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Recovery and morphology of *Pinus resinosa* Ait. trees 50 years after they were displaced by a hurricane

A.E. Akachuku
Harvard University, Harvard Forest, Petersham, MA 01366, USA
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ABSTRACT

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Leaning red pine (*Pinus resinosa*) trees at Harvard Forest in Petersham, Massachusetts, USA, were studied 50 years after they were displaced from the vertical by a hurricane. Objective methods of characterizing leaning trees in process of reorientation to the vertical were developed. The trees were sigmoid- or sinuous-shaped because their upper parts tended to regain vertical growth along a direction that was approximately a continuation of their original vertical growth path before they were displaced. There were large between-tree variations in (i) bole angle of displacement, (ii) external morphological parameters, and (iii) degree of recovery. On average, 63.6% of the leaning tree total height had regained vertical growth, 26.7% of the total height was leaning toward the direction from which the hurricane came, while the remaining 9.7% was still leaning in the leeward direction in which it was displaced. The effect of angle of displacement was significant only on maximum bole displacement on the horizontal plane (positive), concave sweep length (positive), length of bole leaning windward (positive), length of corrected portion (negative) and curvature index (positive). Important relationships were observed (a) among indices of bole and crown size (positive), (b) between curvature index and length of corrected portion (negative), and (c) among indices of bole shape (positive).

INTRODUCTION

The forests of North America are disturbed by natural forces such as wind, fire, snow and avalanche, and consequently the forests are continually changing in structure and composition. Various researchers have studied how the vegetation of the area adjusts to the effects of these forces (Hibbs, 1983; Auclair, 1985; Cogbill, 1985; Lang, 1985; Lorimer, 1985; Oliver et al., 1985; White et al., 1985; Boyce, 1988; Foster, 1988a,b; Webb, 1988). Of all the natural forces disturbing the vegetation of the area, wind is believed to have the greatest impact.

Correspondence to: A.E. Akachuku, Department of Forest Resources Management, University of Ibadan, Ibadan, Nigeria.

In New England, USA, the irregular incursion of hurricanes has become an expected environmental disturbance. From 1635 to 1938, twelve windstorms have exerted the greatest impact on the vegetation of the area, which is continually readjusting to wind damage of varying intensity. The most destructive hurricanes were those of 1635, 1778, 1815 and 1938 (Hawes, 1939; Foster, 1988a,b).

At Harvard Forest in Petersham, Massachusetts, about 70% of the standing volume of timber was blown down by the 1938 hurricane. The trees most affected were those over 20 years old. Many of the younger trees were not blown down, but were only forced to lean by the hurricane. The differences observed at Harvard Forest in the damage to hardwoods and softwoods have been reported by Foster (1988a,b). In the forests of New England affected by the 1938 hurricane, the young leaning survivors, in the absence of most of the older trees, provided shade, controlled erosion and produced seeds for artificial and natural regeneration. Over the years, some of them have completely restored their vertical orientation, while others are at various stages of recovery.

Hurricanes are usually of short duration, but because of their enormous force, trees are wind-thrown, broken or forced to lean in the leeward direction. When trees become inclined for some reason they produce reaction wood, i.e. tension wood on the upper side of the stem in hardwoods and compression wood on the lower side of the stem in softwoods. The effect of tension wood is apparently to pull a leaning hardwood stem back to its normal erect position. In softwoods, the effect of compression wood appears to push the stem back to normal vertical orientation. Reaction wood also tends to maintain a preferred angular orientation of branches in both softwoods and hardwoods. Because reaction wood is a wood defect, a high proportion of it in tree species results in a reduction in wood quality for most industrial purposes (Sinnott, 1952; Wardrop, 1956; Jane et al., 1970; Timell, 1986).

The capacity of compression wood to expand longitudinally and restore a leaning softwood tree to vertical orientation has been discussed quantitatively by Westing (1965), who also examined the possible mechanisms involved (Westing, 1968). Factors that contribute to the process of reorientation to the vertical in leaning conifers are asymmetric activity of the vascular cambium, longitudinal expansion of compression wood, longitudinal contraction of the opposite wood, and increase in osmotic pressure of the cambial cells on the lower side (Westing, 1965, 1968; Boyd, 1973; Timell, 1986; Kubler, 1988). Consequently, a leaning tree is in a process of complete reorientation to the vertical so long as it is forming reaction wood on one side of its bole and opposite wood on the other side. According to Kubbler (1988), in a straight tree severely tilted by a wind gust, reaction wood restores the vertical orientation in the stem's thin top within a few months whereas righting the thick butt section requires many years, so that the stem becomes 'pistol-butted'.

During the process of correction of leaning, a stem assumes a shape which may be characterised as creep, sinuous, S-shaped, bow, crook or bend (Sorensen and Wilson, 1964; Westing, 1965; Embry and Gottfried, 1971; Burdon, 1975; Timell, 1986). Most of the methods of characterizing leaning stems in the process of reorientation to the vertical are subjective (Embry and Gottfried, 1971; Miller, 1975; Cooper and Ferguson, 1981). Some of the objective methods of characterizing leaning trees include determination of their angles of lean, pith eccentricity of their stem cross-sections, and their shapes in relation to standard shapes. These methods have been effectively used to express the severity of lean in forest trees.

There is a need to develop more objective methods of characterizing leaning trees which would indicate to wood users the quality of the bole for the production of various wood products. There is scanty information on the relationships among the external tree morphological features of leaning trees. Their patterns of recovery have not been adequately studied in forest plantations. The most important problem is lack of enough leaning trees (i) of the same species, (ii) growing in the same environment, (iii) which have received the same silvicultural treatments throughout their lives, (iv) of the same age, and (v) displayed at the same time. This is because, in forest management, leaning trees are usually cut to make way for erect stems for economic considerations.

A sizeable population of leaning red pine (*Pinus resinosa*) trees at Harvard Forest satisfy the five criteria stated above. The objectives of this study were (a) to assess the extent to which the trees had returned to vertical orientation 50 years after they were displaced by a hurricane, (b) to characterize the shape of the leaning trees, and (c) to determine the relationships among their external morphological parameters.

MATERIALS AND METHODS

The study area

The study was conducted in a red pine plantation on Prospect Hill at Harvard Forest in Petersham, Massachussetts, USA. Detailed unpublished information on the site and history of the plantation is available in the Harvard Forest Archives of Harvard University. The site has a gentle slope with an elevation of 366 m. The soil is rich sandy loam, fairly rocky and with occasional large boulders. The ground-cover at the time of planting consisted of raspberry, ferns, grass and other herbaceous growth. In 1919 the area was planted with 5-year-old red pine transplants at a spacing of 1.8 m × 1.8 m after cutting nearly pure 30-year-old gray birch coppice growth. The plantation was

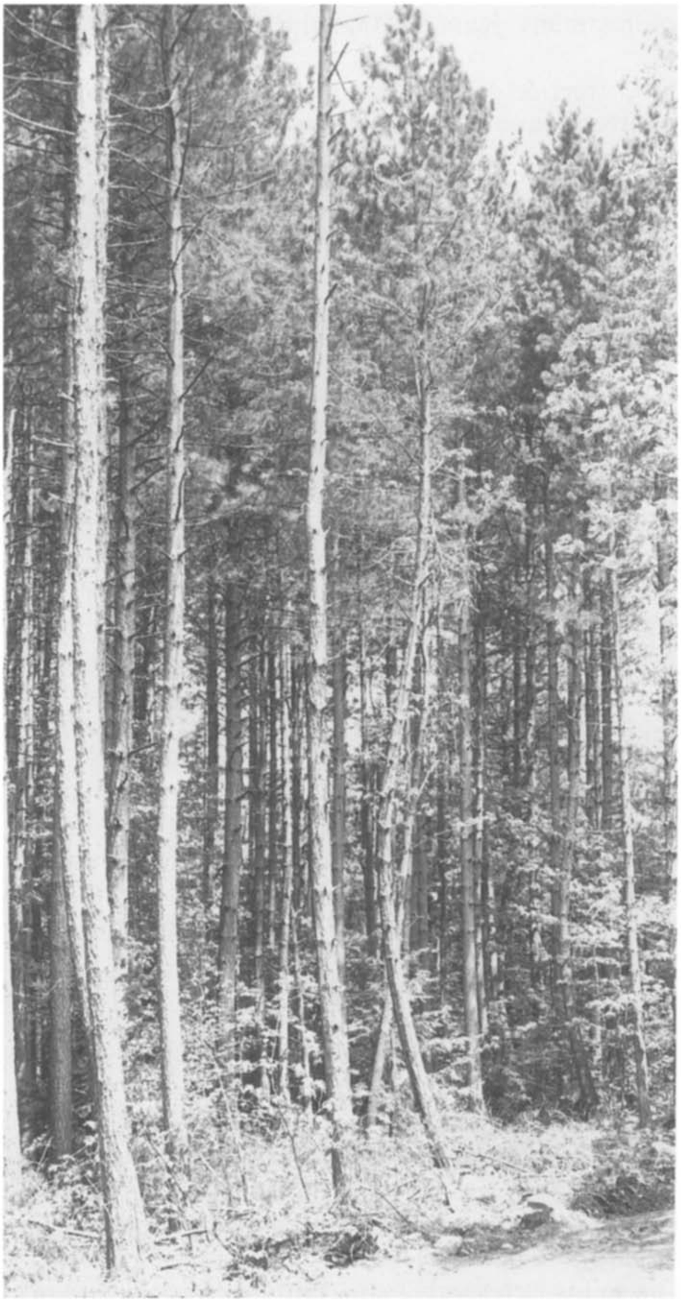

Fig. 1. Leaning red pine (*Pinus resinosa*) trees exhibiting sinuosity 50 years after they were displaced by a hurricane.

weeded, pruned and thinned when the trees were 17, 23 and 25 years old from seed, respectively.

On 21 September 1938, when the plantation was 25 years old from seed and just after it was thinned, it was struck by a hurricane accompanied by 15–35 cm of rain and winds in excess of 200 km h^{-1}. Because the trees were relatively young at the time, most of them survived the hurricane but many were displaced from the vertical. The contributions of the intensity and timing of the weeding, pruning and thinning before the hurricane to the severity of the lean were probably small, because the hurricane had a catastrophic effect on both natural forests and plantations in central New England irrespective of their structure or stocking. Post-hurricane forest management favoured gradual cutting of the leaners to provide space for the erect trees. A part of the plantation containing many leaning trees was preserved after the hurricane for research purposes (Fig. 1).

Field study

Fifty years after the hurricane, 33 leaning red pine trees in the study area were randomly selected and marked. The following parameters were measured on each tree.

(i) Bole diameter at breast height (DBH), i.e. at 1.3 m above the ground measured along the bole (i.e. along CO in Fig. 2).

(ii) Bole angle of deviation from the vertical at breast height, i.e. angle COD ($=\theta$) in Fig. 2. This was measured with the aid of a plumb-line (Burdon, 1975).

(iii) Total height, which is the sum of the lengths CO, ABC and AT (not the vertical line TO) in Fig. 2. These three components, or 'height zones', of the main bole are defined and how they were measured is described below in (v), (vi) and (xi), respectively.

(iv) Mean crown diameter: the mean of maximum and minimum crown diameters measured from their vertical projections (Philip, 1983).

(v) Length of the portion of the bole still leaning leeward 50 years after a tree was displaced. This is CO in Fig. 2, and is the zone of least participation in the overall recovery process of the tree. In this study, it is referred to as Height Zone I. The length of this height zone in all the trees measured was more than 1.3 m and hence the angles of displacement of the trees were measured at breast height.

(vi) Length of the portion of the bole leaning windward, i.e. towards the direction from which the hurricane came. This is ABC in Fig. 2, and is sometimes called the over-corrected portion because it curves away from the vertical in a direction opposite to that of the base of the tree. In this study it is referred to as Height Zone II. The lengths of Height Zones I and II were measured with the aid of an improvised ladder and a tape.

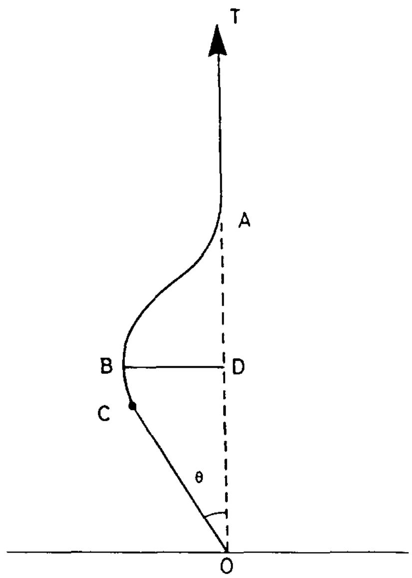

Fig. 2. A diagrammatic representation of a leaning *Pinus resinosa* tree in the process of vertical reorientation. O, ground level; θ, angle of displacement of the bole from the vertical; A, point of correction of the displaced bole; BD, maximum horizontal displacement of the bole on the horizontal plane; C, end of the lower bole leaning leeward; T, tree top; AT, recovered portion of the tree.

(vii) Sweep length, i.e. the length of the curve formed by the initial displacement plus the curvature formed by the recovering leading shoot (leader), ABCO (=CO+ABC in Fig. 2).

(viii) Maximum displacement of the bole on the horizontal plane (BD in Fig. 2).

(ix) Vertical distance from the ground to the point of correction (AO in Fig. 2).

(x) Curvature index of the sweep, defined as the ratio of sweep length (ABCO) to vertical distance between the ground and point of correction (AO).

(xi) Length of corrected portion (AT in Fig. 2). This is referred to as Height Zone III, and is the difference between TO and AO measured with the aid of a modern hypsometer (Loetsch et al., 1973; Philip, 1983; Hamilton, 1988).

Statistical analyses

Regression analysis was used to investigate the relationships among the morphological parameters of the trees. The following models were tested:

linear	$Y = A + BX$
exponential	$Y = Ae^{BX}$
'power'	$Y = AX^{B}$

where X= the independent variable, Y=dependent variable, e=exponential symbol and A and B are constants.

RESULTS AND DISCUSSION

Shape of the leaning trees

The boles of the leaning trees were bent into a sigmoid or sinuous curve exhibiting 'sinuosity', a term used by Dyson (1969) and Timell (1986). The sequence consists of a concave sweep in the lower part of the stem, followed by an upper small convex sweep at the point of correction. The upper convex sweep diminishes considerably with a decrease in the stem angle of deviation.

Path of correction

Each leaning red pine tree tends to correct along a line that is approximately a continuation of its original vertical growth path (AO in Fig. 2) before it was displaced. No matter what the angle of displacement of a bole from the original vertical path, the leader tends to return to that path. There is a number of possible vertical growth paths from C to O in Fig. 2, but it is not clear why the leader regains vertical orientation at O. Since O is the position where the displaced bole is in contact with the ground or the point above the root system, there is a need to investigate whether the root system plays a role in this pattern of reorientation to the vertial. Sinuosity in leaning trees appears to be an over-correction only in the sense that the leader goes beyond the point necessary to resume vertical growth. In reality, it is a tendency of the leader to return to its original vertical growth path. The physiological importance of this phenomenon is yet to be understood.

Parameters of leaning trees

The morphological parameters of the leaning trees 50 years after they were displaced by the hurricane (i.e. at the age of 75 years from seed) are shown in Table 1. The mean proportion of Height Zone III (the recovered portion of the bole) is the highest (63.6% of the total tree height), followed by Height Zone II (the portion of the bole leaning toward the direction of the hurricane as a result of the reorientation process, 26.7%) and then Height Zone I (the lower bole still leaning leeward because of the original impact of the hurricane, 9.7%). The values show that the recovery process reached an advanced

TABLE 1

Means and ranges of growth parameters of *Pinus resinosa* trees 50 years after they were displaced by a hurricane

Parameter	Mean	Range
Role angle of deviation from the vertical at breast height (°)	11.8	5.0 - 24.5
Diameter at breast height (cm)	30.6	21.6 - 43.9
Total height (m)	25.1	23.5 - 26.4
Mean crown diameter (m)	3.9	2.2 - 7.7
Length of lower bole leaning leeward 50 years after displacement (m)	2.4	1.5 - 3.5
Length of portion of bole leaning windward due to recovery process (m)	6.7	3.0 - 11.1
Concave sweep length (m)	9.1	5.6 - 12.9
Maximum horizontal displacement of bole (cm)	68.6	32.2 -147.5
Curvature index(1)	1.02	1.01- 1.04
Length of recovered portion of bole (m)	16.0	11.1 - 20.3

[1]Curvature index was the ratio of sweep length to the vertical distance between the ground and the point of reorientation to the vertical. Number of observations, 33.

stage 50 years after the trees were displaced. The pole value of the leaning trees had increased considerably because, according to unpublished information in the Harvard Forest Archives, even as early as 13 years after the hurricane, the corrected portions yielded short poles for the USA tobacco industry.

Effect of angle of displacement on bole and crown size

There was no significant effect of angle of displacement on DBH, total height and crown diameter; the values of r^2 (coefficient of determination) were not significant for the linear, exponential and 'power' models (Table 2 and Fig. 3). There was little variation in tree height within the stand in spite of the large variation in angle of displacement. Height growth appeared to be controlled by between-tree competition for light in the stand canopy. In each class of angle of displacement there were large- and small-diametered trees, indicating a poor relationship between the two parameters. This shows that angle of displacement did not significantly control diameter growth. Diameter growth appeared to be controlled by the interaction of a tree's genetic constitution and its unique environment. Crown diameter depended on the space available to a tree and not on angle of displacement, probably because the crown was carried on the upper part of the bole that had regained vertical orientation.

The relationship between angle of displacement and tree size immediately after the hurricane is not known and could not be determined retrospectively.

TABLE 2

Regression analyses for determination of the effect of bole angle of displacement on tree growth parameters in leaning *Pinus resinosa* trees

Parameter	Linear model $Y=A+BX$ r^2 (%)	Exponential model $Y=Ae^{Bx}$ r^2 (%)	Power model $Y=AX^B$ r^2 (%)
Diameter at breast height	0.6 NS	0.5 NS	2.6 NS
Total height	4.4 NS	4.4 NS	4.4 NS
Mean crown diameter	0.0 NS	0.0 NS	0.3 NS
Length of lower bole leaning leeward	1.7 NS	1.1 NS	1.4 NS
Length of actively recovering portion leaning 'windward'	33.0**	33.0**	32.8**
Length of the recovered portion	34.8**	34.8**	32.5**
Maximum horizontal displacement of bole	90.0***	85.0***	46.0***
Concave sweep length	34.7**	34.3**	33.6**
Curvature index	60.8***	60.8***	50.4***

NS, not significant; ** significant at $P<0.01$; *** significant at $P<0.001$. Number of observations in each case, 33.

Even if the relationship was significant at the time, the results of this study show that after 50 years of simultaneous reorientation process and tree growth, the relationship was not significant.

Effect of angle of displacement on the lengths of the three height zones

Lower bole angle of displacement had no significant effect on the length of Height Zone I (Table 2 and Fig. 4). This shows that the length of the portion of the bole still leaning leeward 50 years after the bole was displaced was controlled by factors other than the angle of displacement. It is likely that its length depends on the distribution of forces of recovery along the curved part of the bole.

The effect of angle of displacement on the lengths of Height Zones II and III was significant in each case. The wider the angle, the longer the length of the portion of the bole leaning windward (that is, toward the direction from which the hurricane came) and the shorter the length of the recovered portion because, as the angle got wider, it increased the distance to be covered and therefore the amount of work to be done by the leader before returning to the original vertical growth path. However, the values of r^2 show that only 33.0 and 34.8% of the variations in the lengths of Height Zones II and III, respectively, were associated with corresponding variations in angle of displacement (Table 2). The interaction effect of the trees' intrinsic and extrinsic factors accounted for the remaining variations

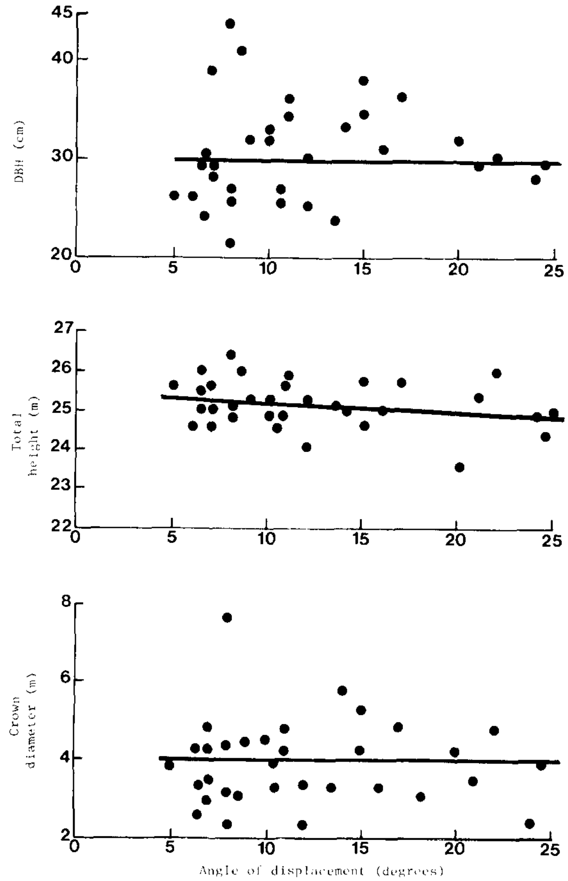

Fig. 3. Effect of bole angle of displacement from the vertical on bole and crown size in leaning *Pinus resinosa* trees. The angle was measured at breast height (1.3 m above the ground).

Effect of angle of displacement on bole indices of shape

Bole angle of displacement had a significant effect on the maximum horizontal displacement of the bole, concave sweep length and curvature index. The values of r^2 were 90.0, 34.7 and 60.8%, respectively (Table 2 and Fig. 5). These three indices of bole shape increased with angle of displacement. These relationships appeared to be modified by the space available to the tree after displacement, the inherent ability of the tree to correct and the leader's initial angle of return to the vertical.

The relationship between concave sweep length and angle of displacement was not as strong as those of the other two indices of bole shape. Each displaced leader had alternative curved paths of return to the original vertical path. Leaders displaced equally returned to the original vertical path along different curved paths and therefore had different sweep lengths. Conse-

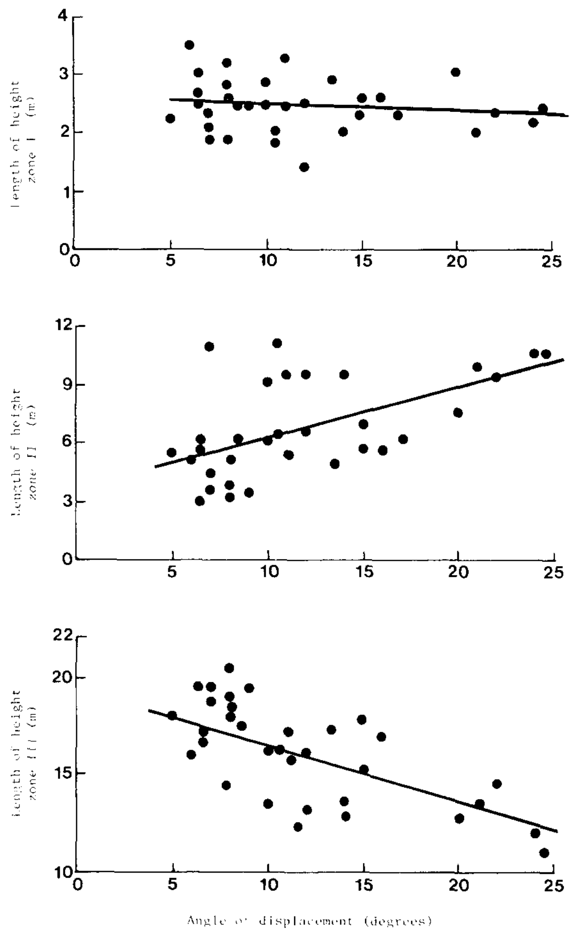

Fig. 4. Effect of bole angle of displacement from the vertical on the lengths of three height zones in leaning *Pinus resinosa* trees. Zone I, portion of the bole leaning leeward; Zone II, portion leaning windward; Zone III, corrected portion.

quently, sweep length depended not only on the angle of displacement, but also on the path of reorientation taken by the leader. A tree of highest recovery efficiency is one that takes the shortest possible recovery path under a given set of ecological conditions.

The post-hurricane thinning or salvage operation in the study area probably had an effect on the morphological parameters of the surviving leaning trees, but it is difficult to quantify it retrospectively. Since all the leaning red pine trees exhibited sinuosity irrespective of their (a) crown diameters which might be indicators of the space available to individual trees (Kozlowski, 1971), (b) angles of displacement, and (c) DBH, it is likely that leaning red pine trees in unthinned stands would also exhibit sinuosity resulting from the

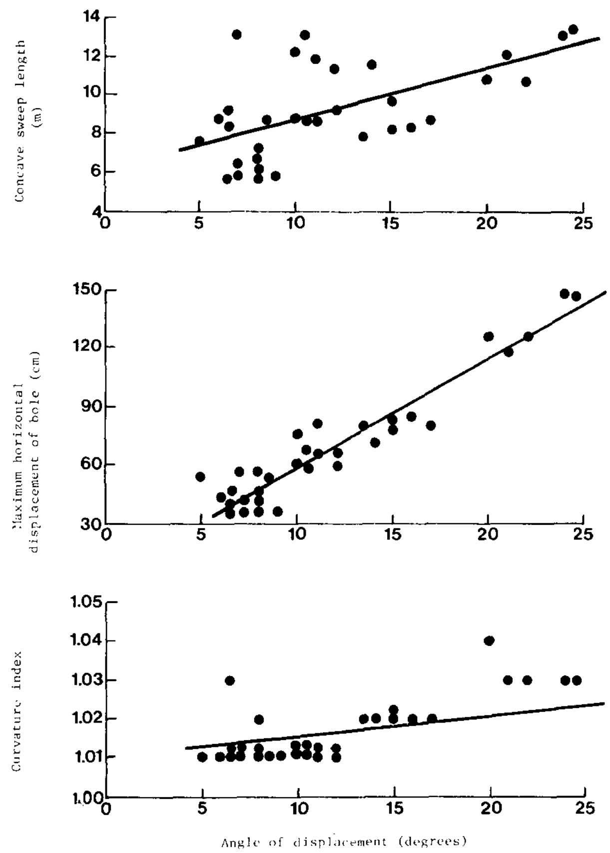

Fig. 5. Effect of bole angle of displacement from the vertical on indices of shape in leaning *Pinus resinosa* trees.

process of reorientation to the vertical. Therefore the methods used in this study would also apply to unthinned stands.

Relationships among the tree parameters

Since considerable evidence is available of hormonal control of (a) shoot expansion in forest trees (Roberts et al., 1963; Nanda and Purohit, 1964, 1965) and (b) cambial meristematic activity in leaning and vertical trees (Wershing and Bailey, 1942; Necesany, 1958; Larson, 1962; Wareing et al., 1964), it is possible that some morphological parameters of a sinous-shaped tree are related to one another. The magnitudes and types of relationships among the parameters of the trees are presented in Table 3. Length of the portion of the bole leaning leeward (Height Zone I) was not closely related to the following parameters: DBH; total height; crown diameter; maximum horizontal displacement of bole; curvature index. The values of r^2 were not

TABLE 3

Relationships among growth parameters of leaning *Pinus resinosa* trees 50 years after displacement by a hurricane

Relationship[1]	r^2 (%) for linear model	Type of important relationship
Height Zone I[2] and DBH[3]	0.4 NS	
Height Zone I and tree total height	1.0 NS	
Height Zone I and crown diameter	0.0 NS	
Height Zone I and MHDB[4]	0.0 NS	
Height Zone I and curvature index	0.6 NS	
DBH and total height	13.7 NS	Positive
DBH and crown diameter	46.9***	Positive
DBH and MHDB	0.0 NS	
DBH and concave sweep length	1.4 NS	
DBH and Height Zone II[5]	1.4 NS	
DBH and Height Zone III[6]	4.0 NS	
DBH and curvature index	0.0 NS	
Total height and crown diameter	13.0 NS	Positive
Total height and MHDB	0.6 NS	
Total height and concave sweep length	4.8 NS	
Total tree height and curvature index	9.0 NS	
Crown diameter and MDBH	0.3 NS	
Crown diameter and concave sweep length	3.2 NS	
Crown diameter and Height Zone II	2.9 NS	
Crown diameter and Height Zone III	6.3 NS	
Crown diameter and curvature index	0.0 NS	
MHDB and concave sweep length	46.2***	Positive
MHDB and Height Zone II	41.0***	Positive
MHDB and Height Zone III	46.2***	Negative
MHDB and curvature index	60.0***	Positive
Curvature index and Height Zone III	12.2 NS	Negative

[1]The parameter on the right-hand side was regressed on the one on the left in each case.
[2]Height Zone I, length of the lower bole leaning leeward.
[3]DBH, diameter at breast height.
[4]MHDB, maximum horizontal displacement of bole.
[5]Height Zone II, length of the bole leaning 'windward' because of the reorientation process.
[6]Height Zone III, length of the corrected portion of the bole.
r^2, coefficient of determination; NS, not significant; ***, significant at $P<0.001$.
Number of observations in each case, 33.

significant. It is therefore clear that these five parameters could not be predicted from the lengths of Height Zone I, and vice versa, in the measurement of similar leaning red pine trees. The length of Height Zones II and III were also not closely related to DBH and crown diameter. The results show that the factors that determine the lengths of the three portions of a bole do not significantly control radial growth of (i) the bole at breast height and (ii) the crown. While length of Height Zone II increased, that of Height Zone III decreased as maximum horizontal displacement of the bole increased. The values of r^2 were 41.0 and 46.2%, respectively, and each was significant. It was because of these opposing (positive and negative) relationships of the two portions of a bole with maximum displacement that total height was not related to maximum bole displacement.

Maximum horizontal displacement of bole, concave sweep length or curvature index, which was controlled by the angle of displacement of a bole, could not be determined from DBH, total height or crown diameter (which was controlled by the availability of growth resources and probably by tree genetic make-up). The values of r^2 were not significant.

Considerable variations in sweep length and curvature index were positively associated with concomittant variation in maximum horizontal displacement of the bole; the values of r^2 were 46.2 and 60.0%, respectively, and both were significant. This was because each of these parameters was positively related to angle of displacement (Table 2). Length of recovered portion (Height Zone III) tended to decrease as curvature index increased, partly because the two variables were negatively and positively related to the angle of displacement, respectively.

To a certain extent the factors that promoted diameter growth also promoted crown and height growth in the leaning trees. The values of r^2 were 13.7% for regression of total height on DBH, 46.9% for crown diameter on DBH (significant), and 13.0% for crown diameter on total height.

Biological basis of the relationships and conclusions

(1) The results show that the severity of sweep (deduced from (i) angle of displacement, (ii) sweep length, i.e. the sum of Height Zones I and II, (iii) maximum horizontal displacement of bole, and (iv) curvature index) had no significant effect on the growth rate of the leaning trees (deduced from DBH, total height and crown diameter). One possible explanation of the results is the fact that cambial meristematic activity, which controls radial growth in trees, depends not only on bole lean but also on several other factors such as (a) basipetal flow of products synthesized in the crown, especially carbohydrates and hormonal growth regulators, and (b) a tree's micro- or macro-environment, comprising soil conditions, space available to the tree and biotic and physical factors that control the number, size and total photosynthetic area of leaves (Kozlowski, 1971). The effect of lean on cambial meristematic activity was therefore less important than the joint effects of other factors that controlled cambial activity. The control of the activity of cambium by-products synthesized in the crown partly explains the positive relationship between DBH and crown diameter in the leaning trees. Crown diameter was probably not significantly controlled by the severity of sweep because the crown was borne on the portion of the bole that had regained vertical orientation. Also, crown diameter usually depends on the space avail-

able to a tree. The total height of a leaning tree was not closely related to severity of sweep because the lengths of the different portions of the sinuous-shaped bole varied differently with the degree of bole displacement.

(2) The indices of severity of sweep were positively related to one another. This was because the greater the displacement of a tree, the greater the distance covered by the recovering leader on its way to the original vertical growth path, which in turn controls sweep length and curvature index.

(3) The positive relationship between total height and DBH in the leaning trees was not as strong as the relationship between the two parameters in vertical trees (Farr et al., 1989). The factors responsible for this relatively weak relationship are not entirely known. Breast height in these trees was at the leaning portion of the bole, and was therefore in the region of asymmetric cambial activity which gave rise to wide-ringed reaction wood and narrow-ringed opposite wood. The asymmetric growth and the sinuous-shaped growth path of the leader probably contributed to the weak positive relationship between DBH and total height.

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