AN ABSTRACT OF THE THESIS OF

Ronald Roy Carlton for the degree of Master of Science

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Title: Influences of the Duration of Periodic Sway on the Stem Form Development of Four-year-old Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco)

Abstract approved: H. Richard Holbo

Stem form development of trees in response to wind has been established in the literature to be a response to stem sway induced by the wind. The response is manifested in modifications to height and diameter growth which strengthen the stem against wind stresses. Experiments in the literature show that significant responses result from short durations of sway daily. An experiment exploring the growth responses resulting from a wide range of daily durations of sway was conducted. Also, the influence of timing of periods of sway during the growing season and during different seasons was examined.

The pooled mean leader length for seedlings swayed different durations daily at a rate of 0.8 Hz was 86 per cent of that for unswayed controls. Leader length for seedlings swayed only 10 seconds daily were not significantly different from unswayed controls. Growth during certain stages of apical bud burst seems to have been retarded by the longer durations of sway. Growth ring increment on the compression side of the stem increased due to swaying, with the greatest response due to a 10 second daily duration and the least due to a 10 hour duration. Growth ring increment on the tension side
responded in like manner, the longer durations of sway were not significantly different from the unswayed controls, but the short durations resulted in significant increases.

In a separate experiment, seedlings were swayed 2.5 hours daily. Treatments were begun with the initiation of bud burst, and terminated after periods of 6, 12, and 18 weeks. Leader length growth was not found to differ between controls and the 6-week swaying treatment, but was reduced due to longer treatment periods. The stem diameter in the direction of sway increased as the period of swaying increased. These results suggest that the response system directing height and diameter growth loses its effect, in time, if swaying is terminated before the completion of bud burst.

A field experiment was conducted measuring growth responses of 17-year-old trees which were prevented from natural wind sway during certain seasons of the year. No differences between treatments were found. Wind strength at the study site may have been inadequate to provide measurable differences.
Influences of the Duration of Periodic Sway on the Stem Form Development of Four-year-old Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco)

by

Ronald Roy Carlton

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APPROVED:

[Signature]
Assistant Professor of Forest Engineering
in charge of major

[Signature]
Associate Professor of Forest Management

[Signature]
Head of Department of Forest Engineering

Dean of Graduate School

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INFLUENCES OF THE DURATION OF PERIODIC SWAY ON THE STEM FORM DEVELOPMENT OF FOUR-YEAR-OLD DOUGLAS-FIR (Pseudotsuga menziesii (Mirb.) Franco)

I. INTRODUCTION

The effect of wind on the stem form development of forest trees has been studied for over one hundred years. It has become established during that time that sway due to wind induces morphological modifications of tree stems manifested by changes both in height growth, and in diameter growth. These modifications to stem form enable the tree to withstand stresses caused by the wind. Forest practices which reduce stem density of forest stands increase wind forces within the forest. The new wind regime has often been responsible for significant losses due to windthrow and breakage. In time, adjustments are made by the stand and by individual trees which stabilize the stand and prevent further losses.

The mechanism which controls the response to wind sway is not well understood. It has been found that only very short durations of stem sway daily are required to induce striking changes in stem morphology (Neel and Harris 1971).

The experiments reported here were undertaken to examine in closer detail the growth responses resulting from controlled manipulations of the amount and timing of the stem sway which is received by a tree. In particular, the experiments address the growth responses in Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, due to the influence of: (1) regimes of different daily durations of periodic stem
sway, (2) differences in timing of the periods of stem sway with respect to plant growth stage during the growth season, and (3) differences in timing of the periods of stem sway with respect to the annual cycle, i.e. the season of the year.
II. REVIEW OF LITERATURE

There are many effects on the development of forest stands and individual trees that result from wind. Spurr and Barnes (1973) note that wind is important in regulating evapotranspiration, carbon dioxide exchange, the illumination of leaves (by the twisting and turning of interfering foliage), the morphology of tree crowns and stems, seed and pollen dissemination, as well as its role in windthrow and breakage. The disruptive influence of swaying trees on the mechanical strength of sloping soils is apparently responsible for mass slope failure in some instances, and this detrimental effect to slope stability may outweigh the beneficial cohering effects of the root mass (Cheng 1972). Many direct and indirect effects are at work in each of the items noted. Wind is, clearly, a major instrument in many processes of a forest biogeocenosis throughout its lifecycle.

In October, 1962, a single storm event in the Pacific Northwest, by means of its associated winds, was responsible for uprooted and broken trees on a magnitude approaching the amount normally harvested annually. The lack of heavy rains accompanying this storm may have spared additional losses (Decker et al. 1962). Such storms are infrequent, but even the more common losses due to wind effects in less dramatic storms may be appreciable. Zavitkovski (1968) notes, for example, that a single storm can be responsible for foliage loss equivalent to one year’s needle growth in young Douglas-fir, i.e. a loss of 17 per cent of the photosynthesizing surface. Losses of this
sort may be reflected in lower harvestable yields, just as the more obvious windthrow and breakage are.

The susceptibility to windfall or breakage is variable among individual trees, and apparently changes over time. Weidman (1920a,b) reports that a September storm resulting in great losses was followed by a storm of equivalent magnitude in January, which resulted in no losses. This observation suggests that adjustments may be made within forest stands to prevent further loss. Considerable work has been undertaken to supply guidelines to foresters for the prevention and reduction of wind losses. Notable among these guides for coniferous forests are those by Curtis (1943), Ruth and Yoder (1953), Gratkowski (1956), Alexander (1964), Boe (1965), Hütte (1968), Scottish Woodland Owners Association (Commercial) Limited (1972), and Gordon (1973). These guides address the topographic, soil and climatic conditions pertinent to wind damage, and also characteristics of individual trees. Indeed, if the available guidelines were more closely adhered to, current windthrow and breakage losses could be reduced.

Many observations by the authors of these guidelines have general applicability, whereas others depend upon the particular site. It is interesting to compare Gratkowski's (1956) comment in Oregon: "Boundaries along creeks were least windfirm of all" (p.69), with that of Alexander (1964) in Colorado: "The fewest windfalls were along cutting boundaries near stream bottoms" (p.131). These conflicting comments obviously reflect different local conditions. Similarly, Ruth and Yoder (1953) advise: "Avoid leaving (Western) hemlock as a
stand border tree; it is believed to be less windfirm than ... Sitka spruce" (p.28), whereas Mayhead (1973a) notes that "there is ... some suggestion that ... Sitka spruce ... is less windfirm than Western hemlock" (p.130). Mayhead bases his comment on data concerning the aerodynamic drag of trees from windtunnel tests, and does not presume to include many other important site conditions, in particular, rooting habit.

A considerable body of data has been established in the literature on the aerodynamical and mechanical properties of many forest tree species, both broadleaf and coniferous. In particular, this data is available in Pong (1956), Fons and Pong (1957), Lai (1955), Storey et al. (1955), Storey and Fons (1956), Storey and Pong (1957), and Mayhead (1973a,b).

Forest practices which result in lower stem densities of forest tracts may modify the above-ground parts of individual forest trees. In their turn, these modifications influence susceptibility to wind-throw and breakage, wind patterns within the stand, and the utility and volume of the merchantable timber. Heiligmann and Schneider (1974) examined the responses of black walnut seedlings grown from seed under different regimes of constant windspeed. They found that a windspeed of 2.8 m s$^{-1}$ resulted in a 50 per cent increase in transpiration rates over those observed for a windspeed of 0.1 m s$^{-1}$. The higher windspeeds resulted in reduced dry weights of all plant parts, but did not affect such parameters as total height, diameter, leaf area, or the shoot:root ratio of dry weights.
Several studies have compared stem form development of thinned and unthinned stands (Yerkes 1960, Lohrey 1961, Groman and Berg 1971). Yerkes, for example, plots stem diameters of Douglas-fir trees released by thinning. After nine years, the released trees had greater diameters along the lower part of the bole, and lesser diameters along the upper bole, in comparison with unthinned controls. These results suggest that the increased wind sway in thinned stands may be responsible for these morphological changes, but obviously thinning also provides increases in available soil moisture, rooting area, insulation, and air movement itself, apart from swaying the tree.

Observations concerning the volume and disposition of the crown space are pertinent, too, when considering the redistribution of the annual increment. The crown shape, above the level where branches touch adjacent trees, was found to be independent of age and stand density (spacing) for black spruce and balsam fir (Honer 1971). The natural pruning of lower branches in denser stands can influence the distribution of wood along the bole. Pruning experiments on loblolly pine have shown that crown size influenced growth below the crown (reduced crown volume resulted in reduced ring increment), but not within the active crown. As a consequence, this tends to make the boles more cylindrical (Young and Kramer 1952). The annual ring increment is greatest at the base of the live crown of loblolly pine (Labyak and Schumacher 1954) and Douglas-fir (Stein 1955). The diameter at the base of the living crown of Douglas-fir moves upward in the tree roughly at a constant rate during the mature life of the
Differences in gross bole morphology and depth of branching between dense and thinned forest stands results in noticeably different locations of the centers of gravity of bole, bark, branches, and foliage (Adamovich 1970). Thus, effects which may be attributable to wind sway may be confused by effects due to changes in crown volume, or other conditions. Farrar (1961), interpreting data available in the literature, discounts wind in favor of increased illumination, as a result of thinning, as an explanation for increased increment growth along the lower part of the bole. This view is not widely held. Though increased illumination may be a significant factor in some cases, wind has been shown to be a major factor.

That wind itself somehow results in redistribution of woody material on the lower portions of the stem has been observed in nature under conditions where strong prevailing winds occur. Bannan and Bindra (1970) found an eccentricity in the cross section of boles of several coniferous species, with a greater diameter in the direction parallel to prevailing winds, which could not be ascribed to insolation. A similar result in Europe resulted in an average ratio of 1.17 for the diameter in the direction of prevailing wind to that in the perpendicular direction (Marsh 1963).

Experiments by Jacobs (1936,1954) clearly demonstrate that it is the stem sway resulting from wind which is a dominant force causing redistribution of the annual increment. Jacobs firmly guyed 30-ft tall *Pinus radiata* at a single point in stands with two degrees of
thinning. Guying resulted in significantly greater height increment and progressively decreasing ring increment below the point of attachment of the guys, in comparison with unguyed trees. If trees were double guyed to eliminate bole oscillation, the ring increment became uniform along the bole. Increased degree of thinning resulted in an increased expression of these results. It is interesting to note that complete suppression of wind sway resulted in reduced overall volume growth and, in time, was reflected in dominance relationships between individual trees within the stand (Jacobs 1954). Greenhouse studies, with fans, on the response of Larix seedlings yielded analogous results (Larson 1965). Guying trees, as here, or staking them, a common horticultural practice, frequently results in trees that are unable to stand upright when released (Jacobs 1939, Leiser et al. 1971, Rasdorsky 1925).

Büsgen and Münch (1931, p. 172) cite examples of experiments in which longitudinal tension and pressure applied along the bole resulted in no anatomical changes. The conclusion reached was that differential tension and pressure on opposite sides of the stem is required for increased diameter growth. They noted in addition that the negative results might be explainable on the assumption that not static pressure or tension, but rather the dynamic stretching and compression of the tissue acts as the growth stimulus.

The above discussion has offered a description of windsway effects on stem form development. It has not, however, discussed the mechanism by which trees accomplish this observed response to wind sway,
nor has it incorporated the observed effects into a theoretical framework. Within such a framework many new questions arise concerning stem form response to wind sway. Excellent reviews concerning the theories of stem form development exist (notably Büsgen and Münch 1931, Larson 1963, Duffield 1968). It will suit the purposes here to discuss their essential arguments.

Before the turn of the century a dispute began concerning the factors which influence stem form development. Notable among the theories developed was the so-called "beam of uniform resistance," which supposes that a tree, with limited woody substance available each year, will distribute that wood along the bole in such a way that the potential for breakage at each point due to wind sway will be equal, i.e. there will be no "weakest link" along the bole.

According to this theory, assuming wood of uniform strength and the base of the tree solidly affixed to the ground, the relationship between stem diameter, \( d \), and distance below the point of application of the deflecting force (essentially, the aerodynamic center of drag of the crown space), \( h \), turns out to be \( d^3/h = \text{constant} \), i.e. a cubic paraboloid. The reduction of this problem to an engineering one has prompted considerable data collection to provide "proof" of the theory, but has been accompanied by some dispute as well. Mathematical refinements to the simple cubic paraboloid model, taking into account variations in wood density with age, and between early and late wood, the lack of rigidity at the base of the stem, and other factors, have appeared periodically in the literature (e.g. Esser 1946, Bryant 1951,
Schniewind 1962, Wangaard 1974, McMahon 1975). Ironically Hall (1969), after extensive strain gauge measurements along swaying stems of mature pine trees, concludes that his trees did not develop as beams of uniform resistance. Appropriately he notes:

Since wind was an ever-present environmental factor during the phylogenetic development of a tree species it is surprising that the inherited pattern is probably similar to that which guyed or staked trees revert. ... It must be therefore assumed that mechanical factors are not overriding in controlling stem form. Rather they constitute part of the environmental complex determining the expression of stem development under these conditions where the growth coordinating system of the tree can function normally. (p.88)

Mathematical modeling has provided some insight to the motivating factors in development of stem form. These models are unable, however, to address some intriguing questions proposed in conjunction with the mechanistic theory.

Fritzsche (1933), for example, discussed the concept of a safety factor which would strengthen the stem beyond the need of ordinary storm events, to sustain it through unusually high wind forces (perhaps those associated with storms with 30-year return periods). Clearly a tall tree species, should it fail to establish such a mechanism, would have had considerable selective pressure against its continued survival. He suggests two mechanisms which may direct the distribution of the woody substance: (1) the absolute value of longitudinal pressure received by the cambium, and (2) the frequency with which a certain threshold pressure is exceeded. Hall (1969) concludes that "no static threshold value for the mechanical stimulus exists" (p.104), but that further resolution of this problem awaits...
additional study. He notes that the trees he studied were not in a particularly windy site, "but the tree stems were almost continuously strained, and must amount to many million cycles per year for the cells" (p.82).

Neel and Harris (1971) examined the result of infrequent stem sway on growth of Liquidambar. Once per day for 27 days, the stems of young trees undergoing a growth flush were swayed by hand for 30 seconds, at a rate of 2-3 Hz. The total leader length attained by the swayed trees during the entire growth season was on the average only 20 per cent of the leader length attained by unswayed controls. Three-fourths of the swayed trees set their terminal bud before the conclusion of the experiment, those not setting bud grew to 31 per cent of the unswayed controls, none of which set bud during the course of the experiment. Unfortunately, Neel and Harris do not provide data on diameter growth responses due to this treatment. These results do not resolve Fritzche's dichotomy, but do suggest directions for further study.

Duffield (1968) defines the need for "detailed descriptions and measurements of stem movement or the induction of movements controlled in magnitude, direction, frequency, duration, and timing in relation to growth stages" (p.356) in order to resolve the true nature of the mechanism directing wood distribution. He additionally reflects upon the concept of a memory system which would direct wood distribution to provide strength against wind forces even during times when direct wind stimulus is not present. Certainly, the 30 seconds per day of
Neel and Harris' experiment must have resulted in chemical precursors which influenced growth while the trees were at rest. Opatowski (1946) explains a mechanism which would provide the required memory system:

The importance of pressure differences for the growth of a tree is suggested by the fact that about 30 to 60% of green wood consists of liquid substance and consequently in the presence of a pressure gradient, a substantial intercellular flow may occur with a possible change of relative concentrations within single cells, if the permeability of the cell walls exhibits a specific differentiation for the various constituents of the cell. (p.42)

Growth responses after the fact are well known. Johnsson (1974), for example, notes that a young oat plant tilted horizontally for less than 30 seconds will, some hours later, respond with a curvature to the stem, due to a relatively greater elongation on the portion of the stem which was briefly the underside. Robitaille and Leopold (1974) found that apple stems bent to the horizontal had increased levels of ethylene arising after 16 hours, which peaked after one to four days and then became insignificant after 21 days. Though these experiments do not address the question of interest here (particularly since the latter does not distinguish between the effects of pressure and geotropism), still they suggest fruitful areas of inquiry.

Besides the chemical precursor, manufactured in response to wind sway, Duffield (1968) extends the concept of memory to include an evolutionary factor (genetic) which may be expressed by certain local populations of a tree species (i.e. a "racial" memory), perhaps with respect to the value of their safety factor. No studies addressing
this question are known.

Recalling, now, the comments concerning windthrow and breakage with which we began this discussion, one might see the practical value of studies of growth responses to stem sway. Forest practices which result in lower stem densities in a forest tract have, not infrequently, met with unfortunate losses due to windfall and breakage. With additional knowledge of how trees adjust to new wind regimes it may be possible to plan more rationally cutting and thinning programs which will result in forest stands with higher stability with respect to wind.

The growth response to wind is manifested in changes in growth ring increment and leader length. In forest stands these responses, resulting from a change in wind regime due to thinning, will not be immediately obvious, due to the small volume of annual growth compared to total tree volume. The importance of these changes, of course, is substantial. Determining the length of time it takes for trees to become strengthened to meet a new wind regime will allow prescription cutting schedules to be developed which satisfy local needs.

The experiments which follow were conducted to examine two basic questions which are pertinent in this regard. First, how do different total amounts of stem sway affect the growth responses of the tree? Is, for example, the response cumulative with increased amounts of stem sway, or is there perhaps a threshold value above which additional stem sway results in little additional response? This latter might be expected from studies noted above, and also on evolutionary grounds
since the failure to make adjustments to occasional high wind loads would surely result in frequent loss of individuals and in a threat to the species as a whole. The second question addressed concerns the responses of trees to the timing of the stem sway received. Is, for example, stem sway required throughout the growth season, or is sway received at the beginning of the season remembered throughout the season? Also, if the greatest winds are received in a season other than the growth season, are those winds remembered? Or is the response only with respect to growth season winds, but with a compensating safety factor?
III. GROWTH RESPONSES DUE TO DIFFERENT DURATIONS OF DAILY SWAYING

Introduction

The eccentric growth of tree rings, with thickening in the direction of prevailing winds, has been often observed in nature and frequently demonstrated under controlled conditions. Larson (1965) found that unidirectional winds from electric fans resulted in both reduced height growth and eccentric ring growth in four-year-old Larix. The fans were apparently applied constantly for the duration of the experiment (approximately four months). Neel and Harris (1971), working with Liquidambar, found that trees swayed for just 30 seconds per day for 27 days had total leader length growth of only 20 per cent of unswayed controls, and that three-fourths of the stimulated trees had set their terminal bud within the month after treatment began.

In this chapter, an experiment is presented in which the duration of daily unidirectional stem sway was varied between treatments. It serves to study the growth response to stem sway for a full range of durations, linking, as it were, the results of Neel and Harris (1971) with those of Larson (1965).

Methods and Materials

In December, 1974, a group of three-year-old Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, were obtained from a nursery, selected
for form and divided into 16 height classes. The heights of these
seedlings varied from 41 to 63 cm. The seedlings were potted in forest
soil in three gallon cans and, after a short period of cold storage
following lifting, were set outside in a group, with sawdust between
the cans for thermal insulation. In March, they were transferred to
a greenhouse constructed of translucent fiberglass walls, and a roof
of two-foot-wide panels of transparent plastic, alternating with two-
foot-wide uncovered sections. The walls and roof sections were de-
signed to prevent entry of wind currents, while the uncovered sections
of the roof were required to allow adequate ventilation during the
summer months, since the use of an evaporative cooler, frequently
employed to reduce greenhouse temperatures, would itself create un-
desirable wind currents.

Individuals from each of the 16 size classes were assigned
randomly to each of the seven treatments. Fourteen rows of trees
were established in the greenhouse, two rows for each treatment, and
the individuals in each treatment were randomly assigned to positions
in the rows for that treatment. The order of treatments to the rows
themselves was randomly distributed, except that treatments 5, 6, and 7,
were assigned to adjacent rows, as were the first four treatments.
Watering was carried out approximately weekly for the duration of the
experiment when rainfall was inadequate.

Except for the unswayed controls (treatment 1), all trees were
provided with a one-half inch wide soft nylon webbing, six inches long,
wrapped once around the stem at a height of 26 cm. The free ends of
the webbing were secured with wire, forming a loop, and attached to a cable that ran the full length of the row. The forward end of the cable was attached to a device that provided a periodic to-and-fro linear motion of the cable with a displacement of 13 cm. This resulted in each row of seedlings swaying, in unison, with the same displacement. The opposite end of the cable was provided with a spring, which maintained the tautness of the cable and returned the seedlings to an upright rest position.

A 0.8 Hz swaying motion was provided, with the six treatments receiving this swaying motion for durations of 10 seconds, 1 minute, 6 minutes, 30 minutes, 2.5 hours, and 10 hours, respectively. For treatments of six minutes or less, the motion was supplied manually. A single automatic swaying mechanism with six arms, powered by an electric motor, was used for the longer treatment times. The motor turned a cam which simultaneously applied the same treatment to each of the six rows. The treatments were applied daily from April 1, until August 31, 1975, with the duration of application centered approximately at midday. The manually operated mechanism was easy to maintain at the required swaying frequency by simply "keeping time" with the electrically powered swaying concurrently underway nearby.

At approximately weekly intervals from the initiation of treatments, the morphological development stage of lateral buds was recorded. A seven stage classification scheme described by Lavender.

Professor Denis P. Lavender, private communication, March 1975.
was employed. In this scheme, numerals are assigned qualitatively to the bud, based on its visual appearance, as follows: 0 is assigned to a closed bud, showing no signs of breaking, 1 to a swollen bud, 2 to an elongated bud, 3 to a bud which has opened just enough to view the foliage within, 4 to the stage where foliage is expanding from the bud, 5 to the stage where all the foliage is free of the bud scales, 6 to the stage where elongation of the new shoot begins. The classification was recorded on the basis of the appearance of the most mature lateral buds.

Also during this growing season, at weekly intervals, the total stem diameter in directions parallel to the direction of sway and perpendicular to it was measured with calipers, at a single position marked on the stem, approximately 10 cm from the ground level.

In December, 1975, the trees were harvested and measurements obtained of total leader growth acquired during the current season and the thicknesses of the annual growth rings for the current and previous years growth. The thickness of annual rings was determined microscopically, measured to the nearest 0.0001 inch (0.00254 mm). The rings were measured in the direction of sway and in the perpendicular direction at three heights along the stem: at 7 cm, 17 cm, and at a point midway between the point of attachment of the nylon loop and the tip of the current year's leader.
Significant differences between treatments were determined by analysis of variance techniques (Snedecor and Cochran 1967, Chapter 10). Table I gives the details of the analysis of variance. Computed $F$ values were compared with tabled values. The number of treatments and size classes in the experiment reported here were: $a = 7$ and $b = 16$, respectively. If the $F$-test indicated a level of $a < 0.05$, a linear correlation was developed according to the form

$$Y = c + d \ln(X),$$

where $Y$ is the dependent variable (e.g. leader length, ring increment) and $X$ is the duration of sway, in seconds; $c$ and $d$ are determined by linear regression techniques (Snedecor and Cochran 1967, Chapter 6). The value of $d$ was then tested statistically, to determine if it differed significantly from zero.
Table I. Analysis of variance table.

<table>
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<tr>
<th>Source of Variation</th>
<th>Sum of Squares</th>
<th>Degrees of Freedom</th>
<th>Mean Square</th>
<th>Estimated Mean Square</th>
<th>F Computed</th>
<th>F Tabled</th>
</tr>
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<tbody>
<tr>
<td>Treatments</td>
<td>$SS_a = \sum_{i=1}^{a} \sum_{j=1}^{b} (\bar{y}_{ij} - \bar{y})^2$</td>
<td>$a - 1$</td>
<td>$MS_a = SS_a / (a - 1)$</td>
<td>$\sigma_a^2 + \sigma_{\text{ab}}^2 / \sigma_a^2$</td>
<td>$MS_a / \sigma_a^2$</td>
<td>$F(1 - \alpha; a - 1, (a - 1)(b - 1))$</td>
</tr>
<tr>
<td>Size class</td>
<td>$SS_b = \sum_{i=1}^{a} \sum_{j=1}^{b} (\bar{y}_{ij} - \bar{y})^2$</td>
<td>$b - 1$</td>
<td>$MS_b = SS_b / (b - 1)$</td>
<td>$\sigma_b^2 + \sigma_{\text{ab}}^2 / \sigma_b^2$</td>
<td>$MS_b / \sigma_b^2$</td>
<td>$F(1 - \alpha; b - 1, (a - 1)(b - 1))$</td>
</tr>
<tr>
<td>Residual</td>
<td>$SS_e = \sum_{i=1}^{a} \sum_{j=1}^{b} (\bar{y}<em>{ij} - \bar{y}</em>{.} - \bar{y})^2$</td>
<td>$(a - 1)(b - 1)$</td>
<td>$MS_e = SS_e / (a - 1)(b - 1)$</td>
<td>$\sigma_e^2$</td>
<td>$\sigma_e^2$</td>
<td>$\sigma_e^2$</td>
</tr>
<tr>
<td>Total</td>
<td>$SS_a + SS_b + SS_e = \sum_{i=1}^{a} \sum_{j=1}^{b} (\bar{y}_{ij} - \bar{y})^2$</td>
<td>$ab - 1$</td>
<td>$MS_e$</td>
<td>$\sigma_e^2$</td>
<td>$\sigma_e^2$</td>
<td>$\sigma_e^2$</td>
</tr>
</tbody>
</table>
Results

Bud development

An analysis of variance was conducted on the morphological development data of the lateral buds. Analysis of the data of weekly observations failed to demonstrate a significant difference between treatments for any week. The data of May 12, however, were close to being significantly different at the 95 per cent level. On this date, bud development tended to be more rapid for trees receiving the least sway. The range of the average values was 3.1-4.3.

Differences between these weekly observations were calculated and an analysis of variation conducted. These data proved to be highly significantly different between treatments (99 per cent) for the differences between the May 12 observations and the weeks immediately preceding and following it. Treatments of 30 minutes and longer resulted in smaller differences (1.0-1.2) than the shorter treatment times and unswayed controls (1.7-2.0), for the difference with the preceding week. The differences between the May 12 readings and those of May 19 reversed this tendency. The longer treatments had the greater difference (1.6-1.8) when compared with the shorter swaying duration treatments and the unswayed control (0.9-1.3).
Leader growth

Leader length growth data, acquired at approximately weekly intervals throughout the growth season, was processed by analysis of variation techniques. Only values of total leader length increment on June 10 and after proved to be significant (95 per cent level). Leader length failed to increase appreciably after June 16, this data is given in Figure 1. Linear contrasts of the average values of leader length of the various treatments for June 10 and June 16 showed that the unswayed controls had greater leader growth than the mean of all swayed treatments, and that the trees swayed 10 seconds per day had greater mean leader growth than the mean of all trees swayed for longer durations.

Annual ring growth

Weekly measurements of stem diameter were found to have too great a variance to yield to statistical interpretation.

The annual growth increment measured midway between the point of attachment of the nylon loop of the swaying mechanism and the tip of the leader did not yield statistically significant differences between sway treatments and unswayed controls.

At the position 17 cm above ground level, the effects of treatments on current ring growth in the direction of sway were found to be highly significantly different. The results are given in Figure 2.
Figure 1. Mean total leader length acquired by seedlings swayed daily for different durations. Data was collected June 16, 1975, no additional elongation occurred after this date. The value for unswayed controls is significantly ($a = 0.05$) different from the overall mean for the swayed seedlings taken together. The value for seedlings swayed 10 seconds daily is significantly ($a = 0.05$) different from the pooled mean for the remaining swayed seedlings.
Figure 2. Mean growth ring increments in the direction of sway, 17 cm above ground level, acquired by seedlings swayed daily for different durations. This increment (increment 8 in the diagram below) for the unswayed controls differs significantly ($p < 0.05$) from pooled mean of all swayed treatments. No statistically significant differences in these values exist between seedlings swayed for different durations.
Swaying resulted in more ring increment in the direction of sway (increment 8 as depicted in the figure) than the unswayed controls, differences between swaying duration are not apparent. The current ring increment 180° from this point, i.e. increment 5, is also found to have significant effects due to the swaying treatment. The results are given in Figure 3. Here the tendency is a reduction in ring increment as the daily duration of sway increases. The current ring increments of the sides of the stem perpendicular to the direction of sway were not observed to be statistically different, from each other nor the controls.

At the position 7 cm above the ground surface, both ring increments 5 and 8 had highly significant responses to the treatments. The mean current ring increment in the direction of sway is observed to increase to a point highly significantly different from the controls for the lowest duration, 10 second, treatment with monotonically smaller magnitude differences from the control for the subsequent treatment durations. These results are given in Figure 4. The current ring increment opposite the direction of sway, increment 5, is observed to follow a similar pattern, but with a lower magnitude increase (see Figure 5). The longest treatments do not result in significant differences of increment 5 from the unswayed controls. Again, the increments perpendicular to the direction of sway were not statistically different from the unswayed controls.
Figure 3. Mean growth ring increments 180° opposite the direction of sway, 17 cm above ground level, acquired by seedlings swayed daily for different durations. This increment is identified as increment 5 in the diagram below. The tendency for decreased growth increment with increased duration of sway is statistically significant ($\alpha = 0.05$).
Figure 4. Mean growth ring increments in the direction of sway, 7 cm above the ground level, acquired by seedlings swayed daily for different durations. This increment is identified as number 8 in the diagram below. All swayed treatments are significantly different than the unswayed controls. The tendency for decreased growth increment with increased duration of sway is statistically significant ($\alpha = 0.05$).
Figure 5. Mean growth ring increments 180° opposite the direction of sway, 7 cm above ground level, acquired by seedlings swayed daily for different durations. This increment is identified as number 5 in the diagram below. The tendency for decreased growth increment with increased duration of sway is statistically significant ($\alpha = 0.05$).
Bud development

The bud classification scheme employed here is based on morphological features easily identifiable visually. The numerals assigned to each developmental stage of the bud are highly subjective. In particular, the numerical difference between stages in no case represents actual numerical changes in either the time it takes to transfer from one stage to the other, nor any other quantifiable variable. That is, the scheme is a linearization of a nonlinear function, though equal time between stages may be a fair order of magnitude approximation. Arithmetic operations with these numerals are, therefore, to be interpreted with care, especially differences between observations made at different times. The highly significant differences indicated by the analysis of variance is to be taken, therefore, as suggestive only.

Apparently, during the week prior to May 12, as the buds were generally passing from classification 2-3 to 3-4, the trees receiving the longer swaying treatments (30 minutes and more) developed at a slower rate than the others. This is the stage where the bud scales are yielding to and exposing the new foliage. It is this observation in which significance may lie. That is, the data indicates that the longer durations of swaying retard bud development.

The following week, a reverse trend was noted: the slower
breaking buds caught up to the faster ones. This observation is due to an artifact of the classification scheme. Many buds in all treatments were at that time reaching a stage of 5 or 6, and the time between stages at that time may have been of longer duration than that of the preceding week. Also, since 6 is the highest stage of classification, the rate of change becomes zero once it is obtained and immediately suppresses the average of the difference of the more highly developed buds.

Leader growth

The great variation present in these data (see Figure 1) prevent one from defining precisely how increasing amounts of stem sway are manifested in leader growth responses. Mean leader length of the control proved to be significantly different from the mean leader length of all swayed treatments taken together. And, the mean of the 10-second swaying treatment was significantly greater than the mean of all treatments of longer duration. The leader extension of all swayed treatments taken together was 86 per cent of the mean for the unswayed controls. This result differs markedly from that of Neel and Harris (1971) with Liquidambar, who found leader height for their 30 second treatment to be reduced to only 20 per cent of their unswayed controls. No comparable work has been conducted on other tree species, but these results indicate an essential difference in response of Liquidambar and Pseudotsuga. It must be noted, of course,
that the conditions of the experiment are not directly comparable. In particular, the swaying frequency employed by Neel and Harris was more than twice that used here.

**Annual ring growth**

The use of calipers (accuracy to 0.001 inch) to measure weekly stem diameter growth proved to be an unfruitful method. Wide variability in the results from week to week is due to an inability to return the calipers to precisely the same point on the stem each week. This could, perhaps, have been rectified by cementing the heads of thumb tacks to the stem, as suggested by Zaerr\(^2\), but the mass of adhesive on the small stems of the trees in this experiment may have resulted in an anomalous localised ring growth response, due to tensions in the thin expanding bark, and therefore itself resulted in unreliable data.

The unstressed portion of the stem, measured midway between the point of attachment of the nylon loop and the tip of the leader, was not found to be influenced by the swaying of the tree stem. The geotrophic effect in this portion of the stem would be the greatest of any point along the stem, and in these experiments this portion of the leader attained an angle of \(45^\circ\) from the vertical at its extreme swayed position. Also, the rate of movement through space of this section of the stem was greater than all other portions of the stem.

\(^2\)Professor Joe B. Zaerr, private communication, March 1975.
In spite of this fact, induced sway had minor, if any, effect on annual ring growth on the portion of stem free of compression or tension. Confidence for this conclusion is strengthened by the highly significant results found for lower segments of the stem.

The current ring growth increment 17 cm above the soil surface, which is 9 cm below the point of attachment of the nylon loop, was found to be significantly affected by the compressions and tensions induced by mechanical swaying. The compressions, at this level, manifested an approximately 35 per cent increase in ring increment in the direction of sway, increment 8, independent of the duration of that sway. The opposite side of the stem, increment 5, was found to generally decrease as the duration of swaying increased. The mean increase to increment 8, for the 10-hour duration treatment, is almost exactly compensated for by the mean decrease on the opposite side. This result suggests that the sum of these opposite effects in current ring increment for the 10-hour treatment could be approximately equal to the controls, and thereby less than the shorter duration treatments. Further examination does not bear this out, however. Values of the ratio of total stem diameter parallel and perpendicular to the direction of sway are given in Figure 6. This ratio will have on the average a value near unity in the case of trees which have not been treated in a manner to cause eccentric ring growth. The ratio of diameters of the unswayed controls and of the initial diameters prior to treatment are seen in Figure 6 to have values near unity, as expected. The means of the ratios of total stem diameters following
The diameters are identified in the diagram below. The post-treatment ratio is A:B, the pretreatment ratio is C:D. The ratios A:B for swayed seedling treatments are significantly greater than unity. The ratio A:B for unswayed controls and the ratios C:D are not significantly different than unity.
treatment are seen in all cases to exceed unity. The average value of this increase is significantly greater than unity. No particular trend with duration of treatment is noted in this data, i.e. all treatment durations appear to increase stem diameter ratios to about the same degree. The 10-hour duration treatment which appeared anomalous before, no longer appears so.

The analogous results for the lower position on the stem, 7 cm above ground level, have a different trend and are also statistically highly significant. Contrary to the result anticipated by the experimenter, the shortest duration swaying treatment resulted in the greatest current ring increment. Increasing the duration of swaying resulted, monotonically, in less ring increment. The 10-second duration treatment increment was three times that of the controls, whereas the 10-hour duration treatment resulted in less than twice the value of the controls. An increase is also noted on the opposite side to the direction of sway which parallels the effect noted above. The shortest duration treatments resulted in a near doubling of the ring increment, and increasing the duration of sway reduced the effect. The 2.5- and 10-hour duration treatments did not result in statistically significant differences from the control.

That the greatest ring increment would result from the least duration of swaying is an unexpected result. Results of ring increment growth at the 17 cm position were seen above to reflect a different picture by examining values of the ratio of total stem diameter in the direction parallel and perpendicular to the direction of
sway. Figure 7 plots these ratios for pretreatment and post-treatment measurements. It is apparent that the unexpected result persists even here, though somewhat less dramatically. The shorter duration treatments still have a significantly greater response than does the greatest duration treatment, but the effect is no longer clearly monotonic. An interaction between the strengthening response in the current ring increment and the initial pretreatment diameter exists. Taking this interaction into account makes impossible a decisive statement about which treatment results in the greatest response. Additional work is required to illuminate further the factors at work here, but this result does offer a new insight to the often reported result of stem thickening.

An increase in ring increment due to the tension induced by stem sway in coniferous species is not known to have been previously reported. Since only the shorter duration treatments responded in this manner, this is not surprising. Aside from being only partially unidirectional, naturally induced stem sway by wind may rather easily exceed the short duration sways necessary for this effect. Unfortunately, Neel and Harris (1971) do not report any stem diameter measurements on their 30 second swaying treatment of Liquidambar, so a parallel result in broadleaf species remains to be explored.
Figure 7. Mean pretreatment and post-treatment ratios of diameters in the direction of sway to that in the perpendicular direction, 7 cm above ground level. The diameters are identified in the diagram below. The ratios A:B for the swayed treatments are significantly different from unity. The tendency for decreased value of this ratio with increased duration of sway is statistically significant.
IV. GROWTH RESPONSE DUE TO DAILY SWAYING FOR DIFFERENT PERIODS DURING THE GROWTH SEASON

Introduction

The effect of timing of stem sway on the stem form response by a tree is addressed only indirectly in the literature. The work of Neel and Harris (1971) showed, for example, that 30 seconds of swaying daily for as little as a month coinciding with the flush of new growth can result in significant decreases in leader growth and a hastening in setting the terminal bud.

The presumed means of directing growth responses to wind sway is a direct chemical system: the mechanical stimulation of stem sway (a pressure flux) causes the formation of chemical precursors which influence cell growth and differentiation. These precursors have a finite active life time, after which their control function is lost. Robitaille and Leopold (1974) found that static bending of an apple stem to the horizontal resulted in peak ethylene levels one to four days after the treatment was imposed, which returned to the level of the controls within 21 days. These experiments do not distinguish between stem stress and geotropic responses, and certainly not to the periodic stem stresses induced by wind sway. They are nonetheless suggestive of the existence of chemical precursor mechanisms which control growth responses and have a definite life time associated with them. The actual role of ethylene in these experiments was unknown.

The experiment presented here was designed to provide comparison
of the growth response in seedlings swayed daily for different periods of the growth season. By comparison of the responses resulting from different periods of stem sway, one may obtain information concerning the lifetime of the chemical precursor, i.e. memory, system.

Methods and Materials

The seedlings used for this experiment were from the same source as that described in the previous chapter and the same handling and maintenance procedures applied. The seedlings were selected for shape and health, divided into 14 height classes, and assigned randomly to four treatments. The trees were larger than those used in the previous experiment ranging in height from 61 to 86 cm. The experiment was conducted concurrently in the same greenhouse as described previously.

One treatment group was designated an unswayed control, the remaining three treatments were swayed mechanically 2.5 hours per day beginning April 1, 1975, which coincided with the initiation of bud burst. The swaying mechanism was disengaged after periods of 6, 12, and 18 weeks, respectively, for the three remaining treatments. The swaying was achieved by an electrically powered swaying mechanism, similar to that in the preceding experiment, that acted simultaneously on six rows of trees (three treatments, two rows of seven trees per treatment). Harvesting occurred in December 1975, with stem sections taken at heights of 9 cm and 24 cm above ground level, and at a point
midway between the point of attachment of the nylon loop and the tip of the current leader.

Significant differences between treatments were determined by analysis of variance techniques (Snedecor and Cochran 1967, Chapter 10). Table I is applicable in this experiment, the number of treatments and size classes are different than for the preceding experiment, being here: \( a = 4 \) and \( b = 14 \), respectively. If the F-test indicated a significance level of \( \alpha \leq 0.05 \), linear contrasts were constructed from the treatment means. These linear contrasts were of the following form

\[
L = \sum_{i=1}^{4} \lambda_i \bar{X}_i,
\]

where the \( \bar{X}_i \) are the mean values of treatment \( i \) (1-4 being the unswayed control, the 6-, 12-, and 18-week swaying treatments, respectively).

Three linear contrasts were then tested for statistical significance according to a t-test (Snedecor and Cochran 1967, Chapter 11). The first contrast compared the mean of the unswayed controls with the pooled mean of the swayed treatments, i.e. \( \lambda_1 = 1, \lambda_2 = \lambda_3 = \lambda_4 = -1/3 \). The second contrast compared the mean of the 6-week duration sway treatment with the pooled mean of the 12- and 18-week treatments, i.e. \( \lambda_1 = 0, \lambda_2 = 1, \lambda_3 = \lambda_4 = -1/3 \). The third contrast compared the means of the 12- and 18-week duration sway treatments, i.e. \( \lambda_1 = \lambda_2 = 0, \lambda_3 = 1, \lambda_4 = -1 \).
Results

Bud development

No statistically significant differences were apparent from analysis of the bud classification data collected during the period of initial growth.

Leader growth

Analysis of variance techniques were applied to measurement data of total leader growth acquired during the growth season. Linear contrasts were constructed to test (a) whether the means of leader growth for the swayed trees were different statistically from the unswayed trees, (b) whether the mean leader growth for the 6-week treatment was different statistically from the means for the 12- and 18-week treatments, and (c) whether the 12- and 18-week treatments resulted in statistically different leader growth.

Highly significant differences (99 per cent) were noted between mean total leader growth for the unswayed controls (151 mm) and the mean for all of the swayed trees. The unswayed controls were on the average 68 mm taller than the swayed trees. Highly significant
differences were also noted between mean total leader growth for the trees swayed six weeks (136 mm) and those swayed longer periods. The trees swayed six weeks were on the average 72 mm taller than the trees swayed for longer periods. No statistical differences could be demonstrated between the mean leader growth of the 12- and 18-week treatments (67 mm and 61 mm, respectively). The means of the unswayed controls and the 6-week treatment were within one standard deviation of each other.

Annual ring growth

Analysis of variance techniques were applied to the annual ring growth increment data, measured at the conclusion of the growth season. Linear contrasts were constructed to compare (a) the mean increment growth for the unswayed controls with the mean for the three swaying treatments, (b) the mean increment growth for the 6-week treatment with the mean for the longer period treatments, and (c) the mean increment growth for the 12-week treatment with the 18-week treatment.

The quantities compared were the current and preceding seasons' growth increments in the direction parallel and perpendicular to the direction of induced sway (enumerated as increments 1, ..., 8, see Table 1). Also compared were the overall diameters parallel and perpendicular to the direction of induced sway, and the ratio of these diameters for both the end of the current growth season, and the end of the preceding growth season. Additionally, the ratios of current
Table II. Statistical results of linear contrasts of mean annual growth increment data comparing the unswayed control treatment with the mean of the swayed treatments. The swayed treatments amounted to 2.5 hours of sway daily for periods of 6, 12, and 18 weeks, respectively, as described in the text. The variables tested are illustrated in the diagram below the table.

<table>
<thead>
<tr>
<th>Increment</th>
<th>9 cm above ground level</th>
<th>24 cm above ground level</th>
<th>midpoint of unstressed stem</th>
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<th>A:B</th>
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<th>C:D</th>
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Notes: - Not statistically significant.
* 95 per cent significance level.
** 99 per cent significance level.

![Diagram of stem cross-section](image)
growth increment in the direction of sway to the current growth increment opposite it, i.e. increment 8:increment 5, were compared.

The results of the statistical testing are given in Tables I and II for comparisons (a) and (b), respectively. Comparison (c), that of the 12-week treatment with the 18-week treatment, did not result in any statistically significant differences.

The growth increment in the direction of sway 9 cm above the soil surface is seen, in Table I, to be significantly smaller for comparison (a). This result is also reflected in the ratios involving this increment. The 6-week treatment resulted in a growth increment in the direction of sway the value of which lies between the unswayed control and the longer period treatments. The magnitude of this increment was significantly different from the longer period treatments but is not apparent in the ratios involving this increment.

At the position 24 cm above the soil surface, which is still below the point of attachment of the nylon loop, increment 5 was found to decrease with increased period of swaying. This was highly significantly different for both comparisons. The ratios involving this increment are also seen to be significant. Increment 8 was not found to be significantly influenced by the treatments. Increment 4, the current season's increment perpendicular to the direction of induced sway, was highly significantly larger for comparison (a).

Midway between the point of attachment of the nylon loop and the tip of the leader, the current season's increment was found to be greater in every direction, for both comparisons (a) and (b). Only
Table III. Statistical results of linear contrasts of mean annual growth increment data comparing the 6-week sway treatment with the mean of the 12- and 18-week sway period treatments. The swayd treatments amounted to 2.5 hours of sway daily for the periods indicated, as described in the text. The variables tested are illustrated in the diagram below.

<table>
<thead>
<tr>
<th>Increment</th>
<th>9 cm above ground level</th>
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<td>C:D</td>
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Notes: - Not statistically significant.
* 95 per cent significance level.
** 99 per cent significance level.
the ratio increment 8:increment 5 was statistically significant comparing the unswayed controls to the mean of the swayed treatments. This ratio increased monotonically with increase of swaying period.

Discussion

The initial period of growth occurred in a period of cool and cloudy weather, and was manifested in a rather slow bud burst. The final stage of the morphological bud classification scheme, stage 6, was not generally observed until the last week of May. The 6-week swaying treatment was terminated in mid-May, so the interpretation of growth response differences between treatments must be made in this light.

It must be noted that the mechanics of this experiment were not as well realized as those of the experiment described in the preceding chapter. The same principles were applied, namely a mechanically oscillating cable to which the trees were attached by means of a nylon loop. Since the seedlings were larger than in the preceding experiment, however, they required a greater displacement distance to achieve the same sway angle at their apogee. A greater leader length was present above the attachment point, and this, coupled with the greater horizontal displacement, resulted in a whip-like motion of the taller seedlings. This motion is some cases snapped off the new leader growth after several weeks, and thus resulted in the loss of the apex. The degree to which this physical disruption influenced the
experiment as a whole is uncertain, but since apical buds are generally believed to control hormone activity, the results must be viewed with this possible complication in mind. This experiment cannot be taken as an examination of solely the factor of stem sway.

Leader growth

The statistical methods applied to the leader length growth data failed to demonstrate a difference between the unswayed seedlings and those swayed six weeks. Since the 6-week treatment terminated before the last stage of bud burst occurred, height growth responses to leader sway may not be important until actual elongation of the leader takes place. The longer sway periods resulted in reduced leader length growth of statistical significance, however breakage of the apex of several seedlings in each group invalidate the legitimacy of this test. It should be noted, however, that elongation of even unbroken leaders in the longer period treatments was never as great as that observed for treatments 1 and 2. This result may, then, reflect that the longer sway periods reduced the elongation potential of the leaders, in spite of the breakage.

Annual ring growth

The three positions where stem cross-sections were examined give different results. The lowest point on the stem examined, 9 cm above
ground level, had significant increment growth increase in the direction of sway for all swaying treatments. There is also evidence that the longer periods had a greater effect, i.e. the magnitude of the increment for the 6-week treatment lies between the value for the unswayed controls and those with longer sway periods. This observation indicates that the activity of the response system established to direct wood distribution diminished in time in the absence of continued stimulation.

Analogous results occurred at the cross-section lying 24 cm from the ground, still beneath the point of attachment of the loop. The response was manifested in increments 4 and 5 rather than 8, but the same type of response with respect to swaying period was displayed. The highly significant result for increment 4 may be due to various causes. The cable used to sway the seedlings stretched along that side of the seedlings, and may have created compression forces in that increment. That is, the direction of sway may have actually been oriented between increments 4 and 8, such that the response was stronger in increment 4. During the first few days of the experiment an abrasion was caused by the cable to many seedlings. A response of the seedlings to this wound may also be an explanation of this result in increment 4, which may also explain why the result was found only for this position on the stem.

The position midway between the point of attachment of the loop and the tip of the leader has two interesting results. First, the unswayed seedlings and those swayed six weeks have a greater ring
increment in each direction than do the seedlings swayed longer periods. This may be a result of the loss of the leader apex by many seedlings swaying for the longer periods. Second, the ratio increment 8:increment 5 is near unity for the unswayed controls, as expected, and is greater than unity for each of the treatment periods. The ratios for different periods are not statistically different from one another. This result is the same as expected below the nylon loop, where stress was applied. Apparently, the whip-like motion of the leader resulted in stresses similar to those deliberately applied on the lower portion of the stem. This ratio increased monotonically with increase of swaying period, though no statistically significant differences between them could be demonstrated.
In certain areas of the Pacific Northwest, the greatest wind forces and therefore potential for windfall and breakage of forest trees occurs in the fall and winter, and not during the growth season. Since wind sway is an important stimulus in the development of stem form, and the ultimate judge of the adequacy of the stem form to resist breakage, it is necessary for a tree to have some form of memory of the magnitude of threatening winds at the time the wood substance is actually distributed along the bole (Duffield 1968).

Wind sway induces the creation of chemical precursors which influence wood distribution along the stem. If the precursors have an active life time of one year, then the precursor might directly influence stem form during the growing season, based upon the magnitude of the strongest winds, even if these winds occurred during the preceding fall or winter.

A second means of insuring adequate strength might be the existence of a safety factor. The safety factor enables stem sway during the growth season to provide all the necessary stimulus to achieve a stem form suitable to resist the strongest winds, even if those winds do not occur during the growth season.

The work of Jacobs (1936, 1939, 1954), investigating the responses of 30-foot-tall thinned stands of Pseudotsuga, prompted an analogous
experiment here to examine the differences in stem form resulting in trees exposed to natural windsaw during different seasons of the year, and prevented from this stimulus during other seasons.

Methods and Materials

A plot of approximately 10 m tall Douglas-fir, 17 years old, grown from a single seed source, were thinned just prior to the application of treatments in October 1974. The plantation is located near Dorena, Oregon, and is described by Rieg (1966). Twenty trees were selected on the basis of straightness of bole and general appearance. They were divided into five size classes based on diameter at breast height (1.3 m). The trees were assigned randomly to one of four treatments: (1) completely unrestrained (controls), (2) guyed until bud burst, then free to move naturally, (3) free to move naturally until bud burst, then guyed throughout the growth season, (4) guyed for the duration of the experiment. The experiment was conducted for a full year. The locations of the trees in the plot are indicated in Figure 8. The northern side of the plot was unobstructed, the western side was adjacent to a sparsely stocked plot of shorter trees, 4-6 m tall, and the plot to the southwest was unstocked. All other adjacent plots were stocked much like the treated plot.

Guying of the trees was accomplished according to the method described by Jacobs (1939). Briefly, three guys were attached by
Vacant area

<table>
<thead>
<tr>
<th>Vacant plot</th>
<th>Fully stocked</th>
<th>North</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 4 4 X 3 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>X 1 2 1 3 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>X X X X X 2</td>
<td></td>
<td></td>
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<tr>
<td>X X X X X 3</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Low, thinly stocked

4 X X
X X X X X
2 X X X X
3 X X X
1
2 4 X

Fully stocked

Figure 8. Locations of individual trees on the Dorena field plot, containing the experimental trees. An 'X' signifies the presence of a tree, a numeral signifies the presence of a tree used in the experiment, and identifies the treatment received, as described in the text.
means of metal eyes, screwed into the bole at a height of 6.5 m. Tension on the guys was adjusted so that the cables were taut and the bole undisturbed from its original vertical orientation.

Measurements of stem diameter were taken with a metal diameter tape to the nearest 0.1 mm at approximately every meter up the bole, beginning one meter above ground level. The exact location of the diameter measurement was dictated by the need to have a portion of the bole free of branching disturbances. Initial diameter measurements were made at the conclusion of the previous year's active growth period, but prior to the attachment of cables in October 1974. Locations of the diameter measurements were marked with paint, and these locations were remeasured at the conclusion of the 1975 growing season, in late September. Height growth was determined to the nearest 1 cm by climbing the trees, and using a metal tape. These measurements were carried out at the same time as the diameter measurements.

Results

The initial height and diameter measurements were processed by a two-way analysis of variance with blocking by size class. Initial height was not different statistically between size classes. All initial diameters were blocked effectively by size class, but to different degrees of significance: decreasing from 99.9 per cent at the 1 and 2 m heights, to barely 95 per cent at the 7 m height.

An analysis of variance was also used to test the differences in
leader length growth during the season and in the diameters measured at the seven heights. No differences were found either for leader length growth or diameter increment, except for the diameter increment at the 2 m height. Differences here were indicated at the 95 per cent significance level. A contrast constructed of this data comparing the increment due to treatment 1 (unguyed) with treatment 4 (guyed) failed to prove significant. Another contrast, comparing the pooled mean of treatments 1 and 2 with the pooled mean of treatments 3 and 4, also failed to prove significant.

Treating all leader length and diameter data as representing only two treatments, either guyed or un-guyed during the growing season, resulted in only one indication of significance in diameter growth. This result was observed for the 3 m height with a 95 per cent significance level. The mean increment growth for the un-guyed trees was less than that for the guyed trees.

Discussion

The results of this experiment may indicate an experimental design failure. That is, the experiment conducted here may not have addressed properly the problem of the effects of non-growing season winds on stem form development. Jacobs (1939), has shown that guying results in modified stem development. Jacobs was able to establish, in fact, that *Pinus radiata* cannot remain stable if guyed between the ages of 16 and 18 years, since trees so treated bent over or fell upon release of the
guy wires. The lack of such a response here is unexpected.

It is necessary, therefore, to examine why differences were not apparent between treatments 1 and 4, which are simply a duplication of Jacobs' experiments. One explanation may be due to the difference in tree species used. In Chapter III differences between Pseudotsuga and Liquidambar are reported, and a similar situation may exist here. Certainly, the low level of leader length reduction brought about by the experiment described in Chapter III may give some credence to this interpretation. The single case in which a significant difference was found cannot be considered important. It simply represents the 5 per cent chance for error which accompany statistical methods.

Jacobs (1939) included heavily and lightly thinned stands in his experiment, and indicated that the lightly thinned stands showed the same result as the heavily thinned ones, but to a reduced degree. The difference in the ground level diameter increment, for example, was 33 per cent of the controls in his lightly thinned stand, and 70 per cent in the heavily thinned one.

It is useful, in light of this, to examine the stand density and wind flow patterns in the area of the plantation. Figure 8 shows the location of the individual trees with respect to one another as they occurred on the field site. Half of the individual trees treated are seen to lie within the first two rows adjacent to the vacant area on the north. These particular individuals would be most likely to receive the greatest wind stimulation, regardless of wind direction. Reduced effects should be received by the trees further within the plot, but
most of the interior experimental trees lie along the western side of the plot, which faces a very thin stand of smaller trees. Thus, these interior trees would be expected to receive wind sway also, but of reduced intensity. Trees were purposely selected on the basis of their exposure.

Since no significant growth responses could be attributed due to stem sway between guyed and unguyed trees, one might wonder if significant differences in stem sway itself actually occurred. Unfortunately, no attempt was made to measure the degree to which the stems moved during the course of the experiment. It is conceivable that the wind received during the course of the experiment was inadequate to result in significant stem sway below 6.5 m. All trees had immediately adjacent neighbors on at least one side. The wind received may have been sufficient to cause movement in the upper portion of the stem and in its foliage, and at the same time fail to cause important differences in stem movement below the guying point.

Considering the topography of the environs of the experimental site suggests further that inadequate windway may be the case. The site lies on a gentle slope near the floor of a wide valley. The wind at the site is probably less than that along the floor of the valley, but no measurements were attempted. The site may have experienced insufficient wind for the purpose of this experiment.
VI. SUMMARY AND CONCLUSIONS

Research conducted during the last 100 years has demonstrated that stem sway induced by wind can modify the height growth and distribution of the annual growth ring increment. The growth response is one which strengthens the tree against wind forces which might break the stem. It is interesting that the inherited stem form does not provide adequate resistance to wind forces, but instead such strengthening is developed only in response to wind sway. Unswayed trees have been found not only to be inadequate against wind forces but also to lose vigor within a few years time. Apparently, trees in a stand which are not free to sway will be less competitive than dominant trees which do receive wind stimulus. Once suppressed, the lack of wind stimulus continues to suppress the tree, in addition to the suppression which may result from reduced illumination (Jacobs 1954).

A recent study (Neal and Harris 1971) found that stem sway of Liquidambar for as little as 30 seconds per day resulted in extreme growth responses. In earlier work, Larson (1965) applied a swaying stimulus to the stem of Larix continuously. It was decided to test the response to stem sway in Pseudotsuga for a wide spectrum of sway durations, from 10 seconds up to 10 hours per day. The mean leader growth of the unswayed controls and of the trees swayed for 10 seconds were each significantly greater than the mean leader growth for the remaining swayed treatments. The leader growth for swaying durations
of 60 seconds per day or more was on the average reduced to 86 per cent of the unswayed controls. No differences between the unswayed controls and the 10 second treatment could be demonstrated. Growth during later stages of apical bud burst seems to have been retarded by the longer durations of sway.

The annual diameter ring increment at a low point on the stem was found to be significantly increased in the direction of sway, as has been often reported. The response, however, was found to be greatest for the shorter durations of swaying. It was also found that the incremental growth 180° from the direction of swaying (the tension side of the stem) was similarly affected. The response on the tension side could not be detected for durations of 2.5 hours or more, but was significantly greater than unswayed controls for shorter durations of sway.

Plant responses to tipping the apical stem are known to result, hours later, in measurable changes in growth or chemistry (Robitaille and Leopold 1974, Johnsson 1974). Since the mechanism directing the response to stem sway is assumed to be of a similar nature, experiments were conducted to shed light upon the active lifetime of this system. In one experiment trees were swayed for different periods during the growth season. Responses to stem sway were not found to be different between periods of 12 and 18 weeks begun concurrently at the initiation of bud burst. The responses in leader growth and diameter increment to these treatments were different from the unswayed controls, however. A 6-week treatment was found to respond at a level
between the unswayed controls and the longer period treatments. Apparently, swaying during the period of bud burst causes the establishment of a response system, but the effect of this system diminishes if the treatment is terminated before bud burst is completed.

An experiment testing the growth responses of forest stand trees to winds received at different times of the year was also conducted. No differences were found in the responses to any treatments. Though this result may reflect some differences between the responses of Douglas-fir and that of Pinus radiata reported by Jacobs (1939), the wind regime at the study site may have been inadequate to result in measurable differences.
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