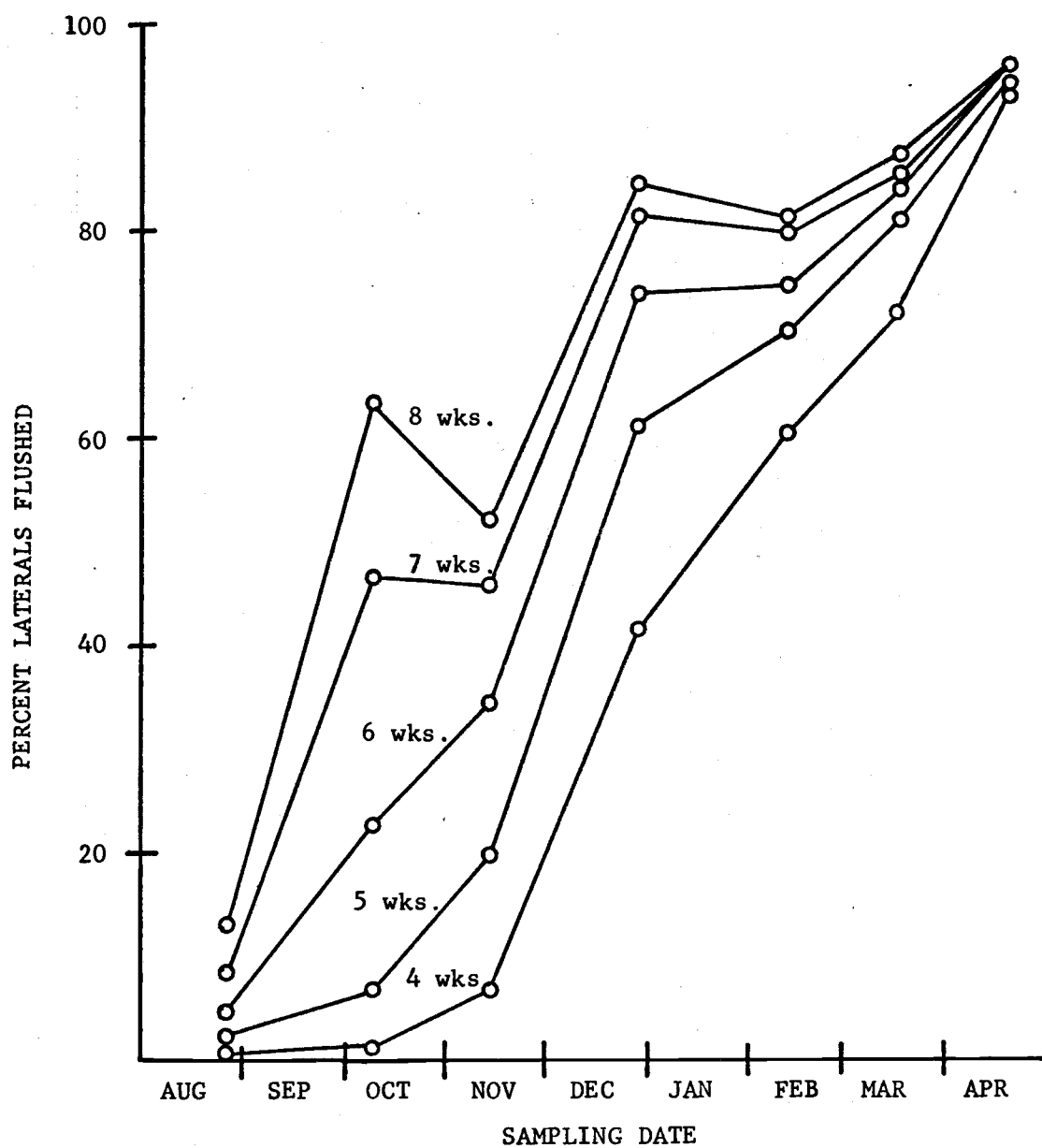
Figure 7. Percentage of Douglas-fir lateral buds flushed by a given
week in the favorable long-day environment.
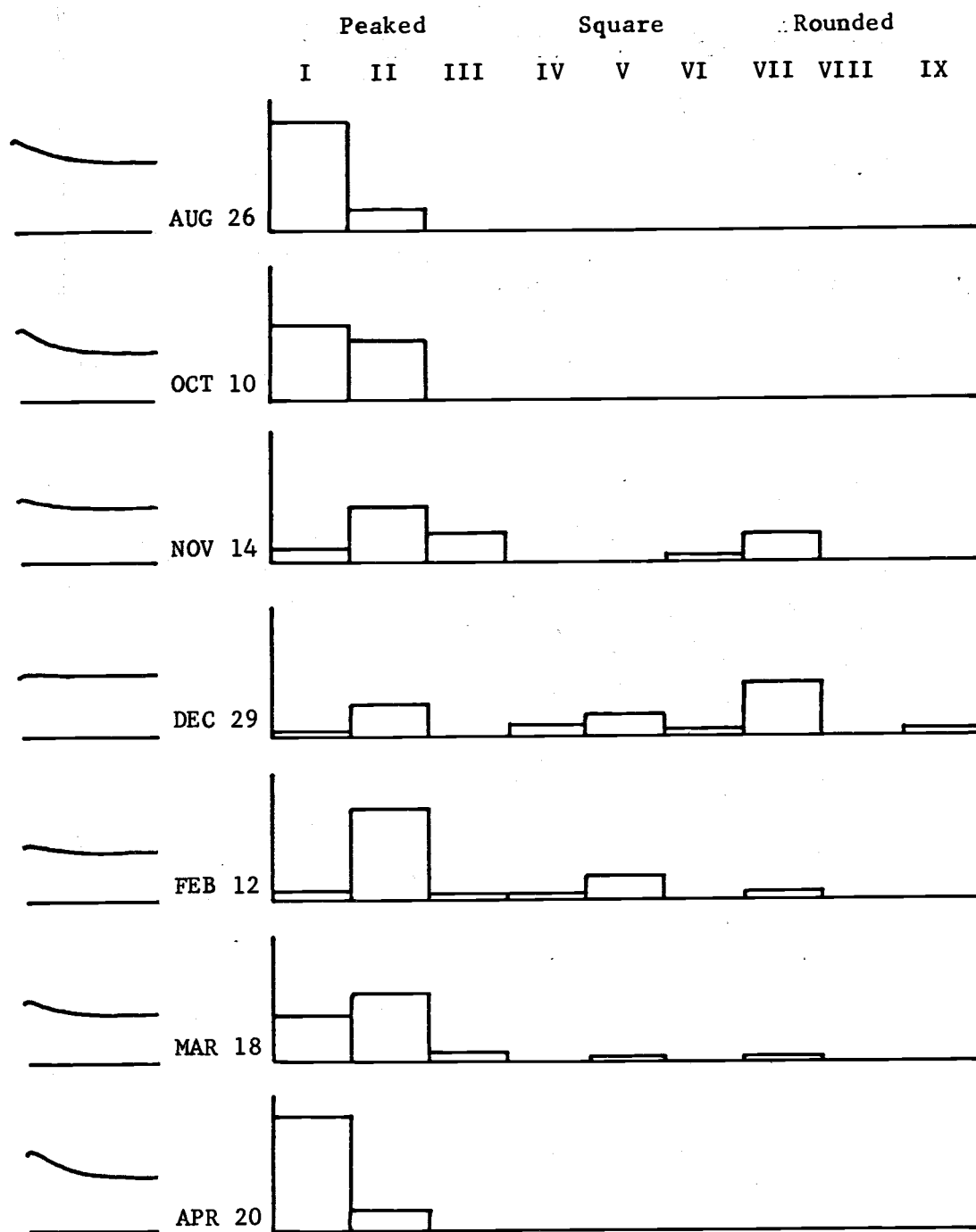
Figure 8. Seasonal change in Douglas-fir trace characteristics. Left: Douglas-fir trace based on means of HFV, MFV, and LFV on each sampling date (vertical scale: 1 mm. = 0.016 V; horizontal scale: 1 mm = 0.035 msec.). Right: Distribution of Douglas-fir seedlings in trace form classes.

Examination of trends in ratios of HFV to MFV, MFV to LFV, and HFV to LFV brings out that trace form undergoes its first major change between October 10 and November 14 (Figs. 9, 10, and 11). Ratios drop to values close to one; the trace becomes square. The ratios of HFV to MFV and HFV to LFV drop slightly more between November 14 and December 29 while the ratio of MFV to LFV shows little change. Ratios then begin to rise, the rate of rise accelerating between March 18 and April 20. The rise in the ratio of HFV to MFV and HFV to LFV between August 26 and October 10 reflects in part a reduction in overall trace amplitude. When differences, rather than ratios, are plotted, this rise is still present but much reduced. Differences do not otherwise present different trends than ratios. The picture presented by ratios is essentially the same as that given by distribution of traces in form classes.

Analysis of variance of each ratio by sampling date and by moisture regime showed the effect of sampling date to be highly significant (F prob. = .000). LSD tests on means ranked by date showed that ratios of HFV to MFV and HFV to LFV changed significantly from date to date. The MFV to LFV ratio did not differ at the .05 level between November 14 and December 29 and between February 12 and March 18.

Investigation of the effect of moisture regime on trace form was limited to consideration of the ratio of HFV to LFV (Fig. 12). Moisture regime had a highly significant effect on the ratio (F prob. = .005). T-tests of differences on each date separately indicated that this treatment difference was significant only on November 14 and December 29. Differences on these two dates could not be directly attributed to any linear relationship between the ratio and diameter at the point of insertion of the oscilloscope electrode.

Trends in individual voltage values differed from ratio trends. LFV and MFV exhibited very similar, somewhat erratic seasonal changes (Fig. 13). HFV exhibited a more regular trend, falling steadily from a high on August 26 to a low on February 12, and then rising again (Fig. 14). Differences between succeeding dates were all significant.

Figure 9. Seasonal trend in ratio of high frequency voltage (HFV) to mid frequency voltage (MFV) for Douglas-fir.

Figure 10. Seasonal trend in ratio of mid frequency voltage (MFV) to low frequency voltage (LFV) for Douglas-fir.
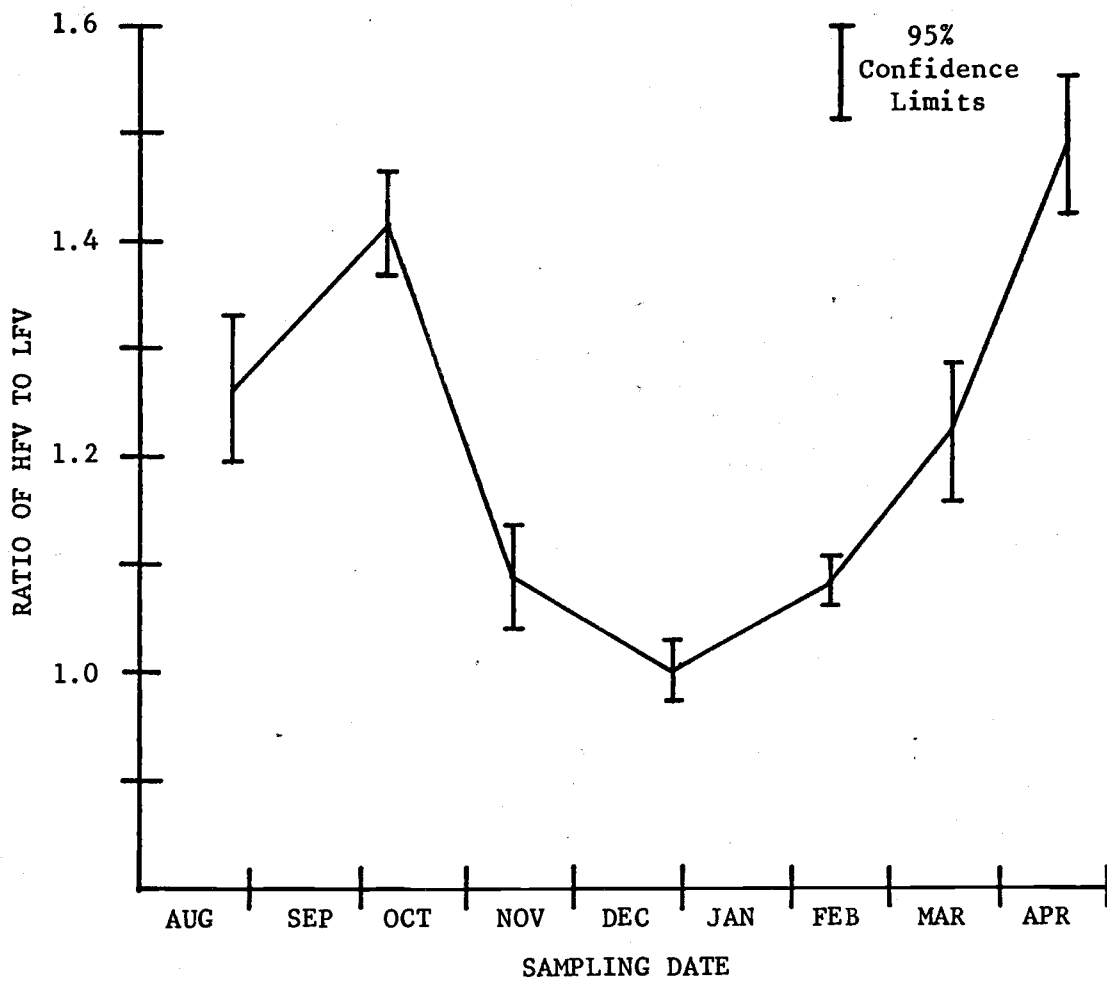
Figure 11. Seasonal trend in ratio of high frequency voltage (HFV) to
low frequency voltage (LFV) for Douglas-fir.

Figure 12. Comparison of seasonal trends in the ratio of high frequency voltage (HFV) to low frequency voltage (LFV) for moisture stressed versus non-stressed Douglas-fir seedlings.
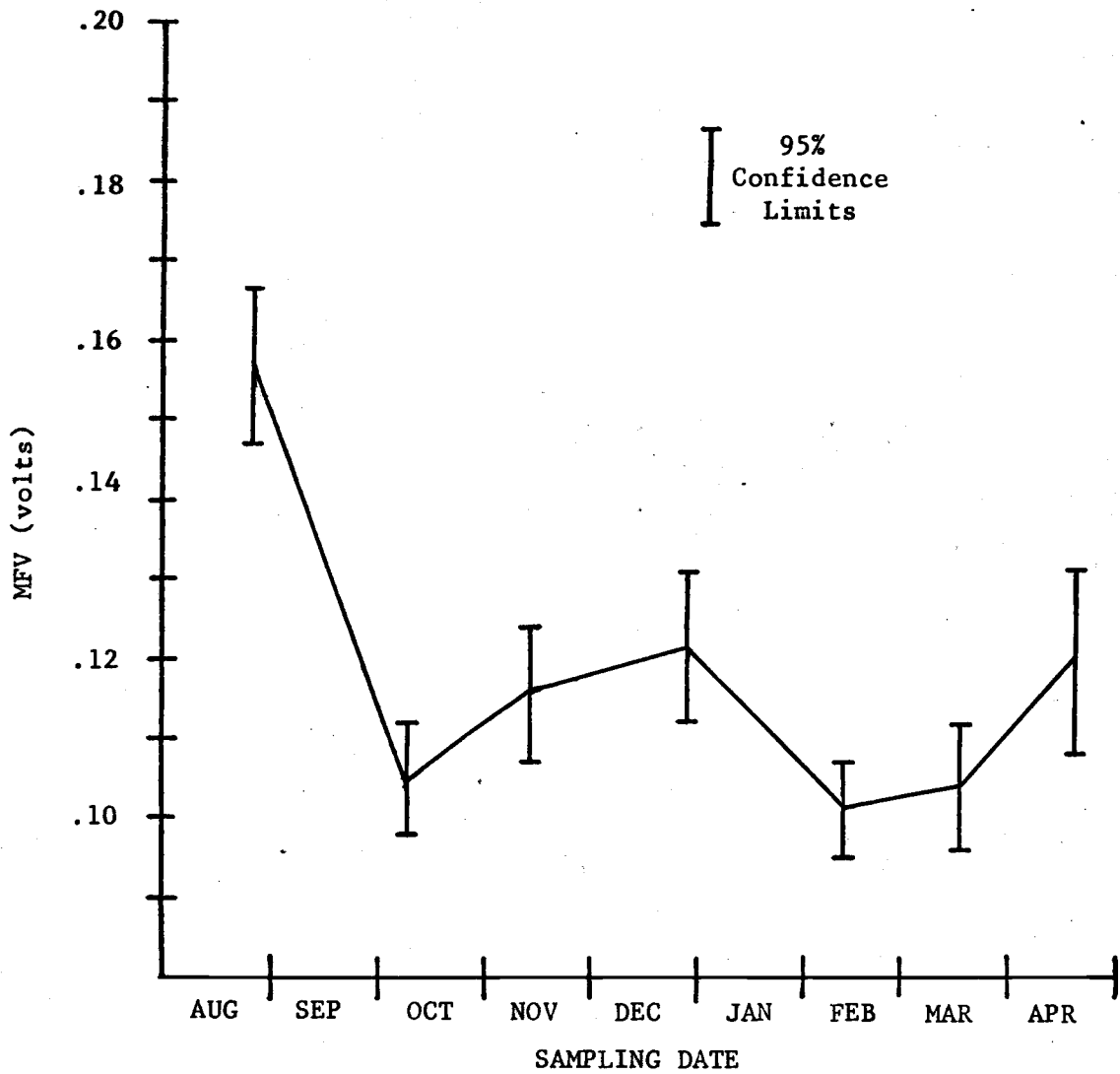
Figure 13. Seasonal trend in mid frequency voltage (MFV) for Douglas-fir. The trend for low frequency voltage (LFV) was nearly identical.
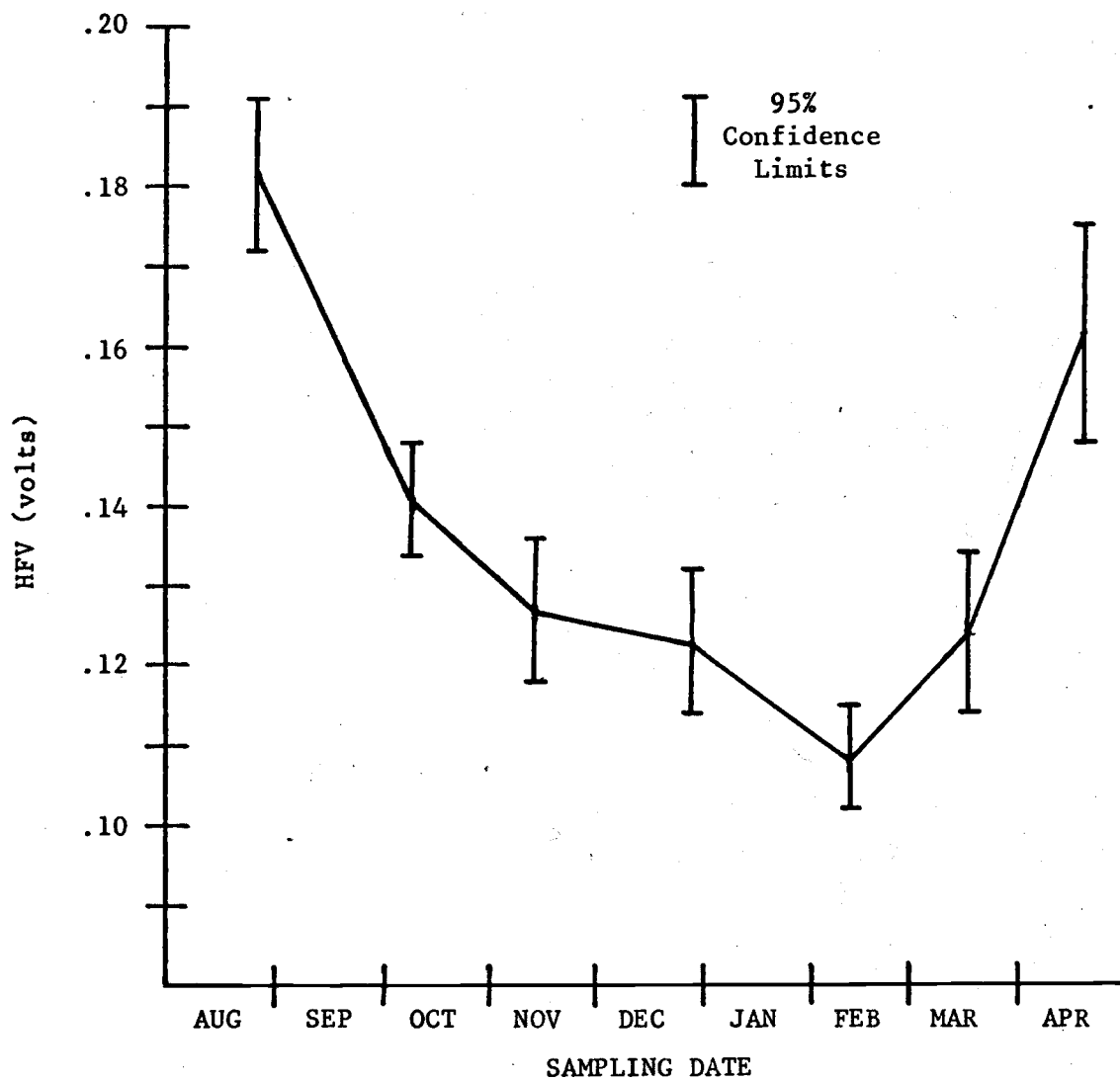
Figure 14.   Seasonal trend in high frequency voltage (HFV) for Douglas-fir.

Relationship Between Oscilloscope Trace Characteristics and Depth of
Dormancy Variables

Terminal and lateral buds exhibit similar seasonal trends in
growth room activity, whether the activity of laterals is viewed in
terms of the speed with which the first bud on a tree flushes or in
terms of the speed with which all the buds on a tree flush. Thus
activity of terminal buds alone can be used to represent apical dor-
mancy development. Similarly, seasonal trends in the ratio of HFV
to LFV adequately represent those in the gamut of trace form charac-
teristics examined here. Of the trace amplitude trends, only that of
HFV shows any promise of relating to seasonal changes in seedling
physiology.

Thus investigation of the relationship between trace charac-
teristics and bud dormancy development can be reduced to examination
of the relationship between growth room activity of the terminal bud
and the ratio of HFV to LFV, and the relationship between growth
room activity of the terminal bud and HFV alone. These relationships
are presented in Figures 15 and 16. The date of cessation of cambial
activity is also noted on these figures. Major changes in terminal
bud activity occur between August 26 and October 10 and between Nov-
ember 14 and December 29. The first major change in the ratio of
HFV to LFV, however, occurs between these two periods, during the
period from October 10 to November 14. There is virtually no change
in terminal bud activity during this period. This is the period during
which cambial growth ceases. The significant increase in flushing
speed between March 18 and April 20 is matched by a considerable in-
crease in peaking of trace form.

Trends in HFV and terminal bud activity are parallel until Dec-
ember 29. At that time bud activity considerably increases while HFV
shows little change. There is little change in HFV during the period
in which cambial growth ceases. The increase in flushing speed between
March 18 and April 20 is paralleled by a significant increase in HFV.

Difference between moisture regimes in ratio of HFV to LFV could
not be related to differences between regimes in terminal bud activity,
since such differences in activity were neither significant nor
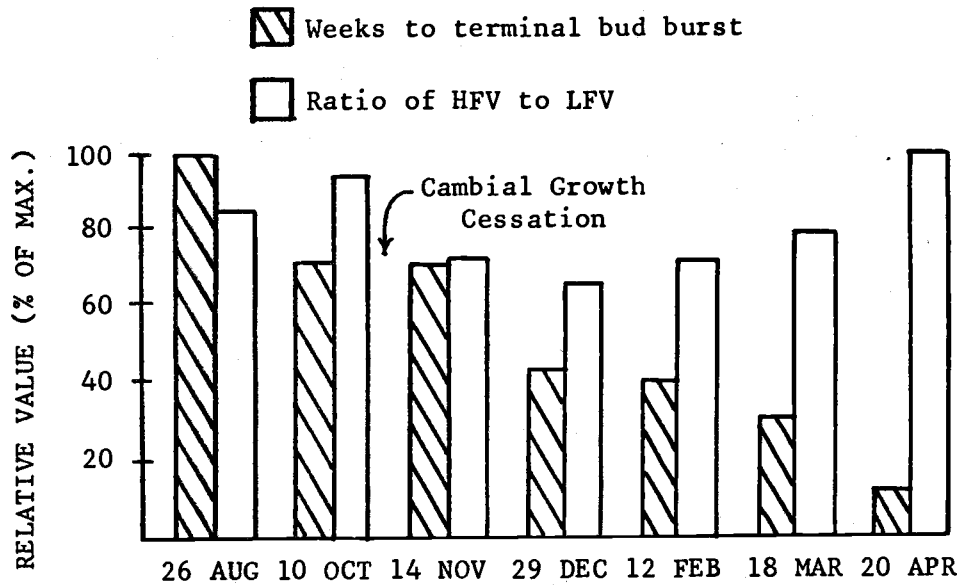
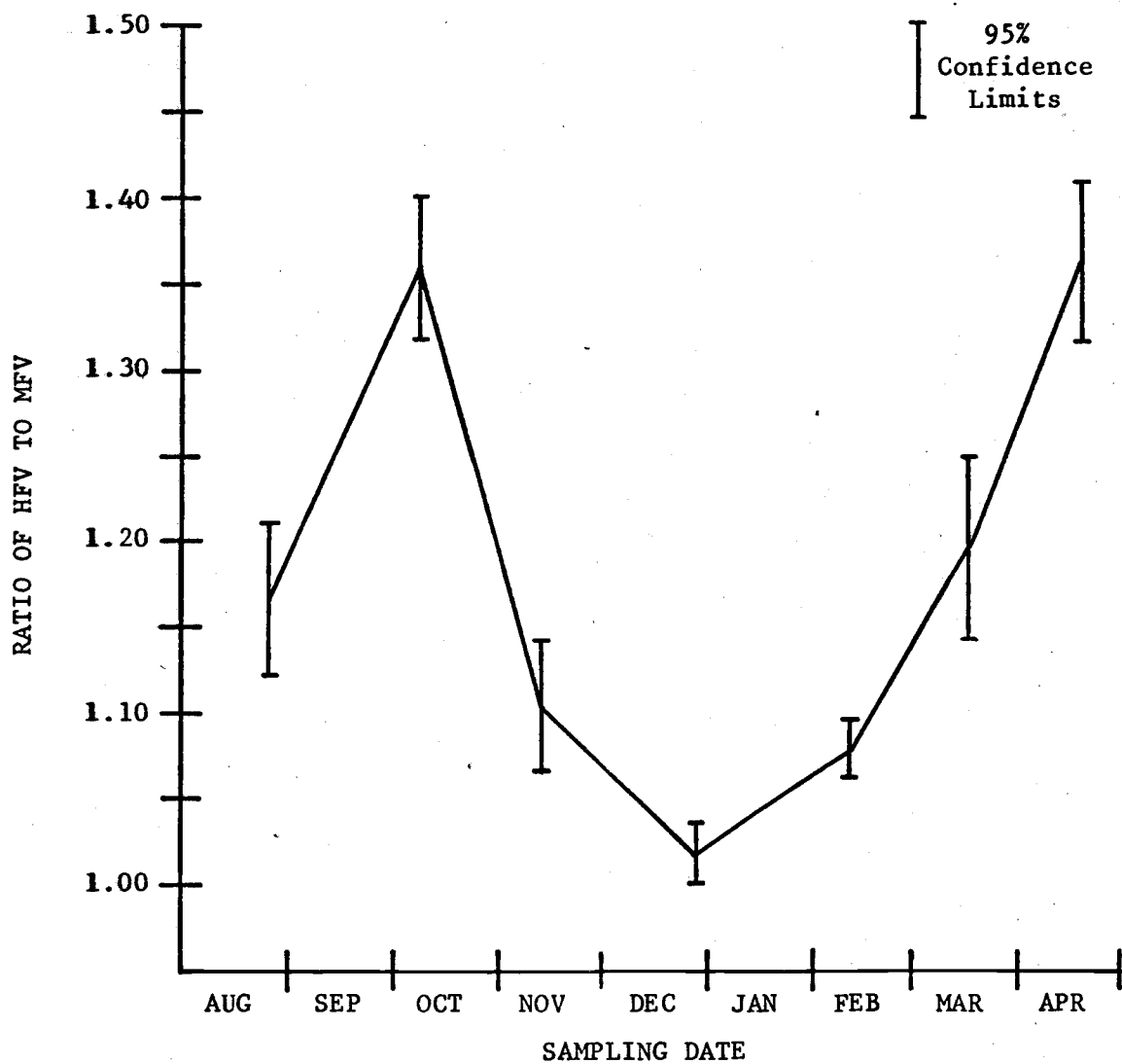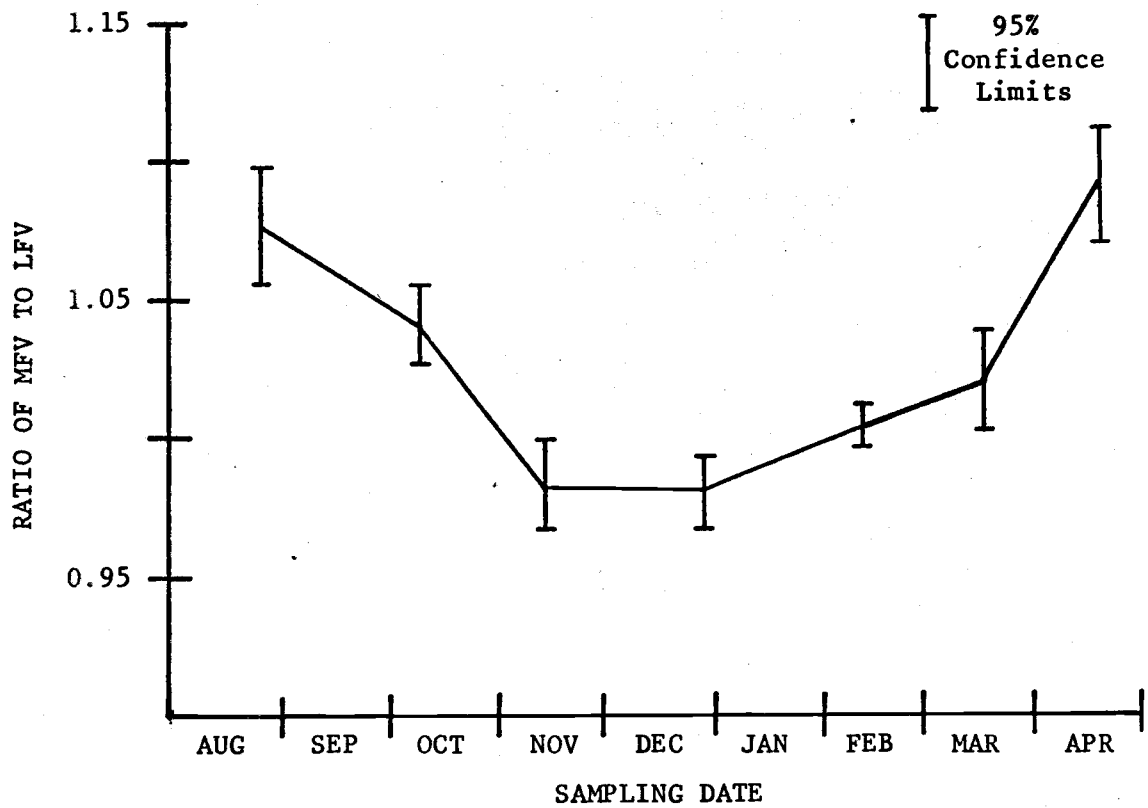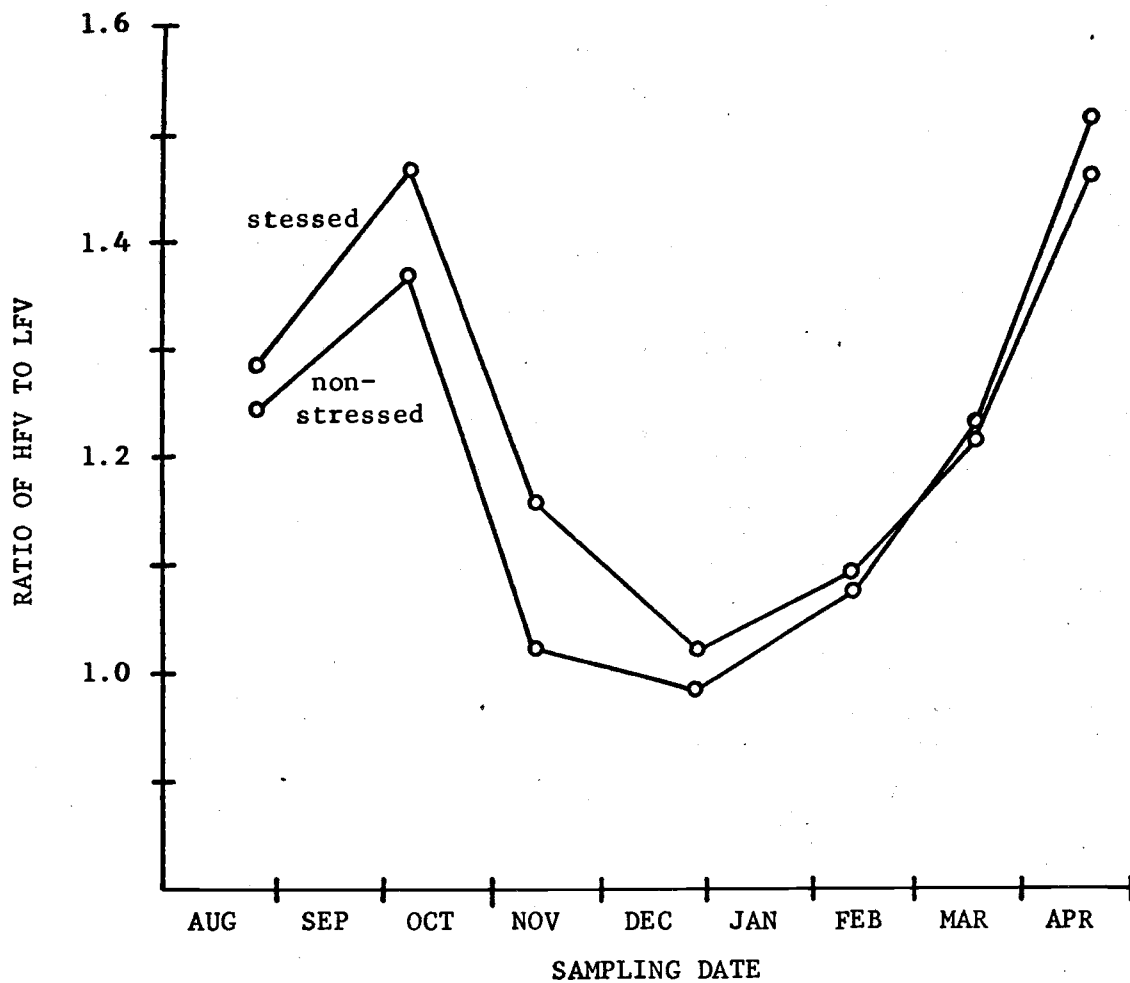Figure 15. Seasonal trends in terminal bud activity and in the ratio of high frequency voltage (HFV) to low frequency voltage (LFV) for Douglas-fir.
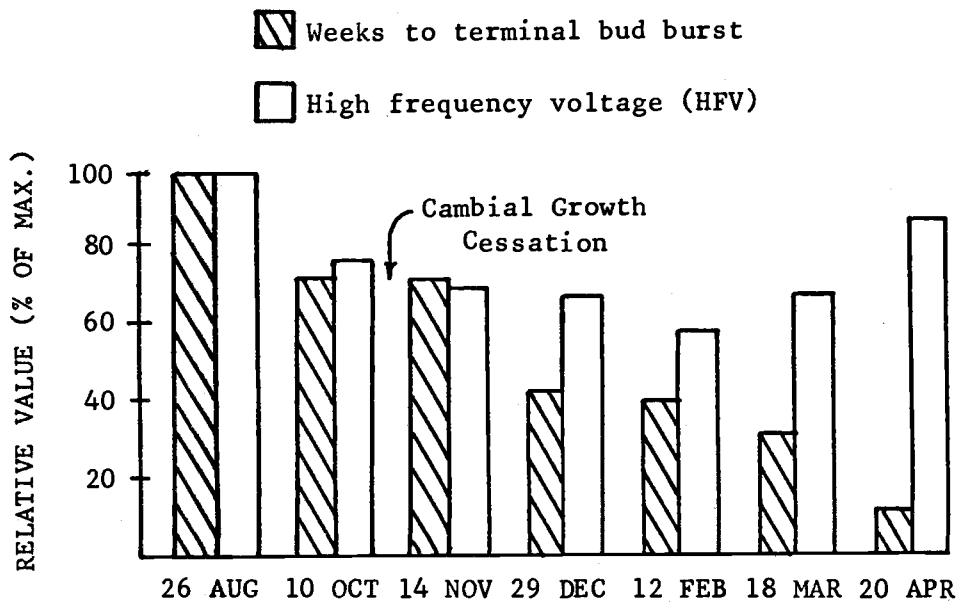
Figure 16. Seasonal trends in terminal bud activity and in high frequency voltage (HFV) for Douglas-fir.

consistent in sign.

Relationship Between Oscilloscope Trace Characteristics and Temperature
Variables

Table 2 gives mean minimum temperature, mean maximum temperature,
and total hours below 4.5°C for the fourteen days previous to each
sampling date. The regression of each of these temperature variables
on each of the trace ratios and on HFV yielded significant results in
only two cases. The correlation coefficient for the regression of mean
maximum temperature on the ratio of HFV to LFV was .91 (significant at
.05 level), and the correlation coefficient for the regression of mean
maximum temperature on the ratio of HFV to MFV was .94 (significant at
.01 level) (Fig. 17). The fall's first frost occurred on October 19;
this was during the period in which the ratio of HFV to LFV changed
greatly.

Seasonal Needle Trace Characteristics

Change in Douglas-fir needle traces was less seasonal and much
less pronounced than change in stem traces. Traces for August 26 and
October 10 resembled those in Figure 18a. Mid-November traces and
traces on all later dates resembled those of Figure 18b. Major change
in form occurring between October 10 and November 14 concurs with the
fall trend in stem trace form.

Results for Ponderosa Pine

Cambial Growth Cessation

Mean date of cambial growth cessation for the ponderosa pine
seedlings was October 27 (95 percent confidence interval October 25 to
October 30). The stressed pine ceased growth an average of five days
earlier than the non-stressed pine. The probability that the stressed
and non-stressed means are equal is less than .07.

Sampling Date	Mean Minimum Temperature (°C)	Mean Maximum Temperature (°C)	Hours Below 4.5°C
October 10	7.4	22.5	7
November 14	4.5	13.2	35
December 29	0.3	5.6	254
February 12	-2.1	10.8	191
March 18	-0.8	11.2	189
April 20	0.9	20.1	85

Table 2. Lath house temperature variables for the fourteen days prior to each Douglas-fir sampling date.

Sampling Date	Mean Minimum Temperature (°C)	Mean Maximum Temperature (°C)	Hours Below 4.5°C
October 24	2.9	18.7	78
December 1	-1.1	10.0	174
January 28	-0.9	11.6	204
March 16	-0.9	10.3	196
April 14	1.7	19.9	101

Table 3. Lath house temperature variables for the fourteen days prior to each ponderosa pine sampling date.

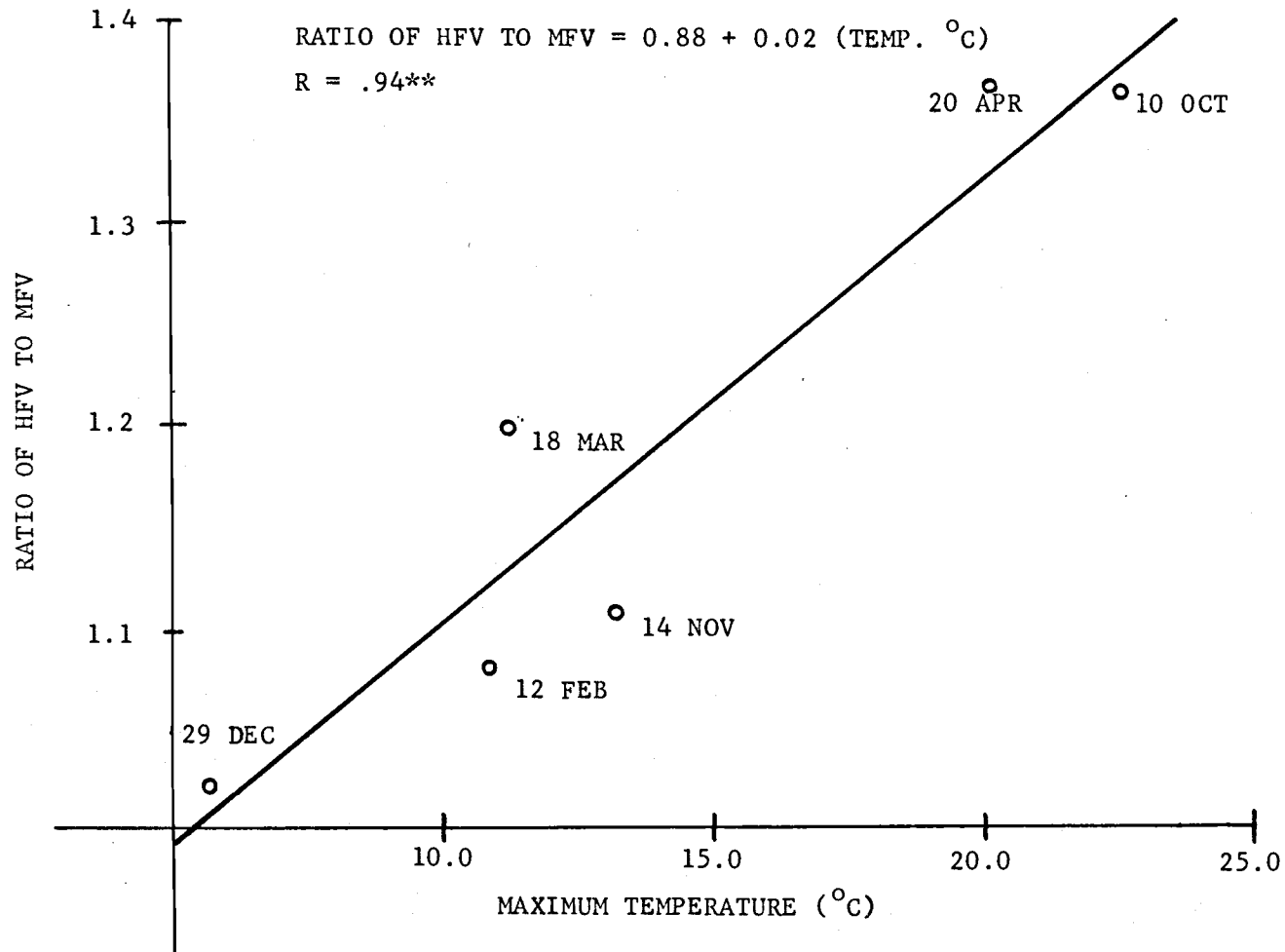Figure 17. Regression of mean maximum temperature for the fourteen days previous to each Douglas-fir sampling date on the ratio of HFV to MFV.

a. Trace form on August 26 and October 10.
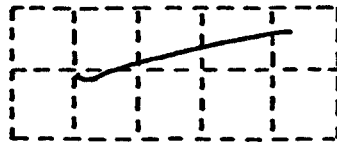
b. Trace form on November 14, December 29, February 12, March 18, and April 20.

Figure 18. Douglas-fir needle traces.

Growth Room Response of Terminal Bud and Needles

Observations of speed of flushing of pine terminal buds in the growth room began on July 18, forty days earlier than those for Douglas-fir. Terminal bud response on this date was very slow; greater than twelve weeks in the growth room were required before buds would burst (Fig. 19). However, needles on the terminal shoot elongated an average of 68 mm. during the first eight weeks the seedlings were in the growth room. By September 2, terminal bud response increased considerably although seedlings were still in the growth room for more than six weeks before buds burst. Needles no longer elongated in the growth room. Mean flushing time decreased significantly between September 2 and October 24. Differences between dates after October 24 were much smaller and only significant between January 28 and March 16. On March 16, thirty-nine percent of the seedlings had swollen terminals when they were placed in the growth room. On April 14, all of the seedlings had swollen terminals.

The analysis of variance of weeks to terminal bud burst by date and by moisture regime showed the effect of date, the effect of moisture regime, and the interaction of date and moisture regime to all be highly significant (F prob. = .001). The difference between moisture regime means held when each date was examined separately. The stressed seedlings consistently flushed sooner than the non-stressed seedlings (Fig. 20). There were also highly significant differences between the two moisture regimes in diameter of the terminal shoot at the point of insertion of the oscilloscope electrode on all dates but July 18 and October 24. For this reason the possibility that the difference between moisture regimes was due largely to differences in diameter alone was investigated. There was a significant linear relationship between weeks to flushing and diameter on only two dates, December 1 and January 28. When diameter was added as a covariable to the analysis of variance, the effects of date and treatment were still very highly significant. Thus moisture regime was exerting an effect on terminal bud-burst above, or at least not linearly related to, its effect on diameter.
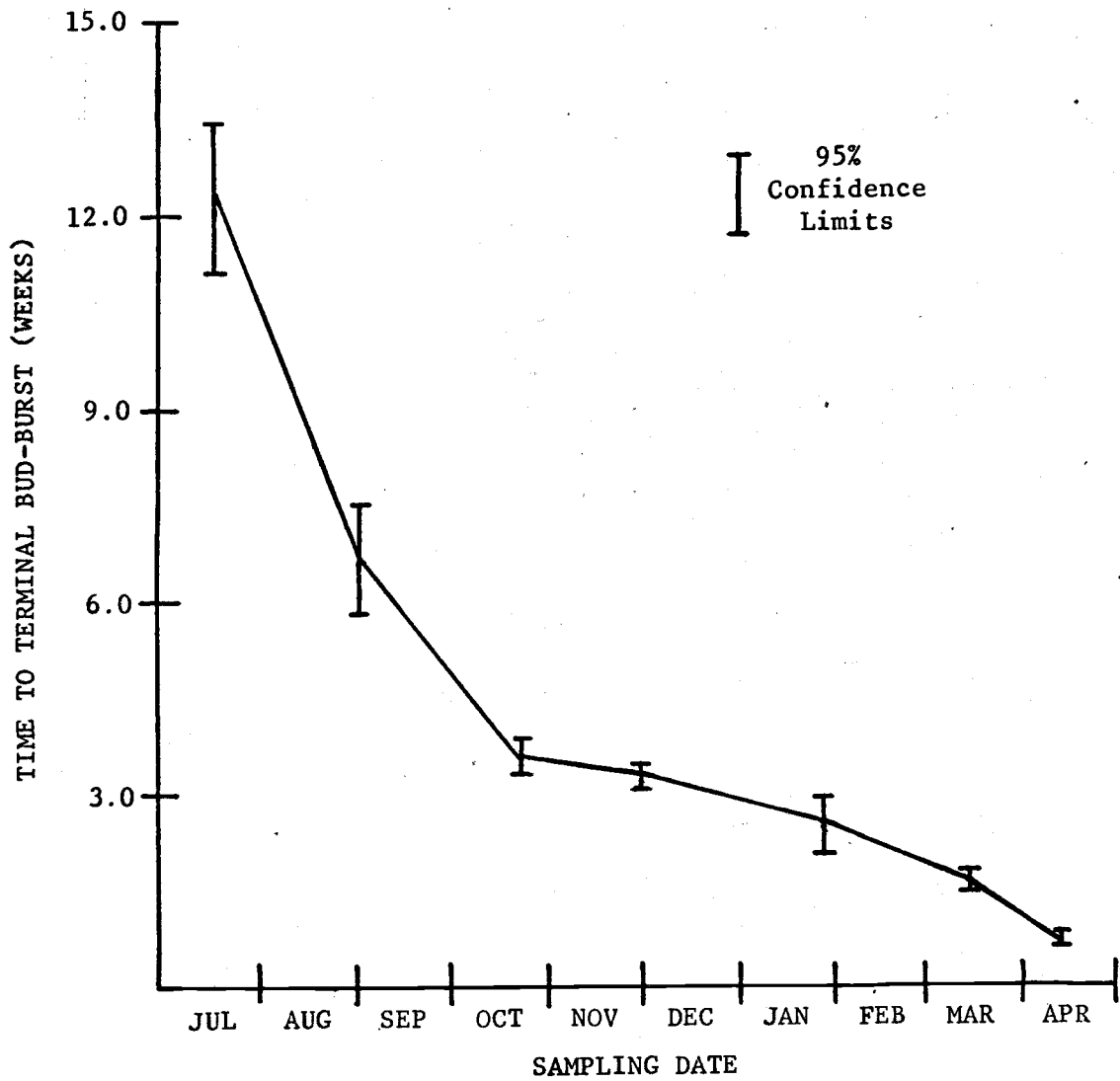
Figure 19. Time required for flushing of terminal buds of ponderosa
pine seedlings brought into favorable long-day environ-
ment.
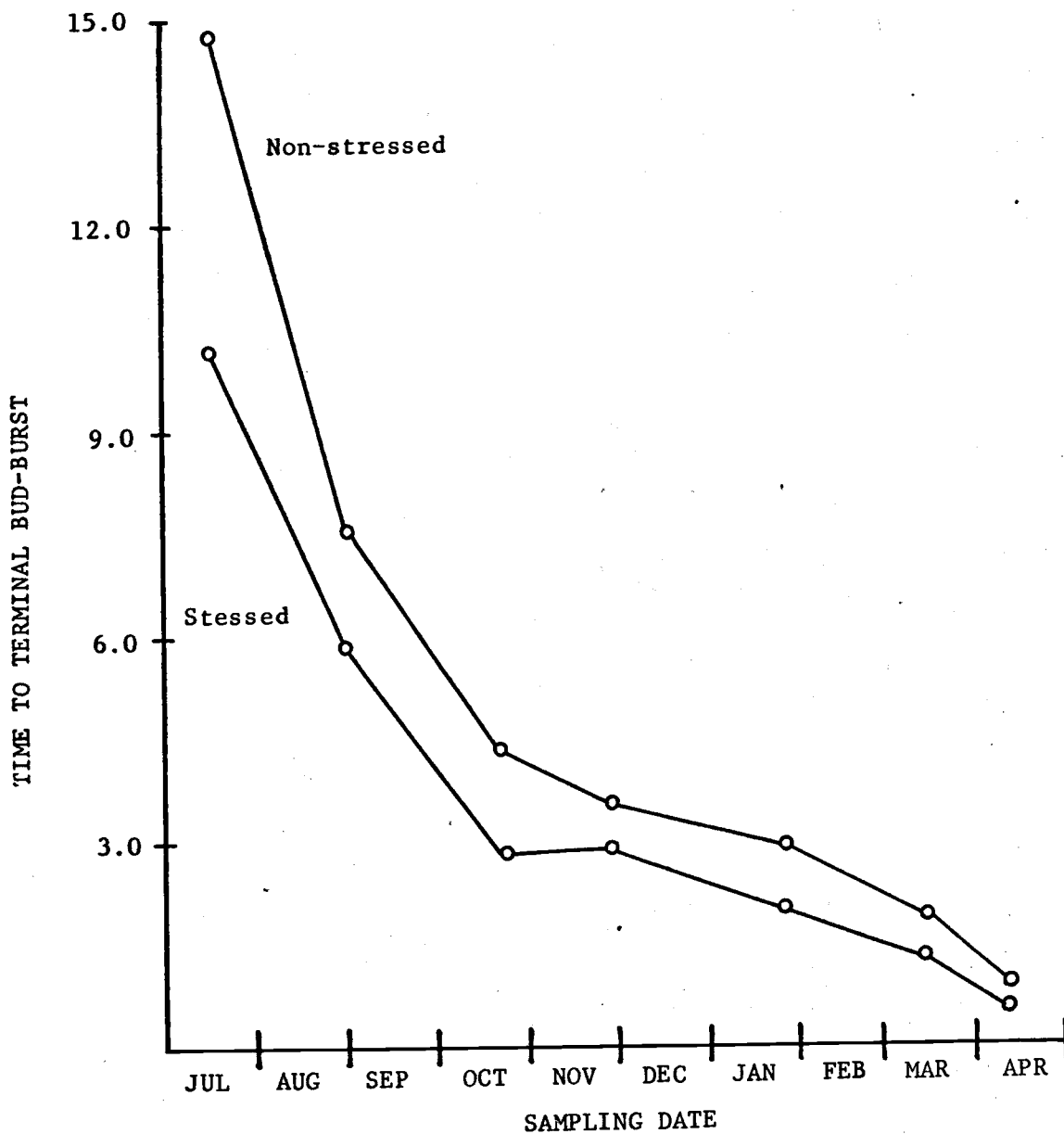
Figure 20. Time required for flushing of terminal buds of stressed versus non-stressed ponderosa pine seedlings brought into favorable long-day environment.

Further Observations on Stressed Versus Non-stressed Seedlings

The stressed pine had reached -20 atm. pre-dawn water potential by the first sampling date, July 18. Terminal buds were set by this date, although many of them were smooth rather than having the scaley appearance of the overwintering bud. No differences were evident in appearance of buds on stressed compared to non-stressed seedlings. Needles of the stressed pine were 10 mm. shorter than those of the non-stressed pine, a significant difference. By September 2, this difference had increased to 51 mm. and was highly significant. There was no difference between stressed and non-stressed seedlings in terminal shoot elongation for the 1976 growing season.

Seasonal Changes in Oscilloscope Trace Characteristics

Seasonal changes in characteristics of ponderosa pine traces were as pronounced as for traces of Douglas-fir (Fig. 21). The transition from traces peaked on the leading edge to traces rounded on the leading edge occurs earlier and more completely than with the fir, however. Examination of distribution of seedlings in trace form classes reveals an almost complete change in distribution between September 2 and October 24. Traces continue to be predominantly rounded to square through January 28. By April 14 only peaked forms occurred, and distribution of seedlings in trace form classes was very similar to that of July 18.

A large number of pine traces fell into class III between October 24 and March 16. Very few Douglas-fir were ever placed in this class. Douglas-fir traces seldom turned down on the leading edge while pine traces displayed definite slopes on October 24 and December 1. Other differences in the character of fir and pine traces can be noted by comparing Figure 21 with Figure 8.

Seasonal trend in the ratio of HFV to LFV reinforces the picture presented by trace form classes (Fig. 22). By far the greatest change in value occurred between September 2 and October 24. The ratio dropped from near 1.4 to less than 0.8. After this date the ratio rose steadily; only the difference between December 1 and January 28 was nonsignificant. Trends for the ratios of HFV to MFV and MFV to LFV
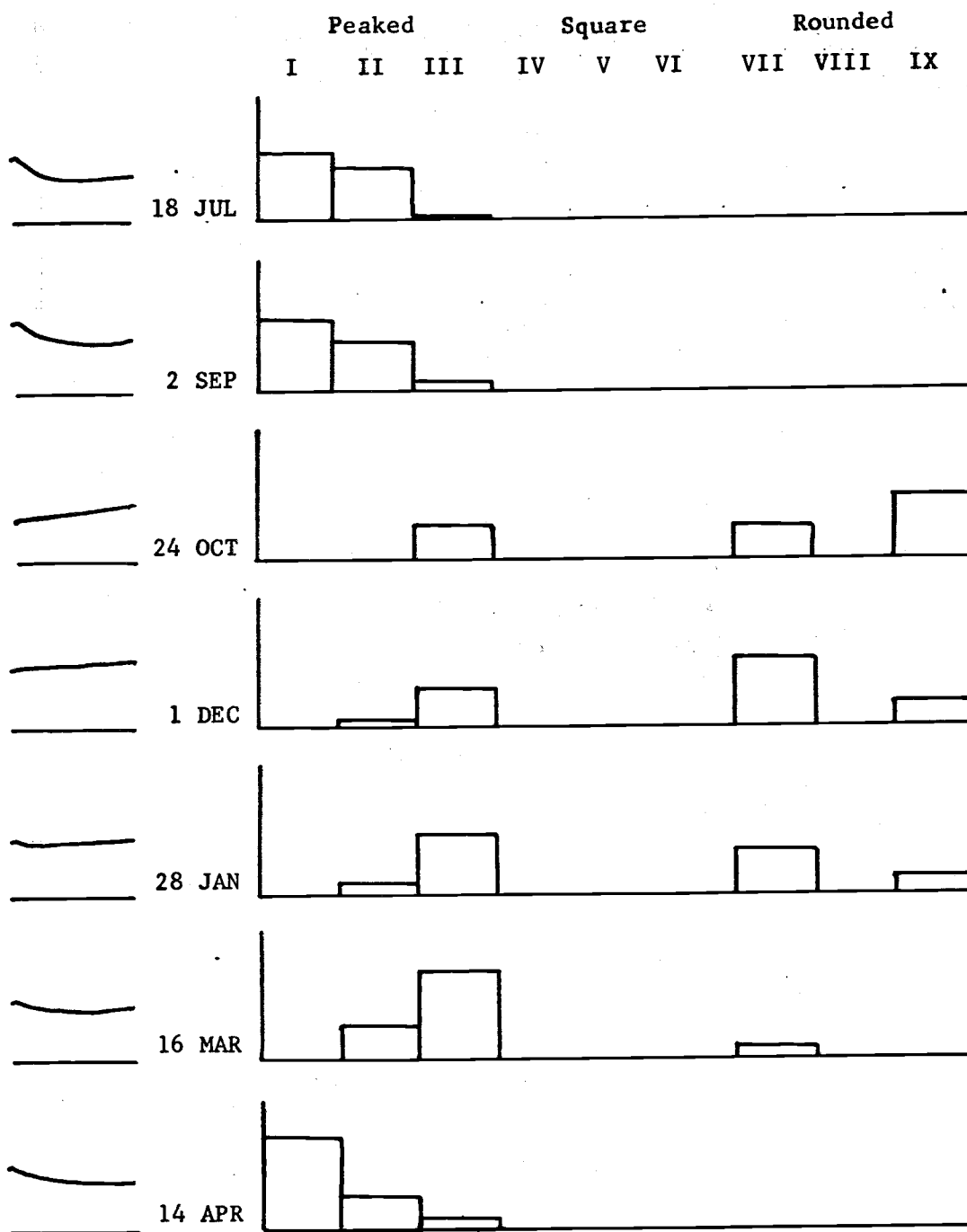
Figure 21. Seasonal change in ponderosa pine trace characteristics. Left: Ponderosa pine traces based on means of HFV, MFV, and LFV on each sampling date (vertical scale: 1 mm. = 0.016 V; horizontal scale: 1 mm. = 0.035 msec.). Right: Distribution of ponderosa pine seedlings in trace form classes.
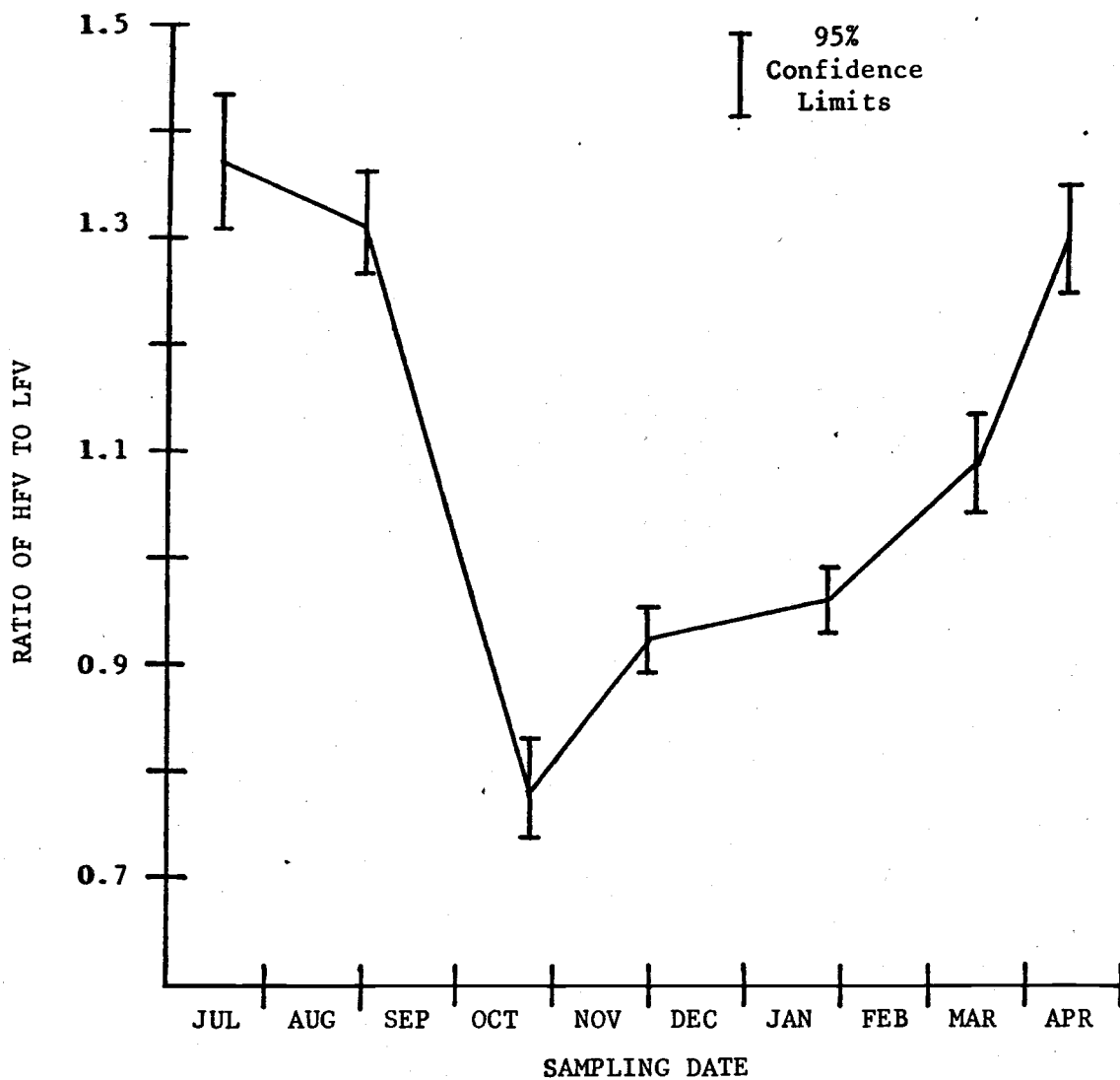
Figure 22. Seasonal trend in the ratio of high frequency voltage (HFV)
to low frequency voltage (LFV) for ponderosa pine.

were similar.

Analysis of variance of each of the three ratios by date and by moisture regime showed the effect of date to be highly significant (F prob. = .001). Moisture regime also exerted a significant effect on the ratio of HFV to LFV and the ratio of MFV to LFV. Examination of the effect of moisture regime on the ratio of HFV to LFV on a date by date basis showed differences between treatment means to be significant only on October 24 (Fig. 23). However, non-stress means were consistently higher on the first five dates. Although there were significant differences between moisture regimes on October 24 in diameter at point of insertion of the oscilloscope electrode, there was no linear relationship between diameter and the ratio of HFV to LFV. Addition of diameter to the overall analysis of variance did not reduce significance.

HFV and MFV taken alone also dipped to low points on October 24. Seasonal patterns were irregular for these two variables and resembled that for fir MFV (Fig. 13). LFV rose steadily to a high on December 1 and then fell steadily to a value on April 14 nearly equal to that of July 18 (Fig. 24).

Relationship Between Oscilloscope Trace Characteristics and Depth of Dormancy Variables

As was the case with Douglas-fir traces, seasonal trends in the ratio of HFV to LFV adequately represent the gamut of seasonal changes in ponderosa pine trace form. Of the amplitude variables, only LFV showed any promise of correlating with seasonal changes in seedling physiology. Therefore, the nature and strength of any relationships between growth room response of terminal buds and the ratio of HFV to LFV, and between bud response and LFV were the foci of this examination. These relationships are presented in Figures 25 and 26. Date of cessation of cambial activity is also noted on these figures. Although given in these figures, variable values for July 18 were not considered in this examination for reasons which will be discussed later.
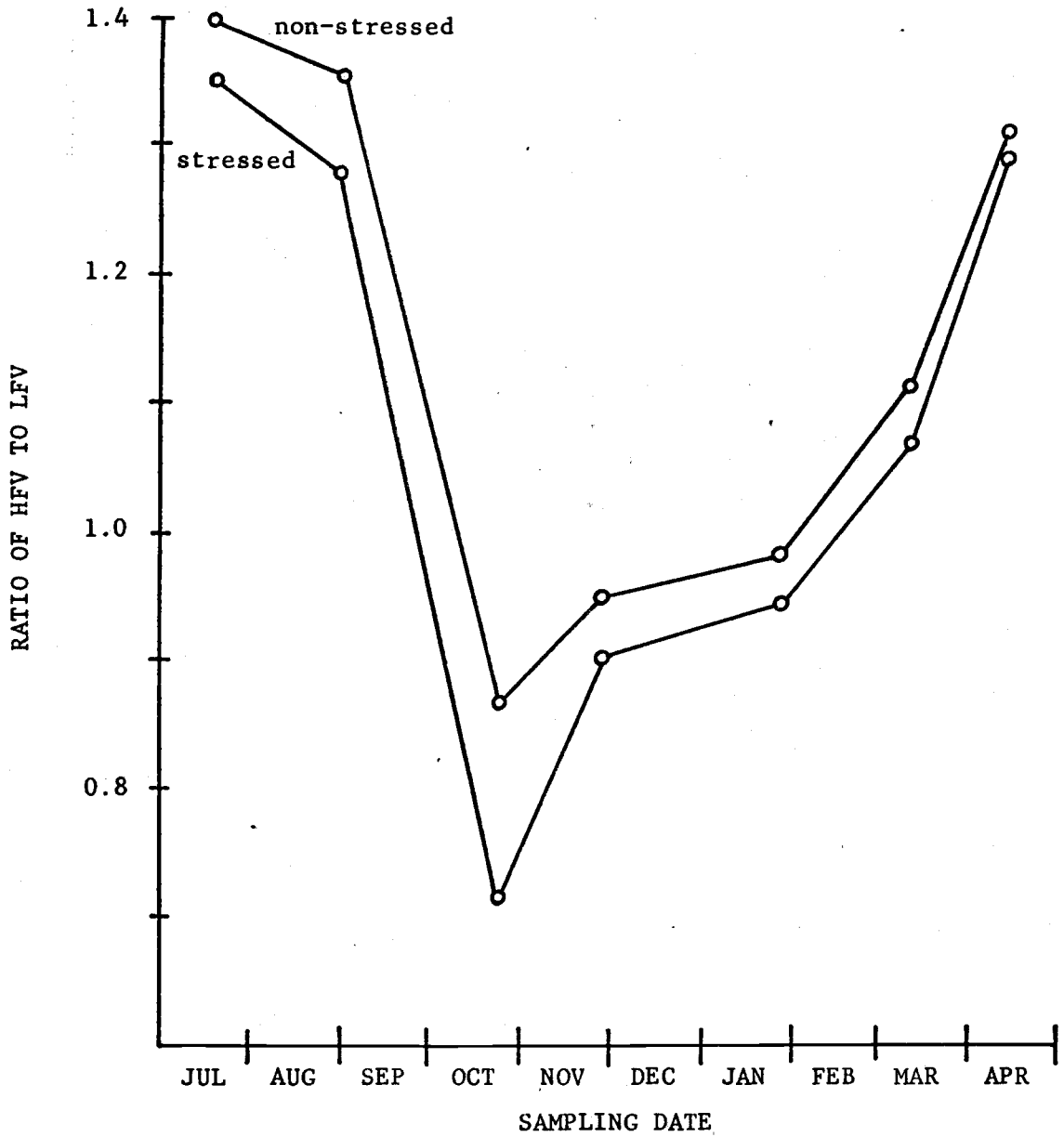
Figure 23.   Comparison of seasonal trend in the ratio of high frequency
             voltage (HFV) to low frequency voltage (LFV) for moisture
             stressed versus non-stressed ponderosa pine seedlings.
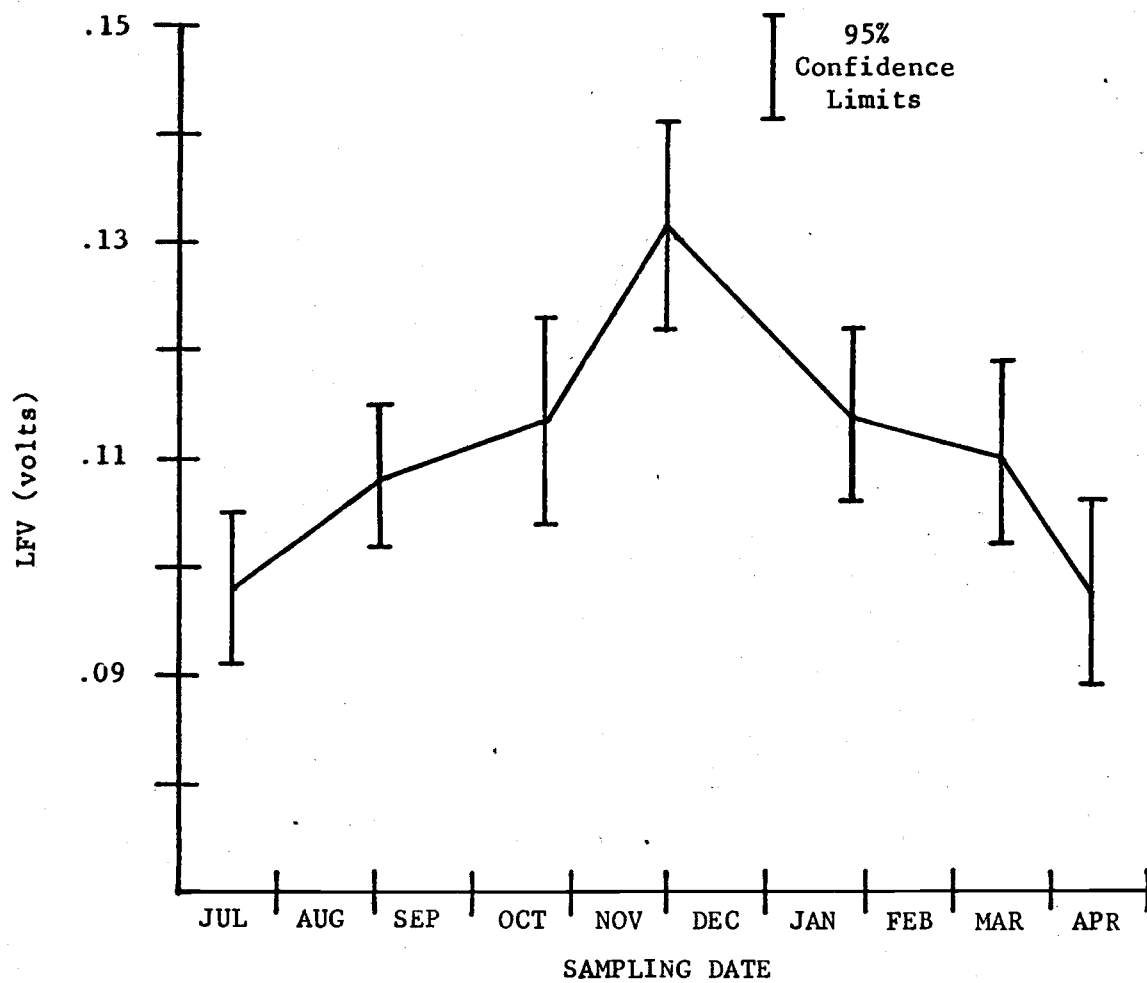
Figure 24. Seasonal trend in low frequency voltage (LFV) for ponderosa pine.
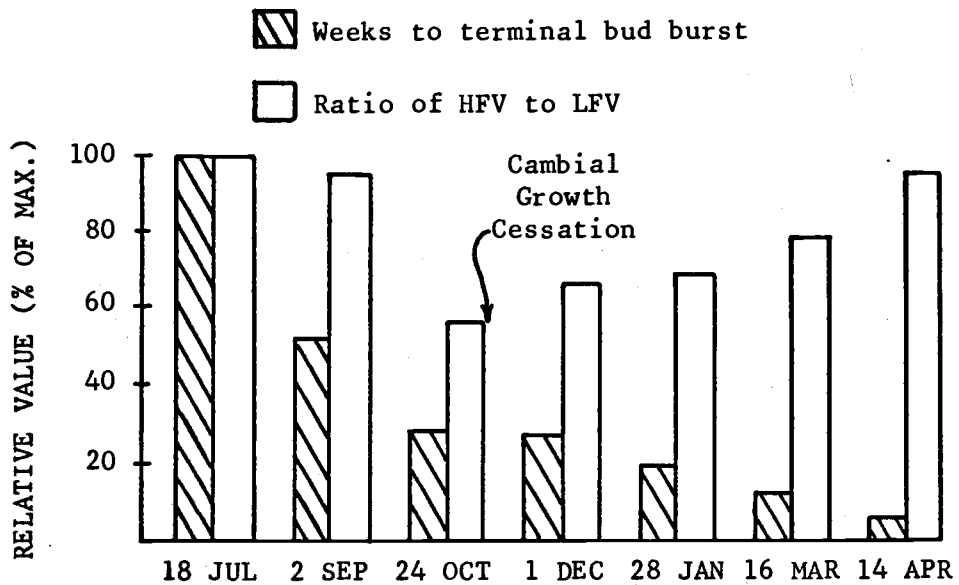
Figure 25. Seasonal trends in terminal bud activity and in the ratio
of high frequency voltage (HFV) to low frequency voltage
(LFV) for ponderosa pine.
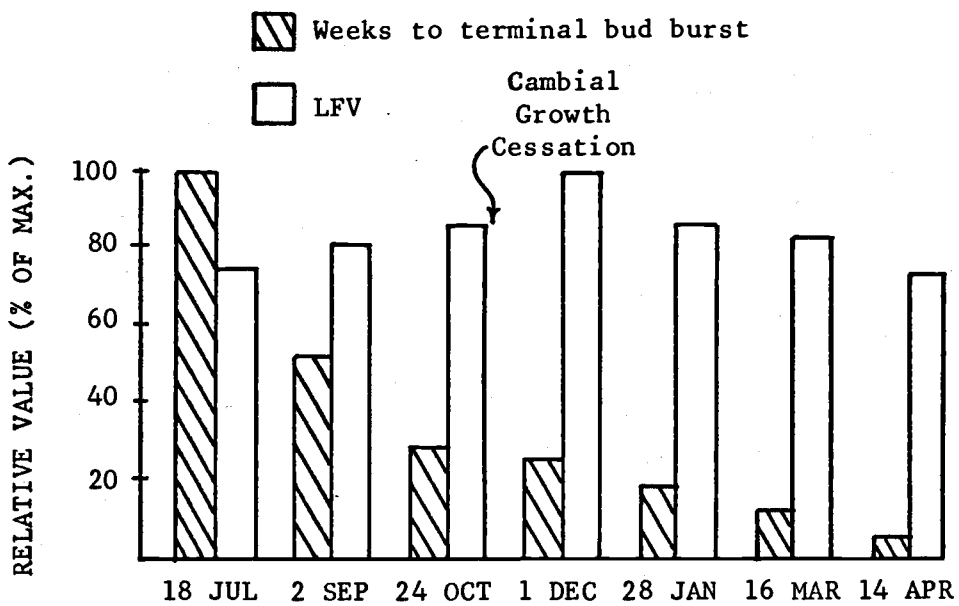
Figure 26. Seasonal trends in terminal bud activity and low frequency
voltage (LFV) for ponderosa pine.

The considerable decline in time to bud-burst between September 2 and October 24 is matched by a large drop in the ratio of HFV to LFV. Cambial growth ceased at the end of this period. From October 24 through January 28 both flushing speed and the ratio of HFV to LFV change little. The magnitudes of increases in bud activity between January 28 and March 16 and March 16 and April 14 are reflected fairly well by rises in the ratio of HFV to LFV.

Seasonal trends in LFV were gradual relative to those in the ratio of HFV to LFV. Change in LFV between September 2 and October 24 was small and did not reflect the magnitude of the increase in bud activity between those dates. Cessation of cambial activity also was not indicated by LFV. Mid-winter and spring trends in LFV paralleled those in bud activity.

Differences between moisture regimes in the ratio of HFV to LFV nearly track differences in flushing speed. Complete tracking would have required stressed seedlings to have had higher ratios than non-stressed seedlings on December 1 and January 28.

Relationship Between Oscilloscope Trace Characteristics and Temperature Variables

Table 3 presents mean minimum temperature, mean maximum temperature, and total hours below $4.5^{\circ}C$ for the fourteen days previous to each sampling date. The regression of each of these variables on each of the trace ratios and on LFV never yielded significant results. Therefore, temperature changes and trace changes were not in phase in ponderosa pine although they were in Douglas-fir. As with Douglas-fir, trace form underwent its most dramatic change during the period in which the first frosts of the fall occurred.

Seasonal Needle Trace Characteristics

As with Douglas-fir, change in ponderosa pine needle traces was much less definite and seasonal than change in stem traces. A trace typical of those on July 18 and September 2 is shown in Figure 27a. Traces for October 24 and all later sampling dates were slightly less

peaked but otherwise very similar (Fig. 27b). Decrease in peaking occurring between September 2 and October 24 parallels major stem trace form change occurring during this period.
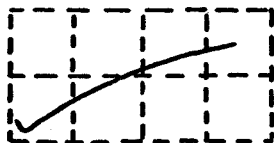
a. Trace form on July 18 and September 2.
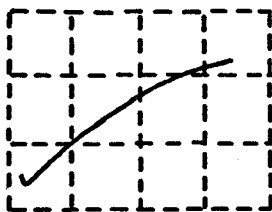
b. Trace form on October 24, December 1, January 28, March 16, and April 14.

Figure 27. Ponderosa pine needle traces.

DISCUSSION OF RESULTS OF PART I

INVESTIGATION OF RELATIONSHIP BETWEEN OSCILLOSCOPE TRACE

CHARACTERISTICS AND DEPTH OF DORMANCY

Converting the speed with which seedlings flush in a favorable long-day environment into a measure of depth of dormancy requires several assumptions. One must assume that depth of dormancy is primarily controlled by the amount of chilling requirement remaining unfulfilled. The need for chilling for release of dormancy in conifers is well documented; but the degree to which other factors, such as endogenous rhythms, may control dormancy depth is at present only a matter of conjecture. Ideally depth of dormancy would have been determined by observing speed of flushing under neutral (12 hour) photoperiods. Use of long-days, however, allowed observation periods to be greatly condensed and made the most efficient use of limited growth room space. It was assumed that response to long photoperiods on a series of dates was proportional to response to neutral photoperiods on that series of dates, i.e. that response was condensed only and not distorted. All results must be viewed with the assumptions in mind.

The eleven weeks necessary for flushing of terminals of the August 26 sample of Douglas-fir indicates that by that date the fir had already entered deep dormancy. By October 10 flushing time had decreased to eight weeks. This is still, however, a long period; and these seedlings are not considered to have left deep dormancy. Between November 14 and December 29, time to terminal flushing decreased to less than five weeks. Considerable increase in activity of laterals, whether viewed in terms of speed with which the first lateral flushed on a seedling or in terms of speed with which all laterals on a seedling flushed, also occurred between these dates. Flushing behavior of the terminal bud began on December 29 to resemble that of the laterals. This is, according to Nigond (1966) and Roberts et al. (1974), a sign that the chilling requirement of the terminal bud is nearing fulfillment. This evidence, and the greatly increased speed

of flushing of the terminal and lateral buds, indicated that by December 29 the Douglas-fir had fulfilled a large part (but not all) of its chilling requirement. The seedlings are, therefore, considered to have left deep dormancy between November 14 and December 29.

Lavender et al. (1970) compared bud-burst rates of seedlings given a supplemental light period of 10,000 lx. with rates of seedlings given a supplemental light period of 500 lx. They found that the high internsity light had a much more stimulatory effect in late October than before or after that date. Part of the increase in flushing speed observed in my study between November 14 and December 29 may be due to a similar uneven stimulatory effect of long days. This could make dormancy release appear to take place early.

Increase in flushing speed between February 12 and March 18 was probably due to the seedlings having received part of their warm day requirement for flushing outside in addition to having their chilling requirement essentially fulfilled. By April 20, the majority of the seedlings had swollen buds on entering the growth chamber; and there was no doubt that most of their warm day requirement had already been met.

As no samples of Douglas-fir were brought in for testing before the date of deepest dormancy recorded (August 26), it is not possible to state that a deeper point did not occur earlier in the summer. This is unlikely, however. Roberts et al. (1974) found a peak of bud dormancy for Douglas-fir seedlings in late August and September using the same criteria employed in this research. Lavender and Hermann (1969) identified September to early November as the middle rest or deep dormancy period for Douglas-fir on the basis of extensive growth room tests of activity of buds, lateral cambia, and roots. This closely agrees with the bounds for deep dormancy here identified.

Ponderosa pine brought into the growth room on July 18 burst their buds after a very long period. This may have been due to inhibition of terminal elongation by seedling resources being channeled into needle elongation or correlative inhibition by mature foliage. It is doubtful that the long period was due to rest of the terminal bud per se. Apical meristems of seedlings on this date are considered to be in

a phase of dormancy development. The September 2 sample required nearly seven weeks to flush. These seedlings were classified as in deep dormancy. The great increase in activity between September 2 and October 24, followed by a leveling off of bud burst response, indicated that by October 24 seedlings had left deep dormancy and entered the phase of dormancy release.

Partial fulfillment of chilling requirements by October 24 was unexpectedly early. By October 24, the pine had received only eighty-two hours of temperatures below $4.5^{\circ}C$. These hours were well interspersed with periods of considerably warmer weather, and one would not have considered them to have been very effective. Stimulatory effect of long versus neutral days may have been high in October compared to earlier and later dates. This would have resulted in early indication of dormancy release.

Chilling requirements for ponderosa pine are not documented. The pine were from a high elevation seed source. At high elevations a long chilling requirement is not necessarily advantageous. In such a climate, winter warm spells which could precipitate untimely growth and reduction of frost hardiness are unlikely to occur. The pine's chilling requirement being satisfied earlier than the fir's can thus be understood.

Increases in bud-burst activity of the pine between January 28 and March 16 and between March 16 and April 14 are clearly due in part to fulfillment of part of warm day requirements ountdoors. Buds were swelling on these dates.

The literature on dormancy and physiological fitness for planting presents evidence that seedlings should not be planted either before their terminal buds have entered the phase of dormancy release or just before and during spring bud-swell. Therefore, the ability of the oscilloscope technique to indicate transition into these phases by change in form or in amplitude was the crux of this evaluation.

The first major change in Douglas-fir trace form occurred between October 10 and November 14. Ratios dropped to values close to one; the trace presented a nearly square impression. This change

occurred during deep dormancy (Fig. 28). The transition from deep dormancy to dormancy release was not reflected in significant change in trace form. Not much significance should be attached to the fact that trace form was squarest on December 29. Dormancy is a continuous phenomenon. Trace form changes also are of a continuous nature. There is no reason to attach particular value to any one point in either cycle. Differences between points or trends are what should be considered. Use of long photoperiods may have made dormancy release appear to take place early. Trace form change may, therefore, be even more out of phase with dormancy release than here indicated.

Approaching spring bud-burst is well indicated by increased peaking of trace form. Similarly, trace amplitude changes indicate spring bud-burst, but lack correlation with dormancy release. Indication of approaching spring bud-burst, while interesting physiologically, is of less potential value to the nurseryman than indication of release from deep dormancy.

Entry of ponderosa pine into the phase of dormancy release between September 2 and October 24 was strongly signalled by change in trace form from peaked to rounded (Fig. 29). As indicated above, such an early date for dormancy release must be viewed with reservation.

Pine trace form change from square to peaked indicated initiation of spring bud-swell. Amplitude of the trailing edge of the trace (LFV) also dropped significantly at that time.

Although differences in trace form between seedlings of Douglas-fir from stressed and non-stressed summer watering regimes could be detected throughout the succeeding fall and winter, no differences in apical dormancy and cambial growth cessaton could be detected. Cheung (1973) was able to induce early dormancy in first year western hemlock (Tsuga heterophylla) seedlings by moisture stress. He reported, however, that the efficacy of the treatment was very much affected by the time at which water withdrawal began. It is possible that stress began too late for the Douglas-fir in this study. This is indicated by failure to find differences between the two treatments in second flushing behavior in July and August. Differences in stress maintained
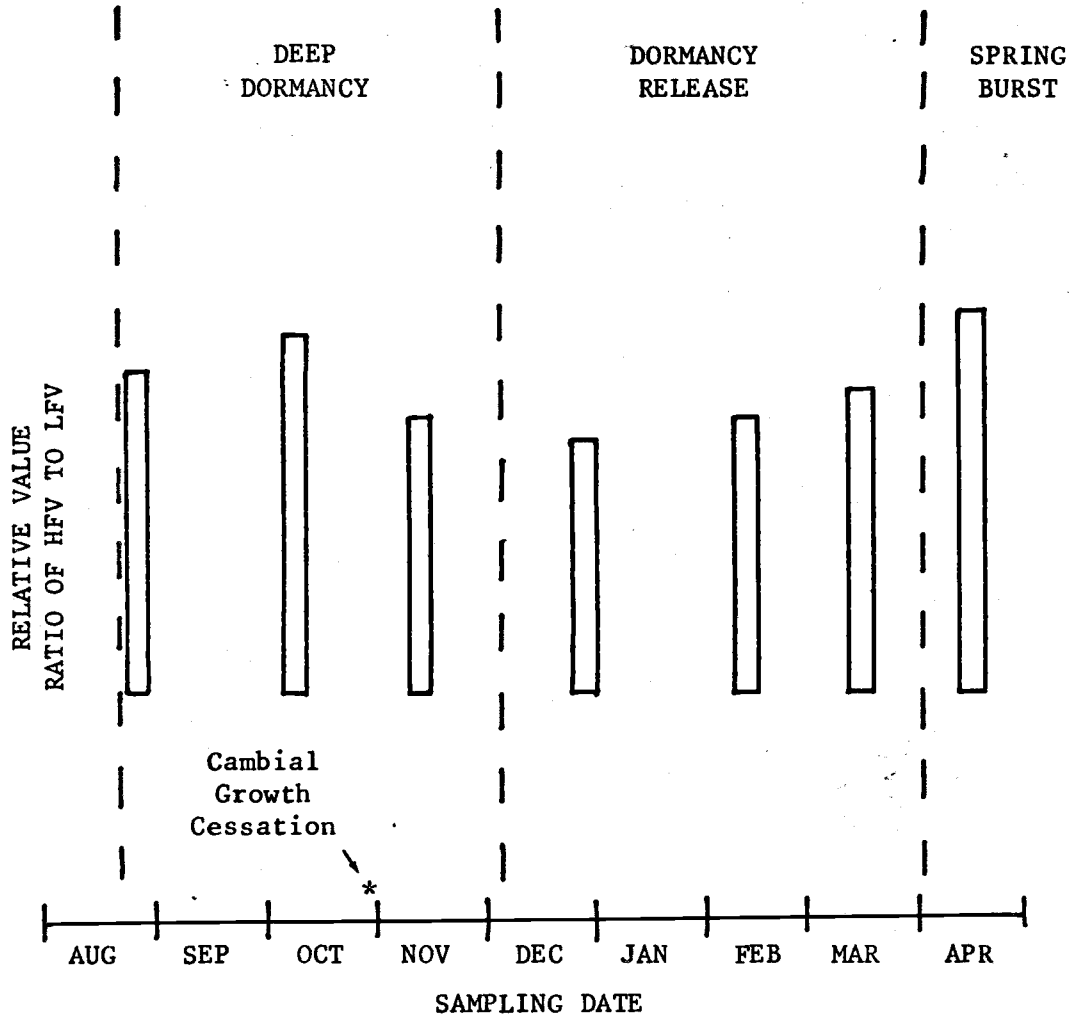
Figure 28. Change in trace form during phases of dormancy in Douglas-fir.
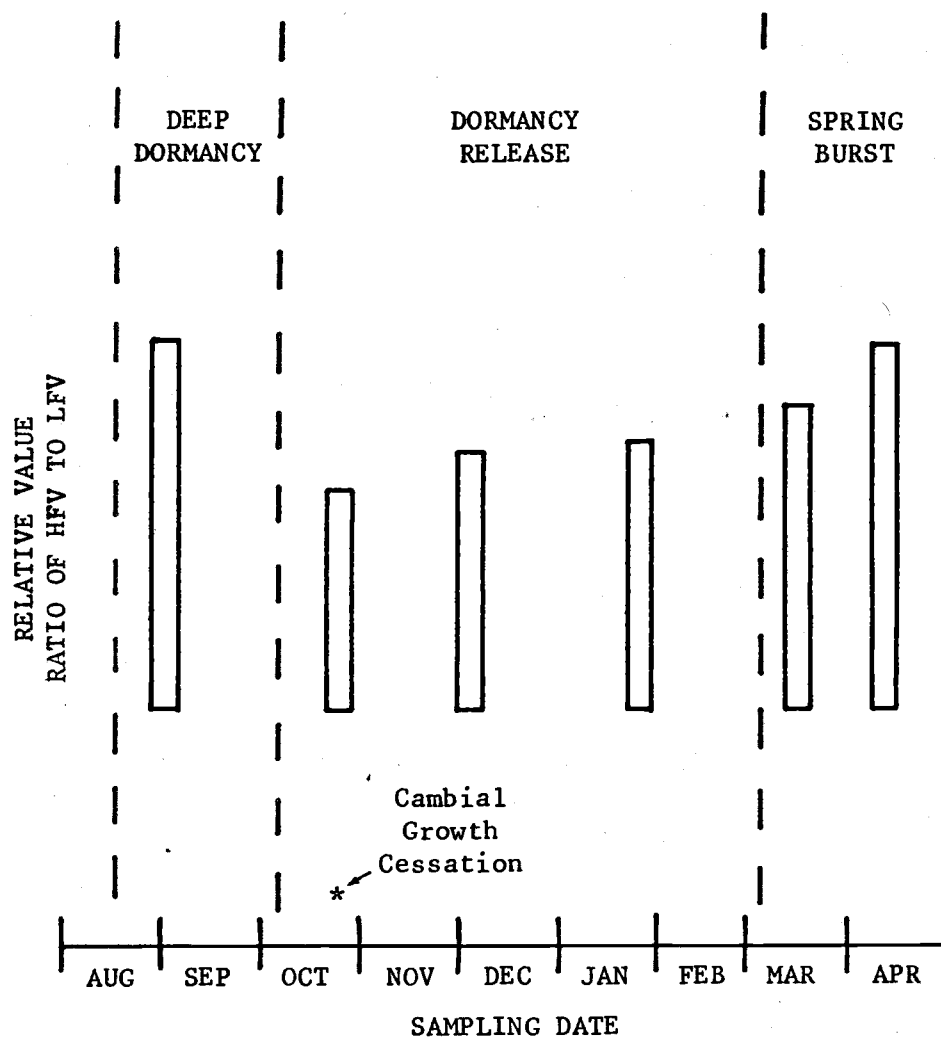
Figure 29.   Change in trace form during phases of dormancy in ponderosa pine.

between treatments also may not have been great enough. These seed-
lings had relatively low root to shoot ratios, and mid-day plant water
potentials of stressed and non-stressed seedlings may have been low
enough in both groups to elict stressed response. The fact that
stressed Douglas-fir seedlings consistently had more peaked wave
forms from August through February is not a random event, however, and
no doubt reflects some factor or factors influenced by water stress.
Differences in diameter at point of insertion of the electrode would
be an obvious possibility. No such differences were found to be
related to trace ratios, however.

Moisture stress affected needle length, apical dormancy, cam-
bial growth cessation, and trace form and amplitude of the ponderosa
pine seedlings. Stressed seedlings ceased cambial growth earlier and
flushed sooner in the growth chamber on all dates. This behavior is,
in general, consistent with moisture stress moving forward the dormancy
cycle of both lateral and apical meristems. Stressed seedlings sampled
on July 18 should have flushed later than non-stressed seedlings, since
the seedlings were entering, rather than leaving, the dormancy cycle.
However, the possibility of inhibition of terminal growth by elongating
needles or mature foliage confounds interpretation. It is possible
that such inhibition peaked earlier than July 18 for the stressed pine,
but was still developing in the non-stressed pine.

Fall and spring trace forms of the stressed pine indicated that
these seedlings entered into and exited from dormancy earlier than non-
stressed seedlings. Mid-winter trace forms did not indicate this
difference, however. Lack of correlation on all dates, as well as the
fact that similar patterns in trace form were observed in the fir where
no differences in dormancy development could be detected, dictates
caution in accepting these results as positive proof that the oscillo-
scope technique can detect differences in dormancy. Neither are the
results negative, however. Further research is indicated. Van den
Driessche (1969) similarly tried to measure the precision of his elec-
trical conductivity method for detecting frost hardiness in Douglas-
fir. He artificially reduced photoperiod in one of his beds to hasten
the onset of frost hardiness. Although conductivity measurements were

well correlated with hardiness differences in other experiments, they
did not indicate the change caused by this reduction of photoperiod.

Trace form indicated early cessation of cambial growth in the
stressed pine. Cambial growth cessation in both the fir and the pine
occurred during the period when trace form changed greatly. Thus there
is a possibility that trace form is influenced by the same factors that
control cambial growth cessation. Cambial growth may be controlled by
innate as well as environmental factors. Innate cambial dormancy has
not been conclusively demonstrated, however. Evidence that the cambium
of Douglas-fir has no innate rest has been presented by Lavender et al.
(1970), Worrall (1971), and Timmis and Worrall (1974).

Peaking observed in fir and pine trace forms with swelling of
buds in the spring may be more directly attributable to activity of
lateral meristems than to activity of apical meristems. Much research
has indicated that spring growth activity of terminal buds initiates
activation of lateral cambia (Perry, 1971). Lavender and Hermann
(1970) showed that growth of lateral meristems of Douglas-fir was stim-
ulated by export of materials from expanding buds. As the electrode
probe in my study was inserted through lateral and not apical meri-
stems, it would not be surprising if lateral activity was better
monitored than terminal activity.

Van den Driessche (1969) has linked cessation of cambial activity
in Douglas-fir with development of frost hardiness. He also noted that
the first large change in electrical conductivity in this species coin-
cided with cessation of cambial activity and the first autumn frosts.
Perhaps corresponding trace changes observed in this study indicate
frost hardiness development, in particular entry into the phase of
hardiness triggered by low temperatures.

Alden (1971) reported that the first substantial increase in
hardiness of Douglas-fir seedlings tested at Corvallis occurred in mid-
October after minimum daily temperatures dropped below 5°C. Similar
timing of seasonal temperature change was recorded during this study.
The strong correlation of changes in Douglas-fir trace form with daily
maximum temperature further suggests that hardiness may be detected by
the oscilloscope method. Prevailing temperature strongly influences

hardiness (Alden and Hermann, 1971). Trace form and temperature changes were not in phase for ponderosa pine, however.

Van den Driessche (1975) and Evert and Weiser (1971) detected frost hardiness by use of a ratio of impedance at two frequencies. The oscilloscope technique is an indirect measure of impedance over a range of frequencies. It would, therefore, not be improbable that the technique could also detect frost hardiness.

Although Douglas-fir and ponderosa pine traces exhibited similar seasonal trends, the character of the two sets of traces was markedly different from October through March. Ferguson et al. (1975) noted that deciduous shrubs exhibited wave forms that sloped to the left to some degree in mid-winter, while all species of the Pinaceae (including Douglas-fir and ponderosa pine) with the exception of larch had no slope to the left. Results with fir and pine in my research indicate less consistency in trace form within the Pinaceae than Ferguson et al. observed. It is doubtful that the oscilloscope method could be used to compare the growth or hardiness status of seedlings of two different species.

No research has related seasonal changes in electrical properties to actual changes in cellular anatomy and physiology. Indeed, anatomical and physiological investigations of seasonal changes alone or electrical properties alone are in their early stages in plant science. Particularly little has been published which relates cellular anatomical changes to dormancy development. However, frost hardiness literature contains observations of anatomical and physiological changes which may be the result of processes linked to dormancy as well as frost hardiness.

The principal cellular changes which are associated with the development of freezing tolerance are in the physical properities of membranes (Levitt, 1972). Electron microscopic studies by Pomeroy and Simenovitch (1971) of changes in phloem parenchyma cells of Robinia pseudoacacia with the onset of winter revealed augmentation of total protoplasm involving the plasma membrane specifically. The plasma membrane changed from relative smoothness and regularity in summer to a highly folded state in winter. In spring, when frost hardiness

decreased, the folding disappeared. Evidence of protoplasmic augmentation has also been found in other deciduous and coniferous species (Pomeroy et al., 1970).

Increases in area of membranes could change their properties as capacitors. Increasing permeability due to changes in the plasma membrane may also affect trace form. The leading edge of the trace reflects higher frequency responses than the trace viewed as a whole. A peaked trace may indicate both strong capacitance and strong resistance in the seedling tissue. Capacitive components of an electrical circuit can more easily pass high than low frequency currents. Thus high frequency currents may be able to bypass resistive components via capacitive pathways when low frequency currents cannot. If either capacitance decreases (as on death), or resistance decreases (as on death or with increased permeability associated with hardiness), differences between the leading edge of the trace and the remainder of the trace would be reduced. The trace would become square. The actual situation in plant tissue is doubtless much too complex for such a simplistic explanation of trace form change, however.

An external electric current must be applied to seedling tissue if impedance is to be measured. This current changes the conditions which it is applied to measure. Among the physiological effects of applied currents are changes of charge on capacitor surfaces and leakages through capacitive resistances (Fensom, 1966). Insertion of the electrode probe in the seedling also causes tissue damage. This damage will distort readings. The significance of these current and damage factors is not known. In a study of a comparative nature such as this one, it is assumed that these factors exert the same influence in all measurements.

In summary, the oscilloscope technique definitely detects seasonal change in seedling physiology. It is not, however, detecting processes which are in phase with dormancy development in Douglas-fir. The technique may be capable of detecting phases of dormancy in ponderosa pine. Further background is necessary on the chilling requirements of this species before a definitive conclusion can be reached. There are strong indications that the oscilloscope technique

may detect degree of cold acclimation in both Douglas-fir and ponderosa pine.

RESULTS OF PART II

INVESTIGATION OF RELATIONSHIP BETWEEN OSCILLOSCOPE TRACE CHARACTERISTICS
AND SEEDLING SURVIVAL POTENTIAL

Effect of Lifting Date and Storage Period on Growth and Survival
Parameters

Flushing Speed and Length of Growing Season

The first lateral bud to flush on a seedling did so an average
of two weeks before the terminal bud. Patterns in lateral flushing
were otherwise very nearly the same as those for terminal flushing,
and only the latter will be evaluated here. Length of growing season
for the terminal shoot was highly dependent on the speed with which
the terminal bud burst in the spring (Figs. 30 and 31). Correlation
between these two factors was very high (R = -.98). Analysis of vari-
ance of growing season by lifting date and storage period showed the
effect of lifting date to be highly significant, the effect of storage
to be significant, and the interaction of the two factors to be highly
significant. Seedlings lifted February 8 or March 24 and stored eight
weeks were planted after flushing of treatments already in the frames
had begun. This resulted in reduction in length of growing season.
Storage increased or had relatively little effect on length of growing
season for treatments lifted in the fall or mid-winter.

Height-growth Ratio

Both lifting date and storage period had highly significant
effects on height growth. That these two factors interact strongly
can be seen in Figure 32. The effect of storage, particularly eight
weeks of storage, was much more deleterious in the fall than in the
winter months. The no storage treatment lifted on October 11 had the
best height growth of all eighteen treatments, while the eight week
storage treatment lifted October 11 had the second lowest height
growth. Lowest height growth of all treatments was made by the treat-
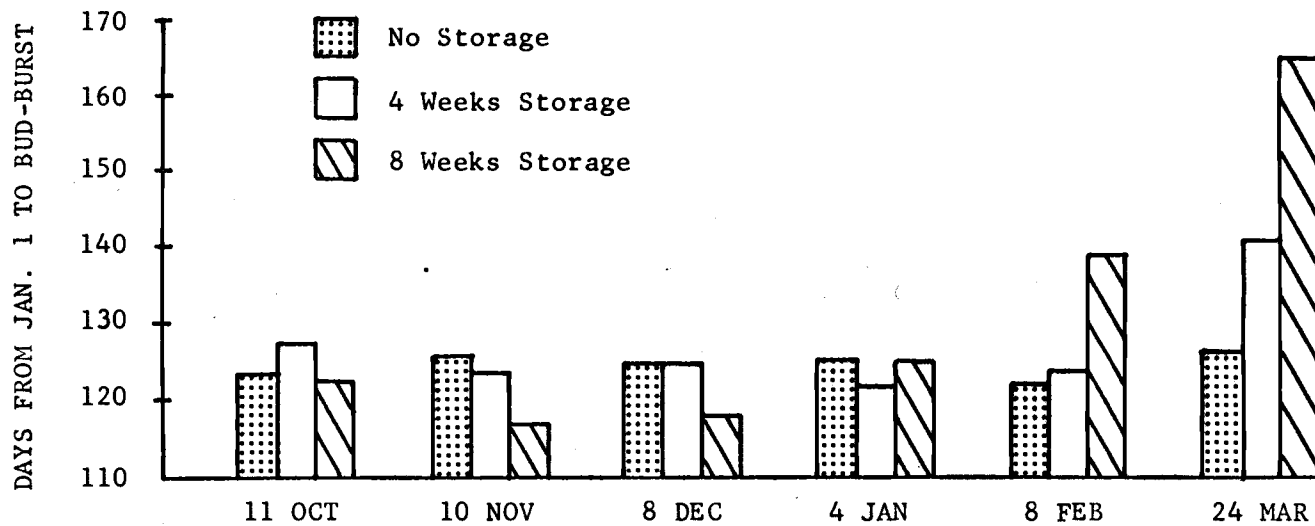ment lifted March 24 and stored eight weeks.

Figure 30. Variation of flushing speed of terminal bud with lifting date and storage period.
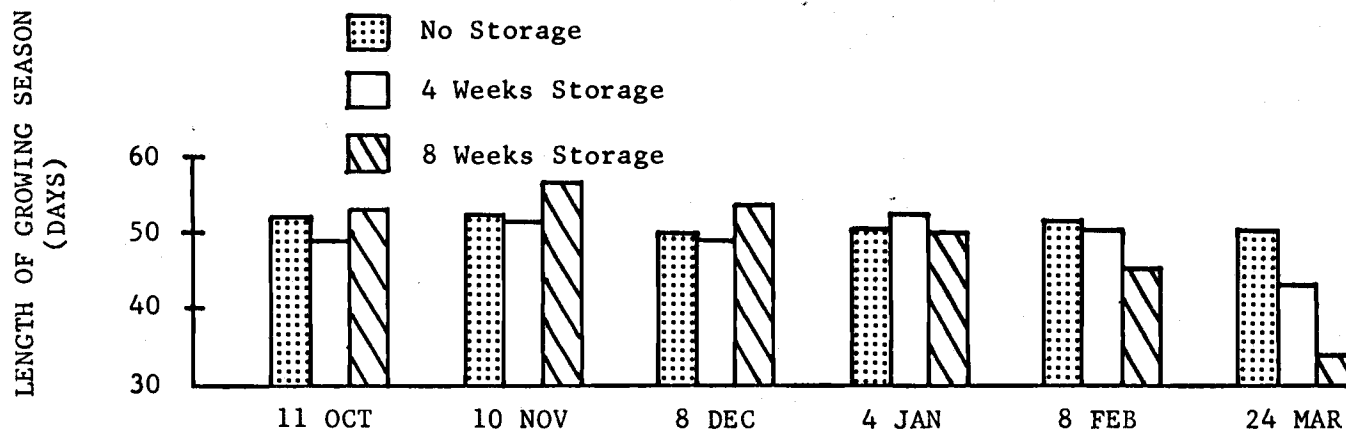
Figure 31. Variation of length of growing season for the terminal shoot with lifting date and storage period.

75

Needle elongation

The effect of lifting date on the length of needles from the mid-section of the terminal shoot was highly significant. The effect of storage was significant. In this case, however, interaction of these two factors was not significant. Figure 33 illustrates the regular drop in needle length with increasing storage on any one lifting date. Although significant interaction of lifting and storage factors was not found, decrease in needle length with increasing storage was most pronounced for the fall lifting dates.

Photographs of typical seedlings from the no storage and eight week storage treatments illustrate the effects of lifting date and storage on height and needle length (Fig. 34). Height-growth ratio and needle length were highly correlated (R = .93).

Survival

Despite seedlings receiving no rain or irrigation after April 15, plant moisture stress never reached levels that would have provided a good test of survival abilities. Lowest mean pre-dawn water potential was -13.1 atm. Survival was 100 percent in all no storage treatments (Fig. 35). Four week storage resulted in reduced survival only when seedlings were lifted October 11 or November 10, and survival for these dates would be considered acceptable in most regeneration efforts. Eight week storage, however, resulted in low survival for both October 10 and March 24 lifted seedlings. All seedlings which survived on the last four lifting dates did so without severe damage to the terminal shoot. Four and eight week storage treatments of the first two lifting dates contained seedlings which survived but suffered winter damage to the terminal shoot. Analysis of variance for the four and eight week storage treatments separately showed the effect of lifting date on survival to be significant for the four week treatments and highly significant for the eight week treatments.
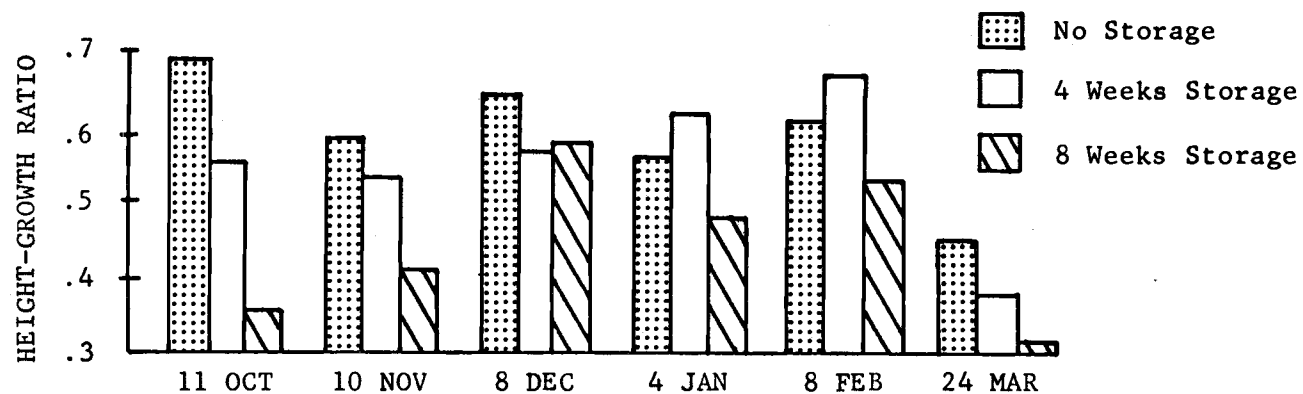
Figure 32. Variation of height-growth ratio with lifting date and storage period.
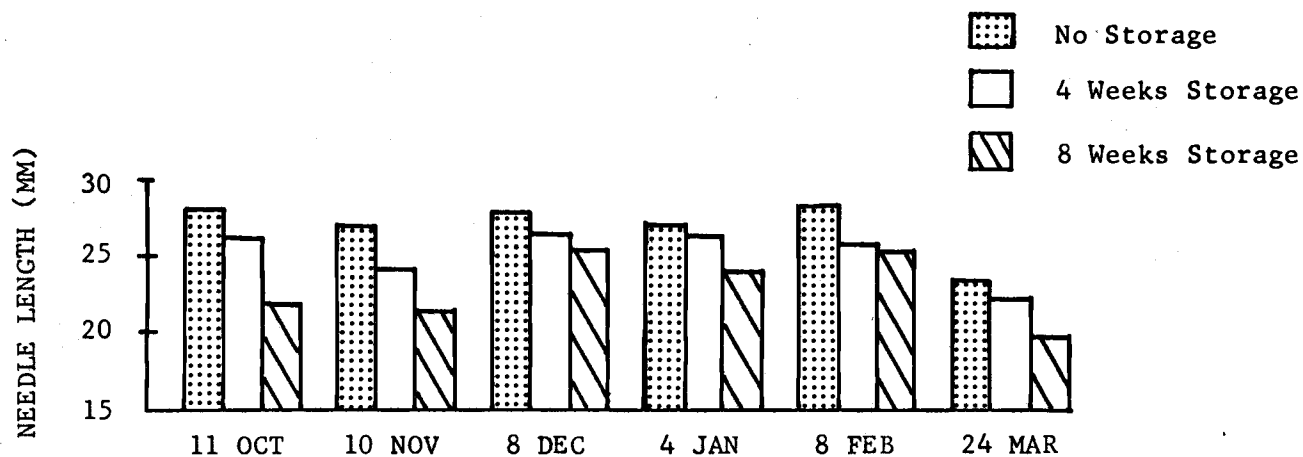
Figure 33. Variation of length of needles on the terminal shoot with lifting date and storage period.

a. October 11 lifted. Left: not stored. Right: stored eight weeks.

b. November 10 lifted. Left: not stored. Right: stored eight weeks.

c. December 8 lifted. Left: not stored. Right: stored eight weeks.

d. January 4 lifted. Left: not stored. Right: stored eight weeks.

e. February 8 lifted. Left: not stored. Right: stored eight weeks.

f. March 24 lifted. Left: not stored. Right: stored eight weeks.

Figure 34.   Effects of lifting date and storage period on height and needle growth of Douglas-fir seedlings.   Photos were taken on September 15, 1977.
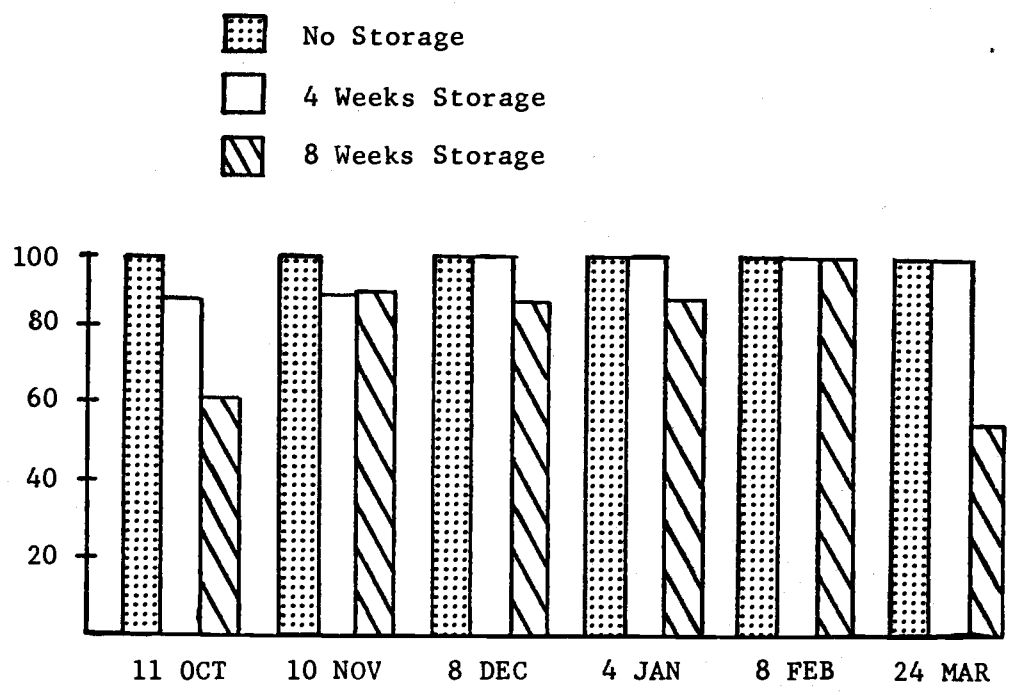
Figure 35. Variation of percentage of seedlings surviving with lifting date and storage period.

Effect Of Lifting Date and Storage Period on Oscilloscope Trace
Characteristics

Trace form at time of lifting had a seasonal trend similar to
that of the potted Douglas-fir in Part I of this investigation (Fig.
36). Forms were peaked on October 11 and March 24, very slightly
peaked on November 10 and February 8, and approximately square on
December 8 and January 4. Eight weeks of storage on October 11 caused
trace form to resemble that of traces of freshly lifted seedlings on
the mid-winter dates, while eight weeks of storage on March 24 caused
trace form to peak considerably more than in any of the other seven-
teen treatments.

Analysis of variance of each of the three voltage ratios assigned
highly significant effects to both lifting date and storage period.
Interaction of these two factors was also highly significant. Changes
in the three ratios were nearly identical and only those for the ratio
of HFV to MFV are presented here (Fig. 37). Both lifting date and
storage period had highly significant effects on this ratio. Inter-
action of lifting date and storage period was significant. The oppo-
site effects of storage on the ratio of HFV to MFV on October 11 and
March 24 are due largely to HFV dropping with October 11 treatments
versus MFV dropping with March 24 treatments. Storage had erratic
effects on LFV.

Correlation of Trace Variables at Time of Lifting With Growth
And Survival

Survival and height growth of unstored October lifted seedlings
was excellent although peaked forms on that date differed greatly from
the square forms of mid-winter lifted seedlings. It was evident that
no correlation of trace form at time of lifting with survival and
growth would be significant if all treatments were used. On the other
hand, there was a very definite relationship between trace form at
lifting and growth and survival of seedlings stored eight weeks. There

Lifting Date	No Storage	4 Weeks Storage	8 Weeks Storage
OCT 11			
NOV 10			
DEC 8			
JAN 4			
FEB 8			
MAR 24			

Scale: Ver. 1 mm. = 0.012 V
Hor. 1 mm. = 0.026 msec

Figure 36.   Trace form at time of planting for lifting and storage
treatments. The trace form at time of planting for the
no storage treatment on a given lifting date is the trace
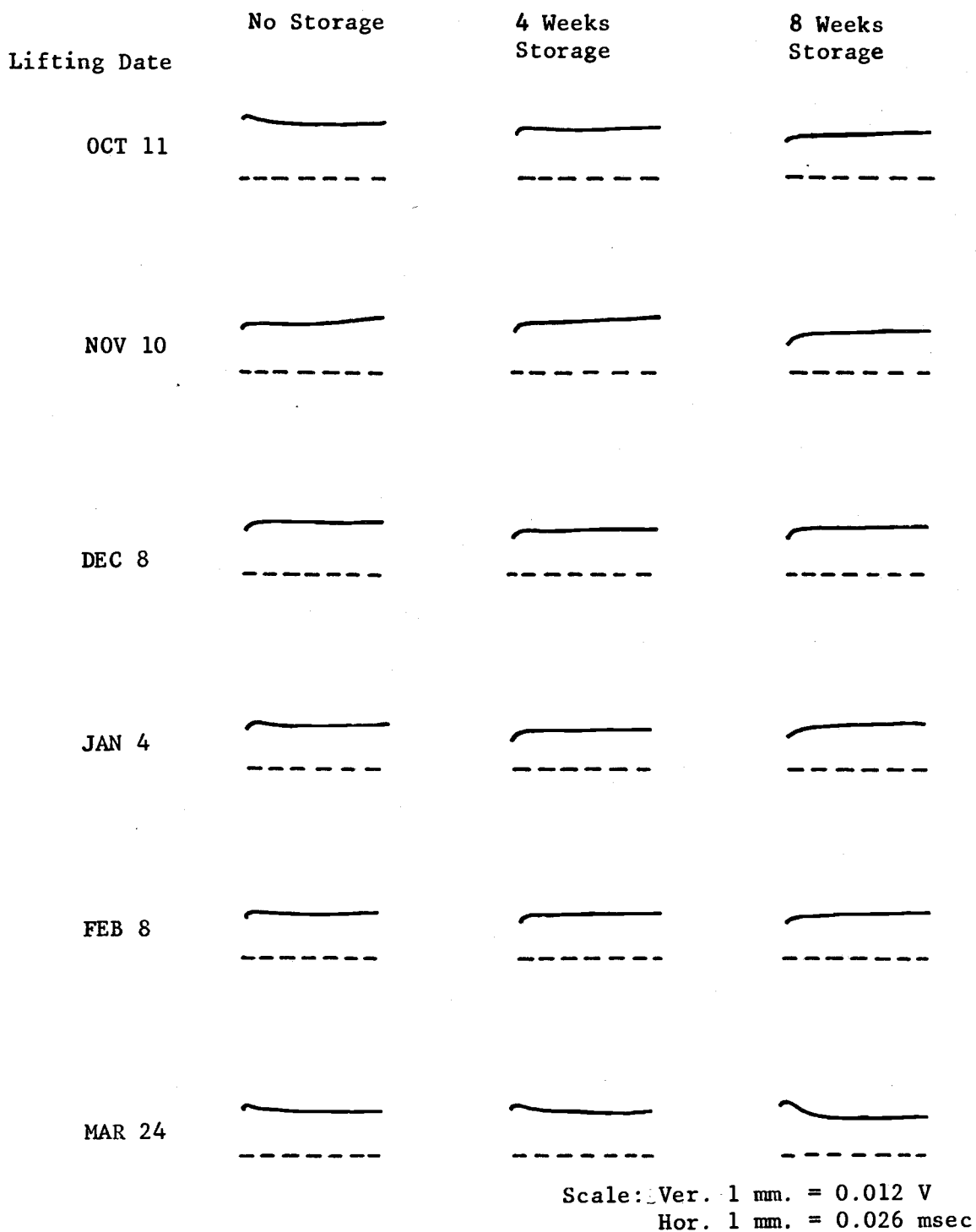form at time of lifting for all three storage treatments
on that date.
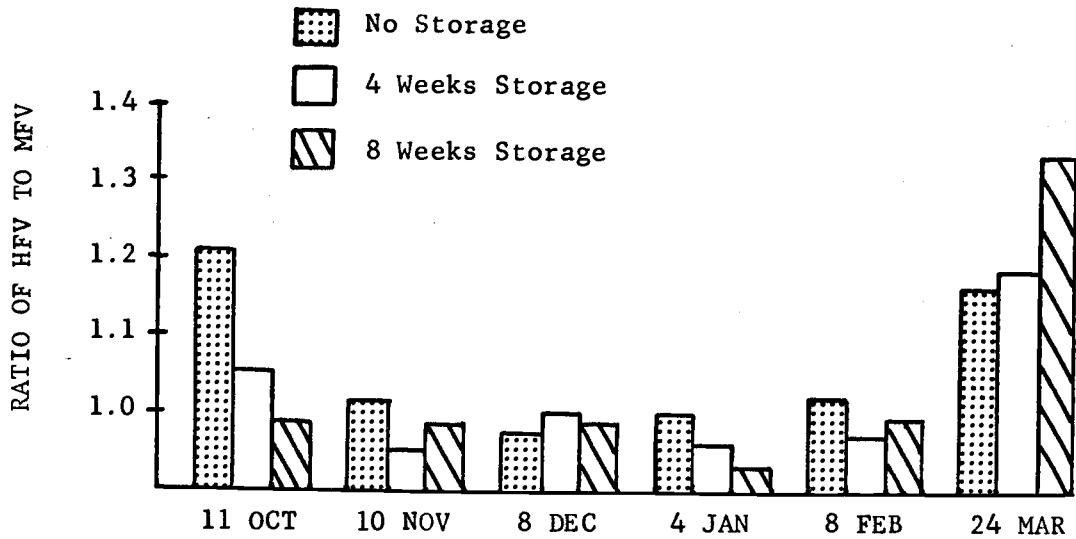
Figure 37. Variation of the ratio of high frequency voltage (HFV) to mid-frequency voltage (MFV) with lifting date and storage period.

were significant correlations of the ratio of HFV to MFV with height
growth (R = -.85), with percentage of seedlings surviving (R = -.90),
and with percentage of seedlings surviving undamaged (R = -.93) (Figs.
38, 39, and 40). Correlation of the ratio of HFV to MFV with needle
elongation was not significant. Scattergrams of survival correlations
highlight the marked difference in survival of seedlings with peaked
versus seedlings with square traces. The same definite delineation
would be present for height growth if it were not for the relatively
poor performance of November lifted seedlings.

Significant correlations of height growth and survival with the
ratio of HFV to MFV were also found when both four and eight week
tratments were used in the regressons, but correlation coefficients
were lower (.63 - .71). Correlations were not improved by leaving
out the February and March lifting dates.

Correlation of Trace Variables at Time of Planting With Growth
and Survival

A cross-tabulation of individual seedlings from all treatments
by trace form class at time of planting and height growth class was
made. Trace form classes were combined to eliminate cells with poor
representation. Values of chi square and gamma indicated that sorting
of seedlings in trace form classes could help predict height growth
but not to a very large degree (Table 4).

Regression of treatment height growth means on voltage ratios one
at a time yielded nonsignificant results in all cases. Only regression
with MFV alone yielded significant results. Correlation was low, how-
ever (R = .47). When only values from the first four lifting dates
were used in the regression, the ratio of MFV to LFV became the trace
variable with the highest ability to predict height growth. However,
this correlation was not significant. Predictive abilities were there-
fore not increased by eliminating spring treatments from the analysis.
Regressions which used all points rather than means yielded correlation
coefficients less than .14, indicating high within sample variablity.

Considering the high correlation between height-growth ratio and
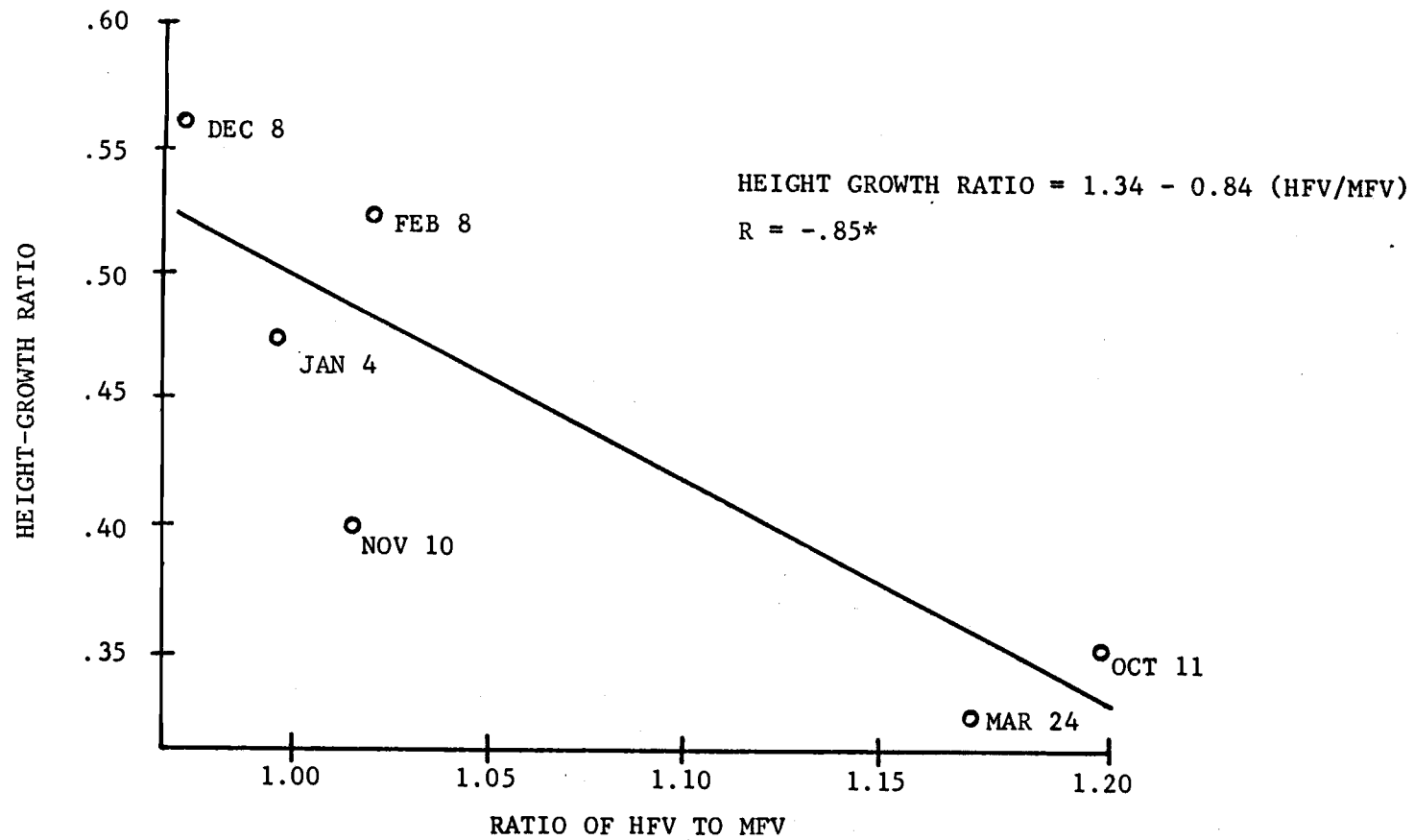
Figure 38. Regression for seedlings stored eight weeks of height-growth ratio on the ratio of high frequency voltage (HFV) to mid frequency voltage (MFV) at time of lifting.
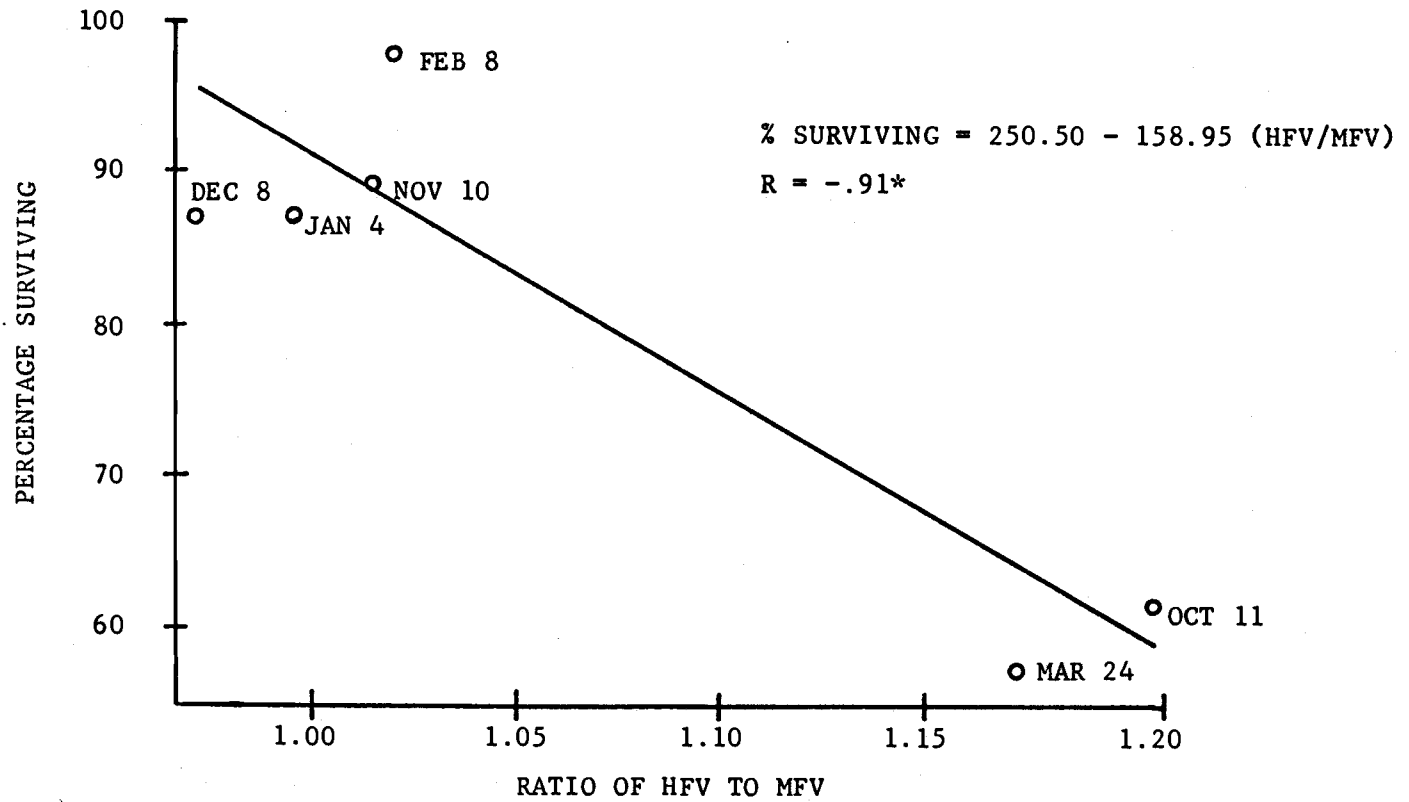
Figure 39. Regression for seedlings stored eight weeks of percentage of seedlings surviving on the ratio of high frequency voltage (HFV) to mid frequency voltage (MFV) at time of lifting.
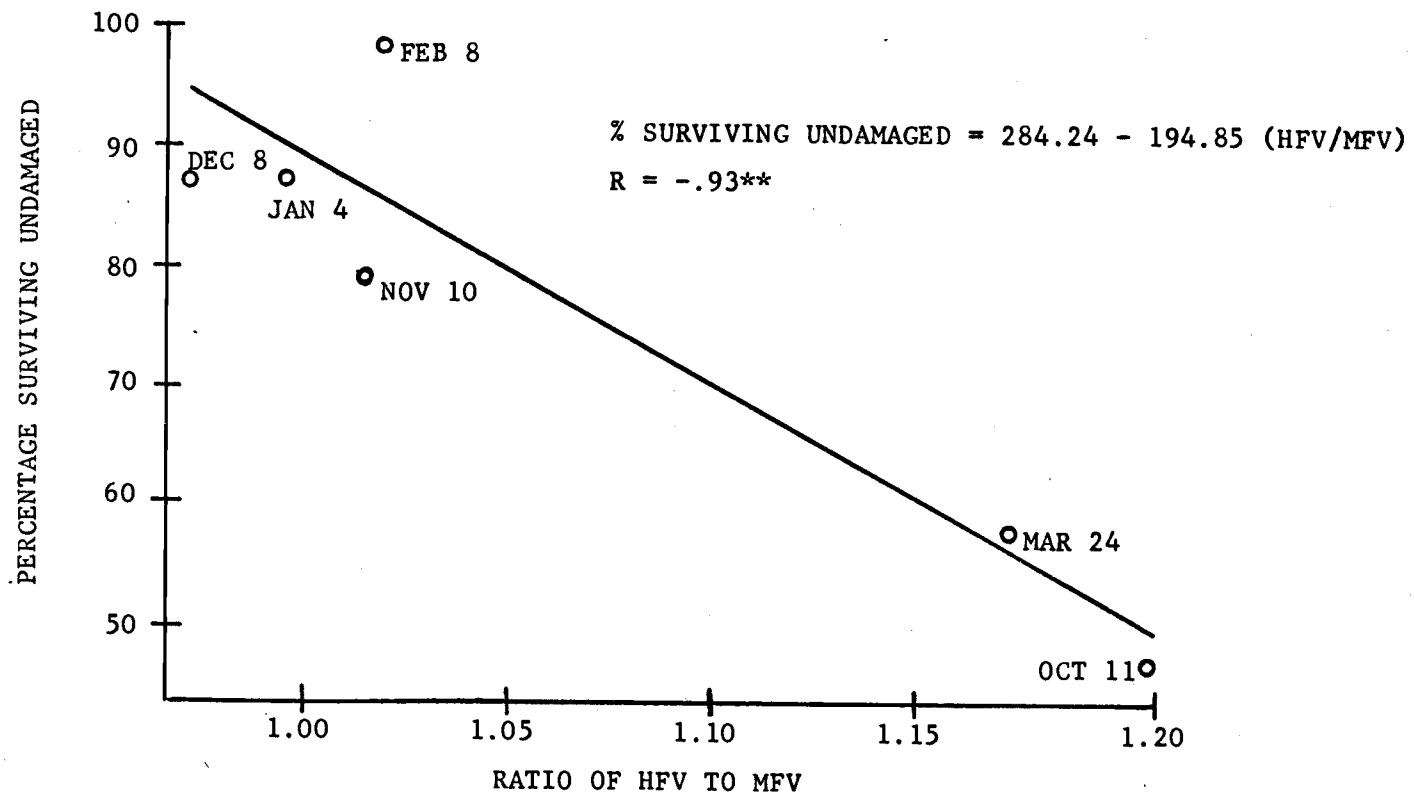
Figure 40. Regression for seedlings stored eight weeks of percentage of seedlings surviving undamaged on the ratio of high frequency voltage (HFV) to mid frequency voltage (MFV) at time of lifting.

	Count Row % Col. % Tot. %	Height-Growth Ratio			Row Total
Trace Form Class(es)		.12 - .319	.32 - .699	.70 - 1.4	
1		10 37.0 20.4 2.4	13 48.1 4.4 3.1	4 14.8 5.6 1.0	27 6.5
2,3		16 16.0 32.7 3.9	69 69.0 23.5 16.7	15 15.0 21.1 3.6	100 24.2
4,5,6		10 9.2 20.4 2.4	82 75.2 28.0 19.9	17 15.6 23.9 4.1	109 26.4
7		5 5.3 10.2 1.2	68 72.3 23.2 16.5	21 22.3 29.6 5.1	94 22.8
8,9		8 9.6 16.3 1.9	61 73.5 20.8 14.8	14 16.9 19.7 3.4	83 20.1
Column Total		49 11.9	293 70.9	71 17.2	413 100.0

Chi-square = 24.7**

Gamma = .18

Table 4.   Cross-tabulation of trace form and height-growth ratio classes.

needle length, one would not be surprised of the relationship between
trace character and needle length was similar to that between trace
character and height growth. This was the case. Sorting of seed-
lings by needle length and trace form classes is given in Table 5.
Although chi-square was highly significant, the gamma statistic for
this contingency table indicates that ordering seedlings as to prob-
able needle growth of the basis of trace form at time of planting
would meet with results little better than random ordering. Regression
of treatment means and individual values of needle length on trace
variables yielded results very nearly identical to those for height
growth ratio. Trace variables taken singly or in pairs are poor
predictors of potential growth.

Overall survival was high, but within certain treatments sur-
vival was low. This made it possible to draw conclusions from sur-
vival data. Table 6 summarizes the distribution of mortality and
damage in trace form classes. Chi-square for this cross-tabulation
was not significant. Combining dead and damaged classes, in effect
testing if traces were distributed differently for healthy versus
injured trees, yielded a chi-square with a lower but still nonsignif-
icant probability.

Single and two factor regression of percentage of seedlings
surviving in each treatment on means of trace variables for each treat-
ment in no case yielded significant results. This was also true when
the percentage of seedlings surviving undamaged was used as the res-
ponse variable. When only the results from the first four lifting
dates are considered, the rato of MFV to LFV can account for a signifi-
cant but small part of the variation in survival (R = .61).

Needle Length (mm)

Trace Form Class(es)	Count Row % Col. % Tot. %	14 – 19.9	20 – 29.9	30 – 45	Row Total
1		9 47.4 20.5 3.1	9 47.4 4.5 3.1	1 5.3 2.2 .3	19 6.6
2,3		12 18.5 27.3 4.2	41 63.1 20.6 14.2	12 18.5 26.7 4.2	65 22.6
4,5,6		6 8.2 13.6 2.1	53 72.6 26.6 18.4	14 19.2 31.1 4.9	73 25.3
7		6 8.6 13.6 2.1	50 71.4 25.1 17.4	14 20.0 31.1 4.9	70 24.3
8,9		11 18.0 25.0 3.8	46 75.4 23.1 16.0	4 6.6 8.9 1.4	61 21.2
Column Total		44 15.3	199 69.1	45 15.6	288 100.0

Chi-square = 26.5*

Gamma = .05

Table 5. Cross-tabulation of trace form and needle length classes.

<center>Survival Classes</center>

Count Row % Col. % Tot. % I	Dead	I	Damaged	I	No Damage I	Row Total
Trace Form Class(es)						
1	4 13.8 13.8 .9	I I I I	0 0 0 0	I I I I	25 86.2 6.4 5.8	29 6.7
2,3	7 6.8 24.1 1.6	I I I I	2 1.9 16.7 .5	I I I I	94 91.3 24.0 21.8	103 23.8
4,5,6	4 3.6 13.8 .9	I I I I	2 1.8 16.7 .5	I I I I	105 94.6 26.9 24.3	111 25.7
7	11 10.6 37.9 2.5	I I I I	4 3.8 33.3 .9	I I I I	89 85.6 22.8 20.6	104 24.1
8,9	3 3.5 10.3 .7	I I I I	4 4.7 33.3 .9	I I I I	78 91.8 19.9 18.1	85 19.7
Column Total	29 6.7		12 2.8		391 90.5	432 100.0

Chi-square = 8.34 (not significant)

Gamma = -.02

Table 6. Cross-tabulation of trace form and survival classes.

DISCUSSION OF RESULTS OF PART II
INVESTIGATION OF RELATIONSHIP BETWEEN OSCILLOSCOPE TRACE CHARACTERISTICS
AND SEEDLING SURVIVAL POTENTIAL

The deleterious effect of lifting date on survival of stored
Douglas-fir seedlings found in this study is in accord with results
of Lavender (1964) and Lavender and Wareing (1972). Lavender (1964)
noted poorer survival of seedlings lifted in October, whether or not
the seedlings were stored. However, in this study unstored seedlings
all survived. Lack of agreement in results here may be due to
Lavender's outplanting site being more severe. Different nursery
irrigation regimes also may account for inconsistency in results.
Irrigation of the seedlings used in this study was reduced in late
July and August to facilitate entry of seedlings into dormancy. Con-
tinued heavy irrigation during this time period can have the opposite
effect (Hermann et al., 1972). The results of this study do agree
with those of Winjum (1963) who found that seedlings of Douglas-
fir planted immediately showed little difference in survival due to
lifting date, while storage in fall or spring reduced survival. He
found, however, that height growth was not reduced for stored seed-
lings, regardless of when they were lifted. In contrast highly signif-
icant interacting effects of lifting date and storage on height growth
were found in this study.

The poor survival of the seedlings lifted March 24 and stored
for eight weeks can be attributed at least in part to the seedlings not
having time to develop a good root system before the onslaught of sum-
mer stresses. Hermann (1967) found seasonal variation in sensitivity
of Douglas-fir seedlings to exposure of roots. Seedlings lifted in
March had greater sensitivity than seedlings lifted in January. Hardly
any difference between March and January lifted seedlings was found,
however, when both were provided with ample water in a controlled
environment. Krueger and Trappe (1967) observed with Douglas-fir seed-
lings growing in the Willamette Valley that root activity was high pre-
vious to bud-break but practically stopped while shoots were

elongating. The Douglas-fir seedlings in my study lifted March 24 and
stored eight weeks began shoot elongation very soon after outplanting.
Little root development may have taken place before this shoot elong-
ation began. Growing season of shoots was short. Seedlings which
could not set buds relatively soon after flushing did not survive.

Poor survival and growth of stored seedlings lifted in October
and November cannot be attributed to the above causes. These seed-
lings had growing seasons equal to or longer than those of other treat-
ments. The treatment lifted November 11 and stored eight weeks was the
first to flush. Previous studies have found early flushing to be a
good indicator of a vigorous Douglas-fir seedling (Heiner and Lavender,
1972). Foliage of many of these November-lifted seedlings, however,
was damaged by winter cold. Early bud-burst may have been a "wound"
response to this damage, and, as such, not a reliable gauge of seed-
ling vigor.

Early fall months correspond to the dormant steady state for
Douglas-fir. Lifting during this period may upset the balance of
growth-promoting and growth-inhibiting hormones in the seedling
(Lavender, 1964). Krueger and Trappe (1967) proposed that later fall
lifting may be more successful due to pre-lifting buildup of food
reserves. A combination of factors is no doubt responsible for the
results obtained.

Although every effort was made to minimize differences due to
weather conditions at time of lifting and planting, these differences
undoubtedly influenced results. Height growth of stored seedlings
lifted in January was lower than that of stored seedlings lifted in
December. This may have been due to the January seedlings being
under high water stress when lifted. Very cold soil temperatures
combined with clear weather to lower plant water potential to less than
-22 atm. during lifting.

Trace form at time of lifting was a good indicator of potential
survival of seedlings that were stored eight weeks. It was also a
fair indicator of height growth of these stored seedlings. The rela-
tively poor height growth of November lifted seedlings with square
traces detracted from the relationship. Poor needle growth of

November lifted seedlings made the correlation between trace form at time of lifting and needle growth of stored seedlings nonsignificant. This poor growth performance of November lifted seedlings indicates that on a site more severe than that of this study, these seedlings may not have survived as well as later lifted seedlings. A square trace form at time of lifting may not be a guarantee of survival for a seedling which will be planted on a severe site.

Of the seedlings lifted and planted immediately, height and needle growth were significantly reduced only for the March lifted seedlings. This difference was well signalled by peaking in trace form. As all seedlings planted without storage on all lifting dates survived, it is not possible to say whether or not trace character was capable of indicating differences in survival potential of these seedlings. Seedlings lifted in October and stored had low survival. However, height and needle growth of October lifted seedlings planted immediately was superior to that of all other treatments. Hormonal and food reserve balances may not be disrupted when seedlings are planted immediately.

In contrast to the good correlation of trace character at time of lifting with survival of stored seedlings, correlation of trace character at time of planting with survival and growth factors was poor. There were cases in which trace form and amplitude at time of planting reflected growth and survival differences. For example, growth, survival, and the ratio of HFV to MFV all drop notably with increasing storage of October lifted seedlings. However, October lifted seedlings stored eight weeks have a form very similar to those of mid-winter lifted seedlings whose survival was far superior. Analyzing the data for all lifting dates or even for just fall and winter lifting dates, only three significant correlations were found of trace character with growth or survival. Two of these were of height and of needle growth with amplitude at one point on the trace (MFV). This bears no relationship to "squaring off" of trace form. The third significant correlation, that of the ratio of MFV to LFV with percentage of seedlings surviving undamaged, also does not reflect peaking or rounding of the leading edge of the trace.

Trace character is apparently not capable of detecting vigor per se but only seasonally related physiological factors. Trace form peaking less and less with increasing storage in early fall suggests that the oscilloscope technique is detecting processes associated with fulfillment of chilling requirements. The results of Part I of this investigation, however, indicated that trace form change in Douglas-fir was not "in phase" with fulfillment of chilling requirements. Trace form change did not indicate release from deep dormancy. This release is a key factor in determination of physiological fitness of Douglas-fir for planting (Lavender and Wareing, 1972). Trace form changes should not be the only guidelines used to determine date of lifting of planting stock.

SUMMARY

1. Oscilloscope technique results should not be used as the sole criterion of depth of dormancy in Douglas-fir.

2. Oscilloscope technique results should not be used as the sole criterion of depth of dormancy in ponderosa pine until other studies have confirmed the low chilling requirements for the species here indicated.

3. The oscilloscope technique may indicate degree of cold acclimation of Douglas-fir and ponderosa pine seedlings. This possibility deserves further examination. Although other electronic methods for detecting frost hardiness have been developed, the oscilloscope technique allows for examination of a wide range of electrical response.

4. Use of the oscilloscope technique as the sole criterion for determination of lifting suitability of Douglas-fir bare root stock is not recommended. A peaked wave form in the fall or spring is a definite indicator that survival and growth of stored stock will be poor, but does not necessarily mean that stock planted immediately will not do well. A square signal does not guarantee that stored stock will survive on severe sites. It must be emphasized that this technique detects lifting suitability based on seasonal changes in physiology alone. The oscilloscope technique shows no promise of detecting seedlings unsuitable for planting for other reasons.

5. The oscilloscope technique may have valuable applications not examined or discussed here. Zaerr (1972) has shown that the technique is capable of distinguishing between live and dead tissue. Further research involving use of the oscilloscope technique should be encouraged based on the results here reported.

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