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# WOOD GROWTH DETERMINED FROM GROWTH RING ANALYSIS IN RED PINE (PINUS RESINOSA) TREES FORCED TO LEAN BY A HURRICANE

by

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## Summary

Leaning red pine (*Pinus resinosa*) trees at Harvard Forest in Petersham, Massachusetts, U.S.A., were sampled for wood growth studies 50 years after they were displaced by a hurricane. Before the hurricane incursion, ring width varied among trees and from year to year but not among radii. After the hurricane, between-tree variation in ring width was again significant but it was not appreciably due to angle of displacement (AOD) of the bole. Wood growth distribution along the bole in the leaning trees was complex. Between-radius variation in ring width was significant in the leaning boles; ring width was largest on the lower side. On the average ring width decreased as tree age increased but the variation was much less on the upper than on the lower side. Ring area tended to decrease with increase in age but the relationship was strongest in the least displaced bole and vice versa. Asymmetric growth ratio increased with AOD of a bole and varied with year of wood formation but was not related to cambium age. Graphs of height above the ground on percentage pith eccentricity exhibited a sinuous shape like that of the trees. Cumulative growth and mean annual increment of height and volume increased with tree age. Current annual increment of height and volume decreased for 9 and 5 years after the hurricane and after the 64th and 69th year of the tree, respectively. Form factor increased after pruning but decreased later with age. Precipitation was not closely related to ring width in the leaning boles.

*Key words*: Red pine, *Pinus resinosa* Ait., leaning trees, wood growth, ring analysis, pith eccentricity, dendroclimatology, hurricane.

## Introduction

Past climatic records show that five to ten hurricanes of varying intensity strike New England, U.S.A. every century while the catastrophic ones strike every 70 to 100 years (Brooks 1939; Foster 1988a, b). They damage tree crowns, break boles, uproot older trees and force many trees, especially younger ones to lean. The effects of wind on stem form and mechanical aspects of windbreakage and windfirmness of trees have been discussed by Mergen (1954). It is important to study the rate of wood formation in surviving leaning trees after a catastrophic hurricane, from growth ring analysis, to assess their contribution to the overall regeneration of the forest. Growth rings are authentic records of growth rates and changes in environment of leaning trees before and after a hurricane.

Variation in ring width is often examined in the horizontal sequence, i.e., from the ring nearest the pith to the outermost one in a stem cross section. Ring width variation along the bole has been examined in a) the oblique sequence, i.e., at a fixed number of rings from the bark at different positions along the bole, and b) the vertical sequence which examines the variation at a fixed number of rings from the pith (Duff & Nolan 1953; Smith & Wilsie 1961).

In normal trees, ring width increases with site quality and it is decreased by environmental pollution (Jagels 1986; Wahlmann *et al.* 1986) and a loss in tree vitality resulting from various causes (Fink 1986; Gregory *et al.* 1986; De Kort 1986; Torelli 1986). There is little information on the distribution of wood growth within leaning coniferous trees other than the widely reported fact that growth rings are wider on the lower than on the up-

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Fig. 1. Leaning *Pinus resinosa* trees exhibiting 'sinuosity' 50 years after displacement by a hurricane.

per side. Such uneven growth results in pith eccentricity, that is, the pith is not at the geometric centre of a stem cross section (usually associated with compression wood in conifers) (Panshin & De Zeeuw 1980; Timell 1986). Eccentricity has been found to increase with angle of bole displacement from the vertical (Fielding 1940, quoted by Timell 1986).

Mergen and Winer (1952) observed compression failures in the wood of a living white pine tree inclined 20° from the vertical by a catastrophic hurricane which struck New England in 1938. The tree was sampled seven years after the hurricane and the compression failures were most conspicuous in the outer rings. Mergen (1958) examined the relationship between the shape of terminal shoot of hemlock trees and the type of wood produced. There was a strong correlation between the curvature and orientation of the leader and the reaction wood produced.

Dendroclimatological studies have been based largely on vertical stems (Akachuku 1985; Kienast *et al.* 1987; Jozsa & Powell 1987; Cook 1988; Robertson & Jozsa 1988). Information on the relationship between climate and rate of wood formation in leaning trees is not readily available.

The objectives of this study were 1) to determine, from growth ring analysis, the rate of wood growth and variation in bole form in red pine (*Pinus resinosa* Ait.) trees before and 50 years after they were displaced by a hurricane, 2) to determine variation in pith eccentricity in the leaning trees, and 3) to briefly evaluate the suitability of leaning trees for dendroclimatological studies.

## Materials and Methods

A red pine plantation at Harvard Forest in Petersham, Massachusetts, U.S.A. was sampled for this study. The plantation was established by Harvard University for research in 1919 with five-year-old transplants at a spacing of 1.8 m × 1.8 m. Important silvicultural operations carried out on the plantation were weeding, pruning and thinning when the pine trees were 17, 23 and 25 years old from seed respectively. On September 21, 1938, the stand was struck by a catastrophic hurricane which forced many trees to lean. Fifty years after the hurricane incursion, numerous discs were extracted from three trees displaced 24.5, 13.5 and 6.5° from the vertical at 1.3 m above the ground. The trees belonged to maximum, medium and minimum classes of angle of displacement, respectively.

Because the leaning trees exhibited 'sinuosity', a term used by Dyson (1969) and Timell (1986) as shown in Figure 1, the bole of each sample tree was divided into three height zones: Zone I, the portion of the bole leaning leeward as a result of the hurricane's impact; Zone II, the portion leaning windward (in relation to the direction of the hurricane) as a result of the tree's reorientation process to the vertical; and Zone III, the corrected portion, i.e., the portion that had regained vertical orientation. The discs were extracted serially from the base to the top of the sample trees, i.e., from the three height zones.

Percentage pith eccentricity (PPE) of each disc was determined; this was the distance between the pith and the geometric centre of the disc expressed as a percentage of the mean radius of the disc (Fig. 2). Tree ring images of the discs were projected and their widths measured on a video screen. The discs were kept wet during the measurements to avoid differential shrinkage and splitting because the boles contain normal, compression and opposite wood. Other growth parameters determined from the ring analysis were a) ring area, b) asymmetric growth ratio (AGR) of each ring defined as the ratio of its maximum width to its minimum width, c) cumulative growth, current annual increment (CAI) and mean annual increment (MAI) of tree height and volume, and d) form factor of the bole reconstructed for each year's cumulative growth.

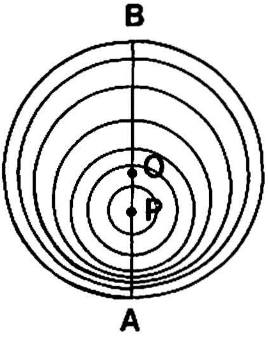

Fig. 2. A diagrammatic representation of a circular stem cross section showing an eccentric pith. O = geometric centre of the cross section; P = eccentric pith; AB = diameter of the cross section, O is its mid-point.

## Results and Discussion

### *Variation in ring width before the hurricane*

Between tree variation in ring width before the hurricane was significant ($P < 0.05$). This was probably because of differences in the micro-environment and genetic constitution of the sample trees. Mean ring width values for trees ranged from 4.6 to 5.3 mm.

Variation in ring width around the bole, i.e., between different radii from the pith was negligible. This shows that variation in cambial activity around the bole was negligible, indicating that before the hurricane, the trees grew in a vertical direction, producing centric pith with concentric growth rings.

Variation in ring width with year of wood formation was significant ($P < 0.001$). The mean widths of the annual rings ranged from 3.5 to 7.1 mm.This was largely because the immediate environment of the trees changed from year to year. For example, the plantation was heavily weeded at age 17 resulting in a very wide ring in the 18th year (Fig. 3), a relatively dry year. In the last four years before the hurricane, within-stand competition was high and annual ring width decreased considerably. That was the reason why the plantation was thinned in its 25th year, shortly before the hurricane struck. The interaction effects assessed were not of practical importance.

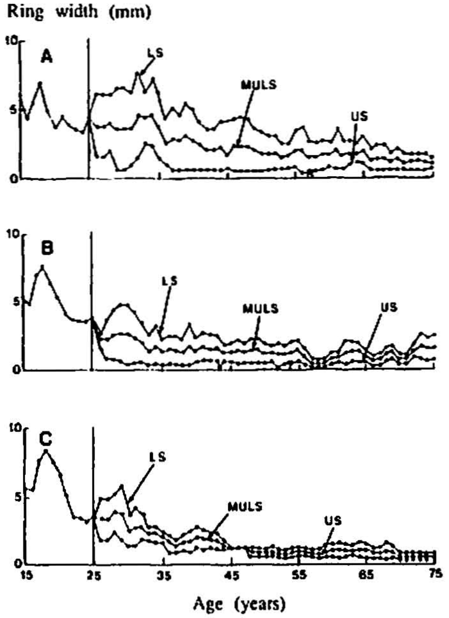

Fig. 3. Variation in ring width of *Pinus resinosa* with tree age before and after displacement by a hurricane. A, B and C are patterns of variation for trees displaced 24.5°, 13.5°, and 6.5° from the vertical, respectively. The trees were displaced at the age of 25 years. LS = lower side of a leaning tree; US = upper side; MULS = mean of upper and lower sides.

Table 1. Analysis of variance of ring width in leaning *Pinus resinosa* trees 50 years after displacement.

| Source of variation | DF | SS | MS | Level of significance |
|---|---|---|---|---|
| Trees (T) | 2 | 55.40 | 27.70 | *** |
| Radial directions | 1 | 263.40 | 263.40 | *** |
| T × Q interaction | 2 | 49.10 | 24.55 | *** |
| Rings (R) | 49 | 163.60 | 3.34 | *** |
| T × R interaction | 98 | 36.70 | 0.37 | *** |
| Q × R interaction | 49 | 67.20 | 1.37 | *** |
| Error (T × Q × R) | 98 | 22.40 | 0.23 | |
| Total | 299 | 657.80 | | |

Radial direction: The lower and upper sides of the leaning trees were sampled.
*** = significant at $P < 0.001$.

Table 2. Analysis of variance of post-hurricane ring width using data obtained from intensive within-tree sampling.

| Source of variation | DF | SS | MS | Level of significance |
|---|---|---|---|---|
| Height zones (HZ) | 2 | 218.77 | 109.39 | *** |
| Discs[1] (D) | 4 | 1.51 | 0.38 | *** |
| HZ × D interaction | 8 | 37.46 | 4.68 | *** |
| Radial directions (Q) | 1 | 82.21 | 82.21 | *** |
| HZ × Q interaction | 2 | 16.41 | 8.21 | *** |
| D × Q interaction | 4 | 12.20 | 3.05 | *** |
| HZ × D × Q interaction | 8 | 19.79 | 2.47 | *** |
| Rings[2] (R) | 19 | 130.50 | 6.87 | *** |
| HZ × R interaction | 38 | 67.31 | 1.77 | *** |
| D × R interaction | 76 | 12.38 | 0.16 | *** |
| Q × R interaction | 19 | 14.64 | 0.77 | *** |
| HZ × D × R interaction | 152 | 38.21 | 0.25 | *** |
| HZ × Q × R interaction | 38 | 5.96 | 0.16 | *** |
| D × Q × R interaction | 76 | 10.41 | 0.14 | *** |
| Error (HZ × D × Q × R) | 152 | 12.65 | 0.08 | |
| Total | 599 | 680.41 | | |

1) Discs : positions along the bole in height zones.

2) Rings: ring width variation was investigated in the oblique sequence along the bole by sampling 20 rings (counting from the bark) at different positions.

*** = significant at $P < 0.001$.

*Between-tree variation in ring width after displacement of trees by the hurricane*

Analysis of variance detected significant between-tree differences in ring width after the hurricane ($P < 0.001$, Table 1). Since the trees were displaced at different angles, had different micro-environments and probably varied in their genetic make-up, the observed differences were not entirely due to the angle of displacement. In one case, two trees with different angles of displacement (the angle of one was 1.8 times that of the other) had corresponding different mean annual ring widths. In another case, two trees with different angles (the angle of one was twice that of the other) had approximately the same mean annual ring width. The angle of displacement therefore contributed minimally to the significant between-tree differences in ring width; they were probably due to the interaction of micro-environment and genetic constitution of the trees.

*Axial variation in ring width after the hurricane*

Along the bole of a leaning tree in the oblique sequence (along annual growth layers), mean annual ring width was highest in the corrected uppermost zone; values for the two leaning zones were close. Analysis of variance detected significant between-height zone variation in ring width ($P < 0.001$, 'Height zones' in Table 2). Within the height zones, the variation in ring width along the bole, though statistically significant, was not practically important because it made only a small contribution to the total variation in ring width.

Interaction effects were significant, indicating that the pattern and magnitude of variation in ring width along the bole differed a) in height zones, b) around the bole, and c) in different years of wood formation. It is therefore clear that the distribution of wood growth in a leaning tree is very complex.

Table 3. Regression analyses for the determination of the effect of tree age on radial growth rate in leaning *Pinus resinosa* trees. Model: $Y = A + BX$.

| Parameter | Sample | $r^2$ | (%) | Significant relationship |
|---|---|---|---|---|
| Ring width | Lower (compression) side of a bole with angle of displacement = 24.5° | 84.6 | *** | Negative |
| Ring width | Upper (opposite wood) side of a bole displaced 24.5° | 29.2 | ** | Negative |
| Ring width | Mean of upper and lower sides of a bole displaced 24.5° | 79.2 | *** | Negative |
| Ring width | Lower side of a bole displaced 13.5° | 50 | | Negative |
| Ring width | Upper side of a bole displaced 13.5° | 0.0 | NS | |
| Ring width | Mean of upper and lower sides of a bole displaced 13.5° | 41.0 | *** | Negative |
| Ring width | Lower side of a bole displaced 6.5° | 65.6 | *** | Negative |
| Ring width | Upper side of a bole displaced 6.5° | 82.8 | *** | Negative |
| Ring width | Mean of upper and lower sides of a bole displaced 6.5° | 74.0 | *** | Negative |
| Ring width | Corrected topmost part of a tree with its base displaced 24.5° | 25.0 | *** | Negative |
| Ring width | Corrected topmost part of a tree with its base displaced 13.5° | 72.0 | *** | Negative |
| Ring width | Corrected topmost part of a tree with its base displaced 6.5° | 45.0 | *** | Negative |
| Ring area | Bole displaced 24.5° | 1.0 | NS | |
| Ring area | Bole displaced 13.5° | 29.2 | ** | Negative |
| Ring area | Bole displaced 6.5° | 72.2 | *** | Negative |

NS = not significant;
** = significant at $P < 0.01$;
*** = significant at $P < 0.001$.
'Negative' indicates that the growth ring parameter decreased as a tree got older.

There was a small decrease in ring width up the bole in height zone I, but in height zone II the small variation had no definite pattern. In the corrected portion, ring width tended to increase up the bole. This appears to agree with the auxin gradient theory (Larson 1964; Wareing *et al.* 1964).

### *Variation in ring width around the bole after the hurricane*

This variation was significant at $P < 0.001$ ('Radial directions' in Tables 1 and 2). Eccentric growth made the largest contribution to total variation in ring width after the hurricane. Significant interaction effects show that the magnitude of variation in ring width around the bole was different in a) different leaning trees, b) position of the bole, and c) years of wood formation. These again show a complex pattern of wood formation in a leaning tree.

### *Variation in ring width with year of wood formation after the hurricane*

Ring width varied with year of wood formation after the hurricane (significant at $P < 0.001$; Tables 1, 2 & 3; Fig. 3). However, the pattern of variation in ring width with year of wood formation differed among and within trees but the general tendency was a decrease in ring width with increase in cambium age on the upper and lower sides of leaning bole (height zones I and II) and in the corrected portion of the bole (height zone III).

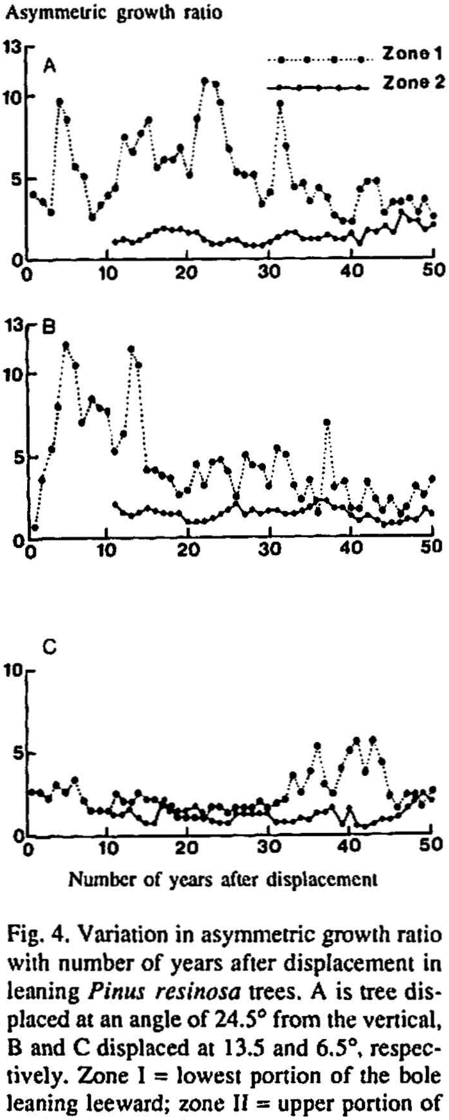

Fig. 4. Variation in asymmetric growth ratio with number of years after displacement in leaning *Pinus resinosa* trees. A is tree displaced at an angle of 24.5° from the vertical, B and C displaced at 13.5 and 6.5°, respectively. Zone I = lowest portion of the bole leaning leeward; zone II = upper portion of the bole leaning windward.

The relationship between growth ring area and cambium age was strongest in the least displaced tree and weakest in the most displaced one (Table 3). On the average, ring area tended to decrease with increase in cambium age. However, variations in ring width and ring area in trees are not always of the same pattern because a wide ring around a young small tree may contain less wood (i.e., may have a smaller area) than a narrower ring around a mature tree with a large diameter.

The decrease in the widths and areas of growth rings with age may be due to the usual decrease in tree vigour associated with ageing. Cambium age was not the only factor that determined ring width and area in different years of wood formation. Changes in the trees' environment and variation in bole angle of displacement resulting from the trees' reorientation to the vertical caused changes in the ring parameters from year to year. Central New England is not part of the favourable range of red pine and this probably reduced the trees' vigour over the years.

### *Asymmetric growth ratio (AGR)*

The mean AGR's were 5.2, 4.5 and 2.5 for the lowest portions (height zone I) of the sample trees displaced 24.5, 13.5 and 6.5° from the vertical, respectively. The mean ratios for zone II (the portion leaning windward) for the trees were approximately equal: 1.4, 1.4 and 1.2, respectively. It is therefore clear that the mean AGR for height zone I increased with angle of displacement. A high AGR is an indication that the tree was in the process of reorientation to the vertical position. A high AGR is usually associated with formation of compression wood and its opposite wood. Compression wood is believed to aid vertical reorientation of a leaning tree through its longitudinal expansion while its opposite wood contributes by its longitudinal contraction (Timell 1986). Since asymmetric growth is known to produce curvatures and bends in different parts of plants (Kang 1979; Palmer 1985) it probably played a role in the overall recovery process of the leaning trees.

AGR varied from year to year but was not related to cambium age. The values of $r^2$ obtained from various regressions of AGR on cambium age were small or negligible (Fig. 4). AGR was probably controlled by the interaction of changing angle of displacement and complex microenvironmental factors.

### *Percentage pith eccentricity (PPE)*

PPE increased with angle of displacement of bole. In the lowest portion of the bole which

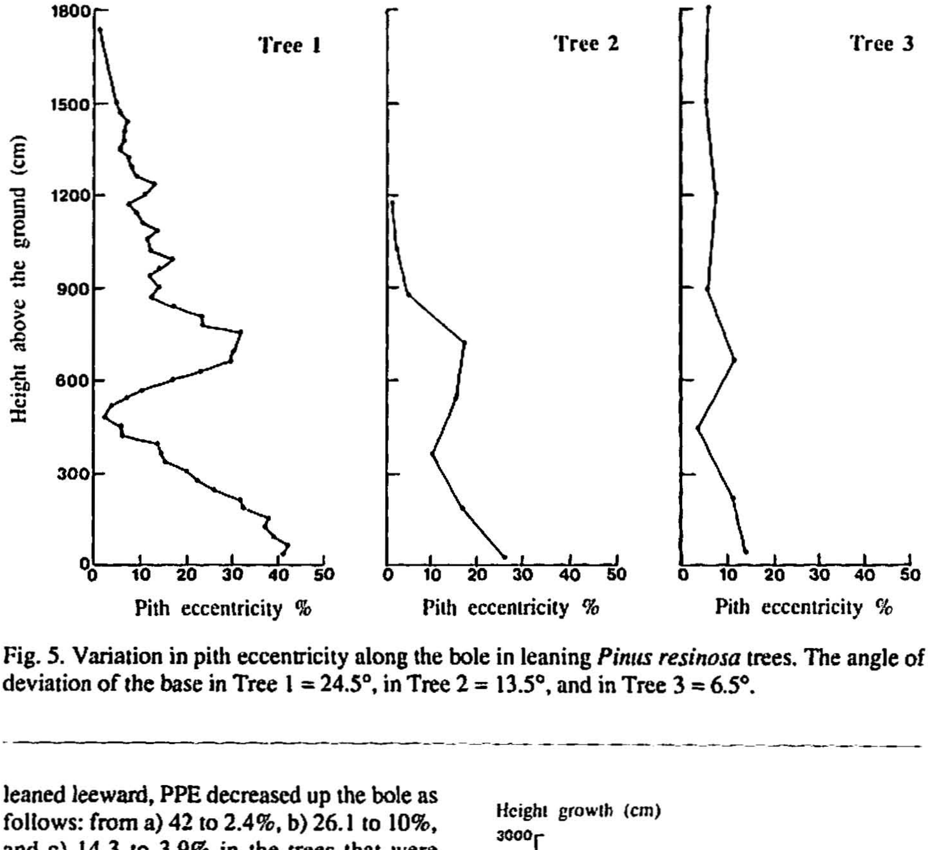

Fig. 5. Variation in pith eccentricity along the bole in leaning *Pinus resinosa* trees. The angle of deviation of the base in Tree 1 = 24.5°, in Tree 2 = 13.5°, and in Tree 3 = 6.5°.

leaned leeward, PPE decreased up the bole as follows: from a) 42 to 2.4%, b) 26.1 to 10%, and c) 14.3 to 3.9% in the trees that were displaced 24.5, 13.5 and 6.5° from the vertical, respectively. Variation in PPE with height above the ground was significant ($P < 0.001$, $r^2 = 97\%$). In height zone II, PPE increased up to the bole to a point and thereafter decreased upwards, fluctuating between 5 and 1%.

Graphical plots of height above the ground on PPE produced figures that closely resembled the shape of the leaning trees (Fig. 5). These show that PPE was closely related to the angle of displacement of different portions of the bole from the vertical.

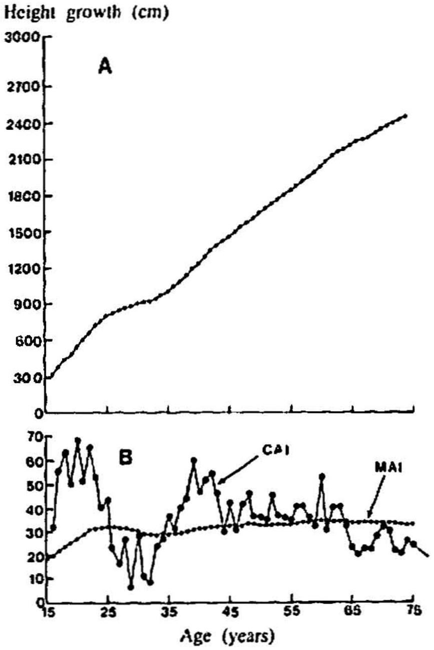

Fig. 6. Height growth in a *Pinus resinosa* tree before and after displacement by a hurricane. Tree age in the year of displacement is 25 years. A: Cumulative height growth; B: CAI = current annual increment of height; MAI = mean annual increment of height.

*Tree height and volume growth and absolute form factor from reconstructed growth layers*

Studies based on the data from the tree displaced at an angle of 24.5° showed that the cumulative height growth increased from 2.9 m in the 15th year to 24.5 m in the 75th year from seed. Current annual increment (CAI) of height ranged from 6 to 68 cm while mean annual increment (MAI) of height ranged from 19.3 to 34.1 cm within the same period (Fig. 6). Cumulative height growth and MAI of height could be determined from tree age; the values of $r^2$ were 99.5 and 54.8%, respectively, which were significant (Table 4). CAI of height was not closely related to tree age.

Cumulative volume growth increased from about $2.6 \times 10^3$ to $8.23 \times 10^5$ $cm^3$ (excluding the bark) within the same period. CAI of volume ranged from about $1.5 \times 10^3$ to $4 \times 10^4$ $cm^3$ while MAI of volume increased almost steadily from about $1.7 \times 10^2$ to $1.1 \times 10^4$ $cm^3$ (Fig. 7). These three indices of volume growth tended to increase with tree age. The values of $r^2$ were 97.8, 32.8 and 98%, respectively, which were all significant (Table 4). Absolute form factor tended to decrease with age ($r^2 = 84.6\%$ significant).

The results show that the tree continued to increase considerably in height and volume every year in spite of its displacement by the hurricane. CAI's of height and volume were relatively low for 9 and 5 years after the hurricane and after the 64th and 69th year respectively, of the tree's life. The first reduction in growth shows that the displacement of the bole from the vertical and the growth of the leader along a curved path probably reduced its growth rate. The second reduction in growth in the later years of the tree's life might have been due to a decline in the tree's vigour with age on the site as stated earlier.

The relatively high values of absolute form factor from the 23rd to 27th year of the tree's life might have resulted from the pruning operation performed on the tree in its 23rd year (Fig. 8). The position of maximum radial growth in plantation trees is the level just below the crown which is the zone of highest concentration of growth promoting substances and photosynthates from all the

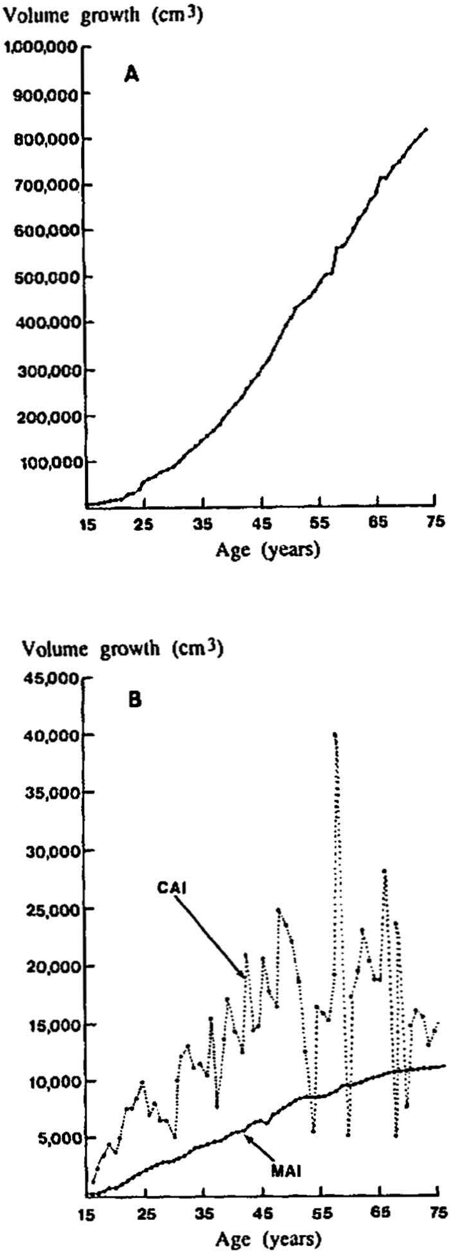

Fig. 7. Volume growth in a *Pinus resinosa* tree before and after displacement by a hurricane. Tree age in the year of displacement is 25 years. A: Cumulative volume growth; B: CAI = current annual increment of volume; MAI = mean annual increment of volume.

Table 4. Regression analyses for determination of the effect of tree age on height and volume growth and absolute form factor in leaning *Pinus resinosa* trees. Model: $Y = A + BX$.

| Parameter | $r^2$ | (%) | Significant relationship |
|---|---|---|---|
| Cumulative height growth | 99.5 | *** | Positive |
| Current annual increment of height | 0.0 | NS | |
| Mean annual increment of height | 54.8 | *** | Positive |
| Cumulative volume growth | 97.8 | *** | Positive |
| Current annual increment of volume | 32.8 | ** | Positive |
| Mean annual increment of volume | 98.0 | *** | Positive |
| Absolute form factor | 84.6 | *** | Negative |

NS = not significant;
** = significant at $P < 0.01$;
*** = significant at $P < 0.001$;
Number of observations for each regression = 61.
'Positive' indicates that the growth parameter increased as a tree got older; 'Negative' indicates that the growth parameter decreased as a tree got older.

branches of the crown. In a tree with a long and vigorous crown, the short branch-free portion which is near the ground is the zone of maximum radial growth giving rise to a decidedly tapered bole. Artificial pruning of such a tree moves the crown, together with the point of maximum radial growth upwards. This decreases bole taper and increases form factor (Kozlowski 1971; Panshin & De Zeeuw 1980).

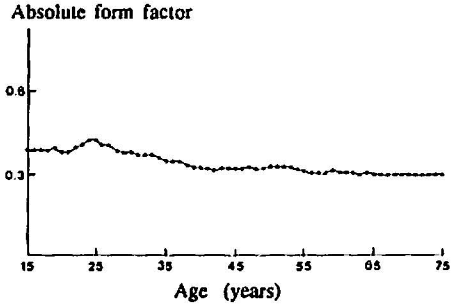

Fig. 8. Variation in absolute form factor with age before and after displacement by a hurricane in a leaning *Pinus resinosa* tree.

*Ring width and total precipitation in the leaning trees*

The widths of growth rings on the lower and upper sides of the leaning trees and their mean widths were not related to a) annual precipitation, b) growth season (May to October) precipitation, and c) five year total precipitation. The values of $r^2$ were negligible: 0.0 to 4.4%.

Rings of leaning trees may not be suitable for reconstruction of rainfall data of an area. Ring width in leaning trees appear to be controlled by complex stimuli which aim at ensuring tree stability and reorienting the trees to the vertical position. Wide rings were formed, not because of an increase in water availability or of nutrients necessary for wood formation, but because there was compression wood produced to aid tree recovery to the vertical orientation.

The effect of precipitation on ring width before the hurricane was not investigated because it was difficult to separate it from the effects of silvicultural operations carried out in the early stages of the plantation. It was therefore difficult to compare the effects of precipitation before and after the hurricane incursion.

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