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Drought and Cold Stress-Induced Morphometric Changes in Tree Rings of Red Spruce

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Technical Bulletin 159



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Drought and Cold Stress-Induced Morphometric Changes in Tree Rings of Red Spruce

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INTRODUCTION

The use of tree-ring width measurements to assess the effects of natural or anthropogenic stresses on forest productivity often relies solely on a single parameter such as radial increment to detect environmental perturbations. But the cambium may respond in several other quantitative and qualitative ways, which can be monitored morphometrically in conifers in the radial files of xylem cells (Bannan 1967; Larson 1969; Jagels and Dyer 1983).

Since radial increment provides only one measure of cambial activity, it is difficult to ascertain the particular trigger for a growth decline response. A decrease in radial increment may reflect any one or combination of events such as drought, frost damage, insect attack, or airborne pollutants (Mott et al. 1957; Glerum and Farrar 1966; Yokobori and Ohta 1983). Morphometric analysis of individual, key growth rings might provide a way of establishing "fingerprints" or unique patterns for growth rings produced following different natural or anthropogenic stresses.

Early attempts at morphometric analysis with wood cross-sections focused on earlywood (springwood)/latewood (summerwood) boundaries to determine the percentages of each produced in a growth ring. In abrupt transition conifers (southern hard pines, Douglas-fir), this boundary is reasonably distinct and can be further defined by Mork's index (Mork 1928). Larson (1969) has pointed out, however, that Mork's index is not appropriate for gradual transition conifers such as spruce and fir. Staining techniques have had only limited success in differentiating earlywood from latewood in such species (Haasemann 1963; Wiksten 1954). More recently, techniques in x-ray densitometry were developed to provide an additional level of sensitivity (Parker and Kennedy 1973; Parker 1976).

Because of the interpretive and/or technical difficulties in assessing earlywood/latewood ratios, we chose two other approaches to cross-sectional morphometry: cell lumen area and double-wall thickness. The development of sophisticated computer systems and digital image analyzers now makes it possible to measure the anatomy of biological systems, both quantitatively and qualitatively, and to graphically plot the changes that occur in space or time (Fischer 1972; Gahm 1972; Quirk 1981; McMillan 1982, Jagels et al. 1982; Jagels and Dyer 1983; Jagels and Telewski 1989; Fritts et al. 1991). These approaches can be applied to coniferous xylem, to quickly assess changes across a growth ring, and the plotted curves can serve as fingerprints for cambial zone activity as manifested in cell division, enlargement, and differentiation (Jagels and Dyer 1983; Jagels and Telewski 1989).

CELL LUMEN AREAS

The cell lumen area (CAL) in any growth ring is greatest in the first formed earlywood and declines through transition latewood into latewood. A large CAL area provides for greater water transport efficiency, but a small CAL enhances "safety" (i.e., reduces the chance of embolism formation as column pressures become more negative under moisture stress [Zimmerman 1983]). Thus, when soil moisture is readily available in spring and early summer, the cross-sectional lumen area is large, while in late summer and early fall when soil moisture may be limiting, cell lumen area is reduced.

In hardwoods (dicotyledonous woods), especially ring-porous woods, only the current year xylem may function in translocation (elm, for example). Thus, a very narrow growth ring provides a smaller volumetric column for water transport, and this may seriously jeopardize the tree during drought conditions (Zimmerman 1983). This is one reason why ring-porous hardwoods are so sensitive to wilting diseases or drought.

In conifers, on the other hand, several growth rings of the living sapwood are functional in translocation. This provides a larger storage reservoir in the trunk to cope with soil moisture deficits (Waring and Running 1978). Evergreen conifers may tap this reservoir during cold months when the soil is frozen, thus permitting limited photosynthesis and associated transpiration.

Conifers growing in dense shade produce narrow growth rings due to reduced photosynthesis. The functional sapwood in these trees is narrow, but is balanced with reduced transpiration rates. On the other hand conifers growing in full sunlight have higher photosynthetic and transpiration rates and thus require more water. This is usually achieved since these trees would be expected to produce wide growth rings and have a wider functional sapwood and increased volumetric water capacity. If the tree is stressed for a single year by drought, the effect on the stem water storage capacity will be minimal, but if the drought continues for several years the effect on water storage capacity is significantly diminished, and some trees may die. Trees that survive might be expected to compensate by producing cells with a larger lumen diameter. A negative consequence of this, however, is increased risk of embolism formation (Zimmerman 1983). A compromise could be achieved by producing larger earlywood cell lumen areas (when soil moisture is not so limiting), and smaller latewood cell lumen areas (when soil moisture is most restrictive). We shall see if either or both of these adaptive mechanisms is employed by red spruce.

If trees undergo a long-term stress (pollutant or climate) and growth rate is reduced, following the logic just presented, trees should be more susceptible to short-term climate fluctuation, particularly drought.

DOUBLE WALL THICKNESS

Double wall thickness (DWT) is a direct measure of cell wall synthesis and an indirect measure of tree vigor (photosynthetic activity in particular). When stressed, a tree can synthesize less cell wall material by (1) producing narrower rings (fewer cells), (2) synthesizing thinner cell walls, or (3) both. Option 1 in conifers should have no effect on physical properties, and studies have borne this out (Rademacher et al. 1986). Options 2 and 3 will reduce strength properties. One or a few rings of this type will have little effect on the tree, but a long-term production of thinner cell walls would significantly affect tree strength—particularly since the rings would be in the zone receiving the highest tensional and compressive stresses in the living tree.

For these reasons, the short-term response of the conifer cambium to environmental stress might be different from the long-term response. We shall examine both the short-term (winter stress and drought years) as well as the long-term changes in DWT in order to assess whether they are similar or different.

Unlike CAL, which measures only a quantitative value (void space), DWT has both quantitative and qualitative aspects. From morphometry we can assess the quantitative differences only. Thus, a caveat needs to be attached to DWT, particularly if cellulose, hemicellulose, or lignin changes are suspected. For the purposes of this study, we assumed that qualitative differences in cell wall composition were minimal and not significant.

The present study is based on the premise that during periods of radial increment change (stimulation or decline) morphometric fingerprints of individual growth rings will mirror the unique environmental conditions defined by edaphic and atmospheric inputs, and that these fingerprints will, therefore, significantly differ among microsites differing in these conditions. The hypotheses to be tested include

1. morphometric features are environmentally sensitive,
2. morphometric features respond differently to separate climate or pollutant stress factors,
3. both short-term (year to year) as well as long-term trends may be a consequence of climate or pollutant stresses, and
4. synchronous climatic or pollutant stresses can interact to initiate more complex morphometric responses.

METHODS AND SITE DESCRIPTIONS

In late July of 1986, coring was commenced on four low elevation sites in Maine, USA. These sites were part of a network of biomonitoring stations assessing fog and rain acidity, ozone levels, and spruce vigor (Jagels 1986). The sites selected were two mid-coast island stands (Head Harbor and Eastern Head on Isle au Haut), a downeast coastal stand (Roque Island), and an inland low elevation site (University Forest, Orono). See Kimball et al. (1988) for further details on these sites. The coastal sites lie on a gradient of acid fog and ozone (Jagels et al. 1989; Percy et al. 1993). Fifteen dominant and codominant trees were cored from each site (2 cores per tree), for a total of 120 cores.

Sites were selected to provide some variation in soils, atmospheric pollutant input, and frequency of tree decline symptoms within the low elevation red spruce forests of Maine. The physical descriptions of the soils are provided in Jagels (1986). In general the soils are high in organic matter and lie over granite or hardpan. Soil depth, pH, percent base saturation, cation exchange capacity, and Ca/Al ratios are presented in Table 1.

Fog pH on Isle au Haut (sites HH and EH) for two seasons averaged 3.26 (min = 2.90), while at Roque Island (RI) fog pH averaged 3.91 (min = 3.32) (Kimball et al. 1988). Fog is generally absent at the University Forest (UF) site. Among the four sites, monitored ozone levels were highest at HH and EH. Other pollutants were not measured. Although fog pH is similar at HH and EH, fog intercept in the canopy of each stand is different. Site HH is an open, rough canopy stand, while site EH is a closed stand with a more even canopy. Based on modeling considerations (Lovett 1984; Lovett et al. 1982) and from actual observation, the open, rough canopy stand (HH) captures more fog. In the closed canopy stand (EH), much of the fog is captured by the white spruce that occupy the shore zone (Jagels et al. 1989).

Table 1. Soil characteristics of 01 and 02 horizons (adapted from Jagels et al. 1989).

	Depth (cm)	pH	% Base Saturation	Cation Exchange Capacity	Ca/Al Ratio
Head Harbor (HH)	22	4.15	45.7	36	0.45
Eastern Head (EH)	14	4.05	70.2	37	4.53
Roque Island (RI)	28	4.10	39.6	35	0.30
University Forest (UF)	14	3.80	26.2	33	0.60

Red spruce growing on HH show foliar decline symptoms of yellowing of upper surface of older foliage and premature needle loss, both of which are described more fully in Jagels (1986). Red spruce on EH have shown late winter needle tip burn (as observed for high-elevation spruce), but the yellowing and premature needle loss is not observed (Jagels et al. 1989). Trees on RI and UF are mostly asymptomatic with regard to foliage. Average tree age and range of ages (as ascertained from cores) for each site follow: HH—63 yr. (36–98); EH—78 yr. (46–105); RI—83 yr. (41–146); UF—69 yr. (56–84).

A 5.0-mm increment corer (Suunto, Finland) was used to extract two cores per tree (at 90° to axis of lean). Cores were dried to constant moisture content (approximately 8%) in a vacuum desiccator and surfaced using a specially constructed jig and abrasive paper (Martin Senour - 220A, 400A, and 600A grades). Abrasive smoothing provided a sharper microscopic image than motorized planing, and microtoming proved to be unworkable.

Ring widths were determined with a Measu-chron (L. Kutschenreiter, Austria) digital micrometer, interfaced with a Hewlett Packard model 85 desktop computer. Cell morphology was measured using a ZIDAS (Zeiss Interactive Digital Analysis System), consisting of a digitizing tablet and ZIDAS interface program version 1.2, which was ported to an IBM-AT personal computer. A Zeiss 20T microscope with incident light optics was used to visualize the wood surface; cores were mounted in a custom-made lucite jig attached to a rotatable mechanical stage. A centered, light-spot cursor was used to trace cell outline (lumen perimeter) and measure cell wall thickness on a virtual image created with a microscope drawing tube extended over the digitizing tablet.

Cell morphology records were transferred via Y-term program from the IBM-PC to a control mainframe IBM 3033. Data points were graphed with a overlaying cubic spline by SAS/graph on a calcomp plotter 1073.

Detailed morphometric analysis was applied to the years 1955 (control), 1956 (winter stress), 1967 (drought), and 1979 (control). Three radial files of cells, from the first formed earlywood cell to last formed latewood cell, were measured by outlining the cell lumen and measuring DWT, using procedures previously outlined (Jagels and Dyer 1983). Circularity index (CI) and CAL were calculated and those parameters as well as DWT were used to generate splined curves as represented in Figure 1, 2, and 3. Although CI had proved useful in a previous study (Jagels and Dyer 1983), it was not sensitive in the parameters investigated in this work and, therefore, is not considered further.

Since our initial intention was to compare different sites and years, data were plotted on a percentage of total ring width basis (Figure 1, 2, 3). Thus, for any ring width the x-axis becomes standardized. This strategy was applied so that morphometric curves could be directly compared.

Maximum cell lumen area (CAL max) was taken from the highest point of the curves on the CAL graphs (see Figure 2). The boundary between earlywood and latewood was arbitrarily determined as the midpoint between the lowest and highest point on the spline of the DWT graphs (see Figure 3). The low point was taken between the 10% and 30% points on the x-axis to avoid transition latewood.

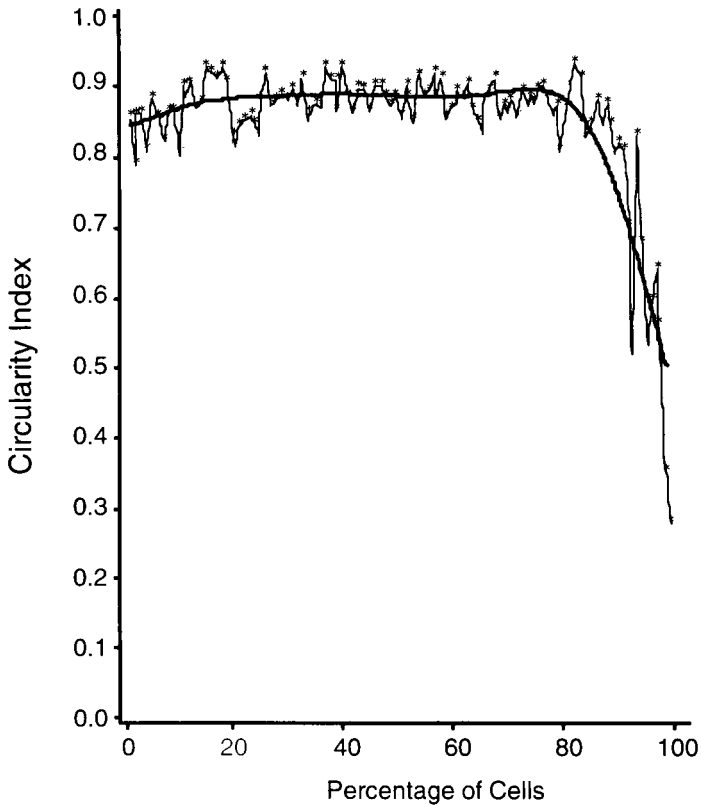


Figure 1. Splined curve of circularity index (RI, Tree 38).

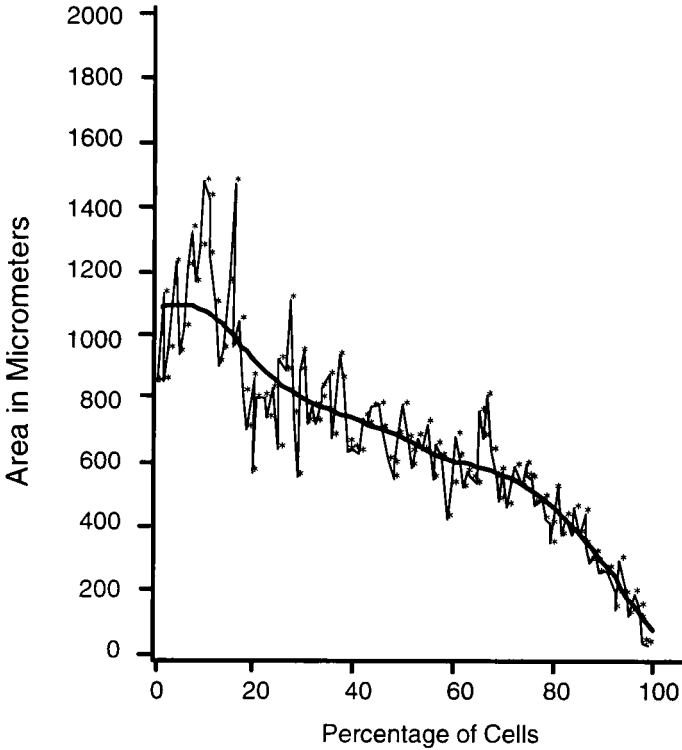


Figure 2. Splined curve of cell lumen area (CAL) (RI, Tree 38).

Weather Data

From September through December of 1955, temperatures were below normal in New England. December of 1955 was the coldest since the record cold of 1917, and the fourth coldest December on record in northern New England. The month was also notable for extremes (-35°F at Fabyan, NH, on the 22nd, followed by 53°F at Readsboro, VT, three days later). Deficit snowfall for the month helped to produce unusually deep frosts. January 1956, had excessively warm temperatures in northern New England, and February and the first week of March were warm, but then the weather turned colder than usual, and this continued into April. April ended with a warm spell, but this was followed by the coldest May since 1917. Some stations recorded the second coldest May on record.

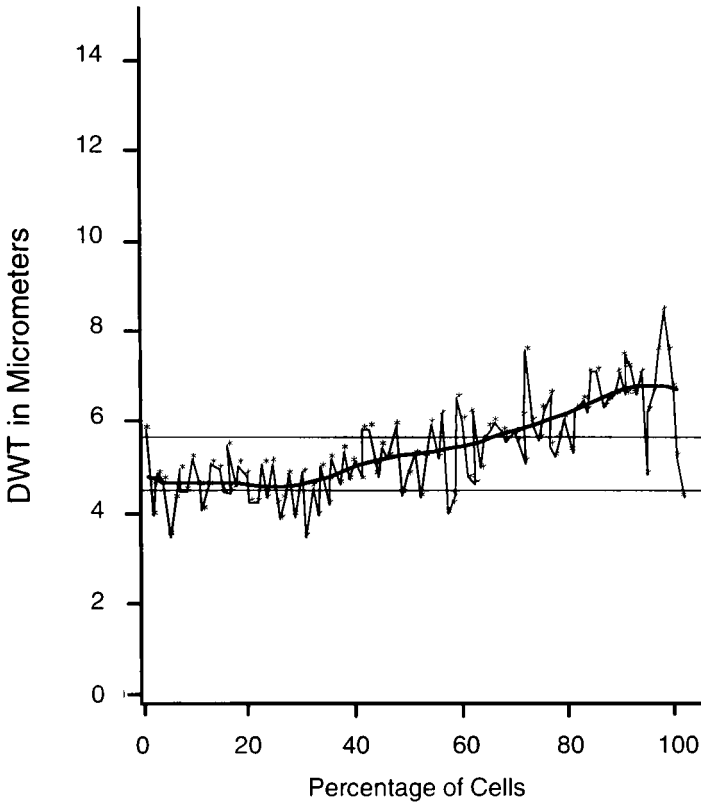


Figure 3. Splined curve of double wall thickness (DWT) (RI, Tree 38).

From the 12th to the 16th of June, a record heat wave occurred (temperatures above 96°F in each state). The rest of the summer was cooler than usual, and some stations reported that September was the second coldest on record. Cool temperatures continued into October. Precipitation during 1956 was above normal along the coast of Maine.

The 1960s were marked by successive well-documented drought years throughout New England, particularly the years 1962–67. Coastal Maine weather stations reported below normal rainfall during these years, but Coast Guard Station reports indicated normal or above normal fog incidence during the early to mid-1960s. This seeming contradiction is common for dry years with higher temperatures—conditions that favor fog formation over cold waters.

RESULTS AND DISCUSSION

Figure 4 is a plot of ring-width chronologies from 1915 to the present for each of the four sites: Head Harbor (HH), Eastern Head (EH), Roque Island (RI), and University Forest (UF). Stand histories, as represented by ring chronologies, vary between sites. Of particular note is the marked increase in radial increment for RI beginning around 1940. Subsequent to core collection we learned that part of the stand had been thinned during that period, releasing trees that had been growing very slowly.

The winter stress year of 1956 is mirrored in all four chronologies, to varying degrees, by a distinct radial growth increment decrease (arrow). Similarly, all four chronologies were responsive to the 1960s New England drought. The coastal sites reached the point of least growth in 1967, while the inland (UF) site reached this point a year earlier (1966). Trees on all sites demonstrated a consistent growth rate decline trend beginning in the late 1950s, regardless of whether trees displayed visible foliar symptoms in 1986. The two

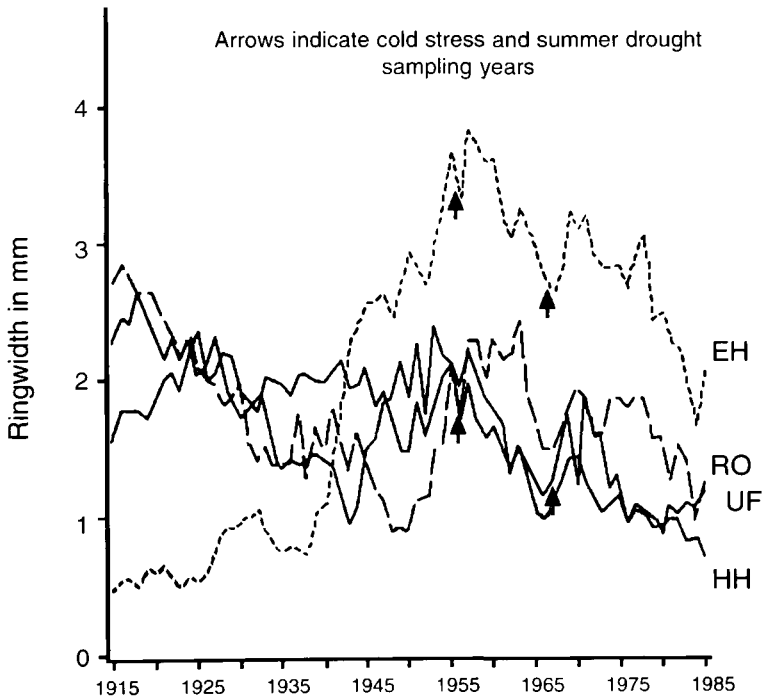


Figure 4. Average ringwidth chronologies.

sites that have shown the greatest and nearly synchronous growth reduction are HH and UF, the sites where foliar symptoms and pollutant loading are greatest (Jagels 1986; Kimball et al. 1988; Jagels et al. 1989; Percy et al. 1993). Each have poor soils and the lowest % base saturation, but UF has a high stand density and the HH stand is more open. Ring width chronologies seem to reflect a combination of factors, including, perhaps, airborne pollutant loading.

Because all trees show a declining growth rate during the study period (1950s–1970s), this downward trend must be taken into account when comparing morphometric features from one year to another. Since morphometric features may be directly or inversely correlated with ring widths, failure to recognize long-term ring-width trends is the same as assuming a level trend. Thus, in all but level-trend situations standard ANOVA testing would be invalid. Once a trend line is established, one can test whether a morphometric feature falls within or outside the confidence limits.

The approach of this analysis was to fit regression lines to the cell parameters for the years 1955, 1958, and 1979. The resulting lines were then used to predict corresponding values for the years 1956 and 1967. These predicted values were compared to observed values to determine if they could reasonably have been observations from the same model.

The models and estimates are dependent upon several factors that must temper any conclusions. First, the fitting of three points must necessarily produce “good” fits, therefore, R^2 values are not presented. Second, the spacing of the points, 1955 and 1958 close together and 1979 far from the others, makes the 1979 point very influential. Even small changes in the 1979 values will produce changes in the parameters. Third, even though a simple linear regression fits in most situations, the spacing of the points could easily allow for equally good fits of more complex models that could change the predictions for the 1967 point.

Cell Number (CN)

As would be expected, cell number is correlated with ring width. We examined whether the relationship between ring width and cell number was constant or varied significantly based on site or stress year. Table 2 shows the ratio between ring width and cell number by site and year.

Table 2. Mean ratios of ring width to cell number.

Year	Head Harbor RW/Cell #	Eastern Head RW/Cell #	Roque Island RW/Cell #	UM Forest RW/Cell #
1955	.029 (.0077)	.029 (.0078)	.028 (.0040)	.028 (.0027)
1956	.027 (.0076)	.028 (.0056)	.029 (.0073)	.029 (.0028)
1958	.028 (.0046)	.028 (.0075)	.029 (.0033)	.029 (.0032)
1967	.029 (.0052)	.029 (.0096)	.031 (.0031)	.027 (.0043)*
1979	.027 (.0045)	.031 (.0055)	.031 (.0030)	.027 (.0029)

() = Std. dev.

*Year 1966

The ratio varies very little among years or sites. Thus, cell number can be reliably used to assess ring width variation. Table 3 displays the average number of cells per annual ring by site and year and reflects the ring width chronologies in Figure 4.

We also wanted to test whether the number of cells in the earlywood (EW) and latewood (LW) declined equally as ring width decreased, or whether one was affected more than the other. Linear regression models with the same slopes fit all of the data, but Roque Island had an intercept different from the other three sites. The regression equations for total cell number follow.

Sites

UF,EH,HH

RI

$$CN = 165.3 - 1.59 \times \text{year}$$

$$CN = 214.7 - 1.59 \times \text{year}$$

Table 3. Average number of cells in annual ring.

Year	Roque Island	Univ. Forest	Eastern Head	Head Harbor
1955	129 (28%)	76 (24%)	74 (30%)	73 (29%)
1956	116 (35%)	66 (42%)	64 (32%)	64 (32%)
1958	128 (34%)	79 (37%)	81 (36%)	64 (34%)
1967	87 (29%)	45 (38%)	53 (34%)	38 (34%)
1979	82 (28%)	38 (40%)	53 (34%)	34 (38%)

() Denotes percentage of mean comprised of latewood. Each mean is based on 30 observations.

From Table 4 it can be seen that the number of cells produced in both 1956 and 1967 were significantly fewer than the number predicted by the regression equations for all sites except RI (see also Figure 4). The linear regression equations for cell number in EW follow.

<u>Sites</u>	
UF,EH	$CN = 126.4 - 1.28 \times \text{year}$
RI	$CN = 159.8 - 1.28 \times \text{year}$
HH	$CN = 119.6 - 1.28 \times \text{year}$

Table 4. Actual and predicted cell numbers per ring for stress years.

Sites	Year	Actual	Pred	SE
UF,EH,HH	1956	64.67	76.28	5.32*
	1967	45.33	58.79	5.10*
RI	1956	116.00	125.72	8.91
	1967	87.00	108.23	8.78

With the exception of the HH site in 1956, EW cell number was significantly less than predicted for all sites for both 1956 and 1967 (Table 5). The linear regression equations for cell number in LW follow.

<u>Sites</u>	
UF,EH,HH	$CN = 48.1 - 0.45 \times \text{year}$
RI	$CN = 62.9 - 0.45 \times \text{year}$

Table 5. Actual and predicted earlywood (EW) cell numbers per ring for stress years.

Sites	Year	Actual	Pred	SE
UF,EH	1956	39.82	54.70	3.71*
RI	1956	73.97	88.15	5.12*
HH	1956	41.50	47.49	5.17
UF,EH	1967	26.52	40.62	3.61*
RI	1967	60.30	74.07	5.09*
HH	1967	23.27	33.42	5.09*

* (1) In the regression formulas presented in this paper, year = calendar year 1990.

With the exception of RI site in 1967, cell number in latewood was not significantly different from predicted values (Table 6). Thus, regardless of environmental cue, when rings become narrower, the effect is primarily on the number of cells in the earlywood, not the latewood. This result fits with the cambial activity model proposed by Wilson (1969), which suggests that the width of the latewood is predetermined by the width of the cambial zone as it expands in the spring, and this in turn, is controlled by growing conditions the previous year. Therefore, factors in the current year that reduce total ring-width must have their primary effect on this year's earlywood.

Table 6. Actual and predicted latewood (LW) cell numbers for stress years.

Sites	Year	Actual	Pred	SE
UF,EH,HH	1956	23.76	23.28	3.05
RI	1956	40.90	37.62	5.11
UF,EH,HH	1967	14.06	18.33	2.92
RI	1967	22.17	32.66	5.04*

Double Wall Thickness (DWT)

Regression analysis for DWT revealed zero slope, indicating that this morphometric feature is not affected by the long-term trend of declining growth rate (progressively narrower rings). Analysis of variance of DWT in earlywood and latewood revealed, using Duncan-type underlining, the following.

EW	<u>55 56</u>	67	<u>58 59</u>
LW	<u>55 56</u>	58	<u>67 79</u>

The winter stress year (1956) is not significantly different from the previous year in DWT, but is different from the other years. The drought year is significantly different from all other years for EW, but is not different from 1979 for LW.

These results suggest that, as in the case for cell number, the strongest influence is in the EW zone, but only in the case of a drought cue, not for winter stress. Although regression analysis failed to reveal any slope other than zero, the ANOVA separations, especially for LW suggest a trend from 1955 to 1979.

Cell Lumen Area (CAL)

CAL was measured for all cells and analyzed for two categories: (1) CAL max (maximum cell lumen area reached in the earlywood), and (2) CAL lw (average cell lumen area of the latewood).

A simple linear model regression equation fit CAL max, with HH site having a different intercept from the other sites.

Sites	
UF,EH,RI	CAL max = $827.3 + 3.15 \times \text{years}$
HH	CAL max = $739.3 + 3.15 \times \text{years}$

Actual values were not significantly different from predicted values for any site in the winter stress year (1956), but were significantly different for all sites except HH in 1967. (Table 7).

Table 7. Actual and predicted maximum cell lumen area in earlywood for stress years.

Sites	Year	CAL max (EW)		Standard Error
		Actual	Predicted	
UF,EH,RI	1956	970.5	1003.9	27.70
HH	1956	891.0	916.0	43.07
UF,EH,RI	1967	1038.6	1038.6	24.63*
HH	1967	964.0	950.7	42.44

A simple linear model would not fit the CAL lw data. After testing several different linear, quadratic, exponential, and nonlinear models, the best fit was with a quadratic term in year. This fit all sites with no intercept differences.

$$\text{CAL lw} = -4819 + 154.51 \times \text{year} - 1.125 \times \text{year}^2$$

Using this regression equation, actual values were not different from predicted values in 1956, but were different in 1967 (Table 8).

The results from these analyses suggest that following a winter stress, CAL is unaffected in either EW or LW. In drought years, however, CAL in EW is larger than predicted, and smaller than predicted in LW. The Head Harbor site, being the most stressed, fails to respond significantly in the earlywood, but does show a slight, nonsignificant increase.

The lack of response in the winter stress year suggests that the major response is the production of fewer cells due to the reduced length of season and excessively cool growth conditions.

Table 8. Actual and predicted cell lumen area in latewood for stress years.

Sites	Year	CAL max (EW)		Standard Error
		Actual	Predicted	
All	1956	329.5	305.8	19.08
All	1967	329.4	482.6	44.89*

The drought also resulted in a reduced number of cells, but also triggered an increase in per cell water capacity in EW and a decrease in LW. Both of these responses fit with the model already presented for drought stress. From our data, it appears that drought years can be distinguished from "winter stress" years most readily by analyzing the morphometric feature of CAL lw. A significant reduction from predicted CAL lw would be a strong indicator of drought stress.

It should be noted that average CAL of earlywood (CAL ew) was also tested, but it was not possible to fit any kind of linear, quadratic, exponential, or nonlinear regression model to this data. The erratic nature of this parameter is probably due to the fact that CAL ew is declining at different slopes toward CAL lw, and this would necessitate an analysis of the difficult-to-define transition latewood (Jagels and Dyer 1983). CAL max avoided these difficulties and provided a morphometric parameter that fit a simple linear regression model.

CONCLUDING REMARKS

The initial premise that morphometric analysis master curves would provide unique fingerprints for narrow rings produced during different environmental stimuli proved to be too optimistic. The between-tree variation was too great (particularly in the transition zone between earlywood and latewood) to permit generating meaningful master curves for a particular year, even on a per site basis.

In part, this variability reflects genetic heterogeneity but in addition, tree vigor and microsite differences may play important roles. Therefore, the effect of a drought is not manifested uniformly throughout a stand. Even ring width varies considerably within a stand for a particular year, but the mean is an indicator of general stand response. Quantitative analysis of selected parts of the morphometric curves proved useful in delineating stand response. In this study, CAL was the most sensitive to drought and permitted us to distinguish narrow rings produced by drought from those produced by winter stress. For other environmental stresses, different morphometric features might be useful.

Because morphometric features may be directly or inversely related to absolute ring width, regression curves must be established for each quantitative parameter to be tested. In future studies, a better distribution of reference years around test years might provide more accurate regression lines against which the anomalous years could be tested. With only three reference years, curvilinear regressions are meaningless.

Under conditions of a level growth rate, standard ANOVA testing would suffice, but this rarely occurs in natural stands. A more difficult problem arises when long-term growth rate is increasing in some stands while decreasing in others (not encountered in this study). The analytical approach used here could not be applied under those circumstances, unless the feature is independent of growth rate (which may be the case for DWT).

The analysis of wall thickness yielded mostly ambiguous results. Quite likely, environmental factors other than the ones we examined were influencing wall thickness variation. No clear short-term or long-term relationships between wall thickness and ring width could be discerned. The only consistent relationship was the HH site influence on wall thickness. As previously noted, the thicker cell walls on this site may be a response to enhanced wind stress on the site.

The morphometric feature of cell lumen area—a measure of water conduction capacity—was the most differentially responsive to separate environmental cues. In particular, during drought stress the maximum earlywood lumen capacity increased and average latewood lumen area decreased. Thus, comparing average CAL_{lw} to a constructed regression curve would seem to provide a reliable indicator of whether narrow rings were initiated by a drought or some other stress. An example of the potential reconstructive value of this parameter can be seen in Figure 5. We initially chose 1979 not as a reference year, but because we were told by the caretakers of Roque Island that it was an excessively dry year. Examination of state weather records failed to support this contention, but Figure 5 suggests that 1979 may, indeed, have been a dry year on Roque Island (reduced CAL_{lw}), and that it was an anomaly for the region (CAL_{lw} increasing on the other three sites).

One pitfall in this kind of reconstructive analysis lies in the possible interactive effect of multiple stresses in one year. Further study will be needed to assess this problem. However, our data would suggest that the consistently strong influence of drought on CAL may be revealed even if other stresses are affecting tree growth

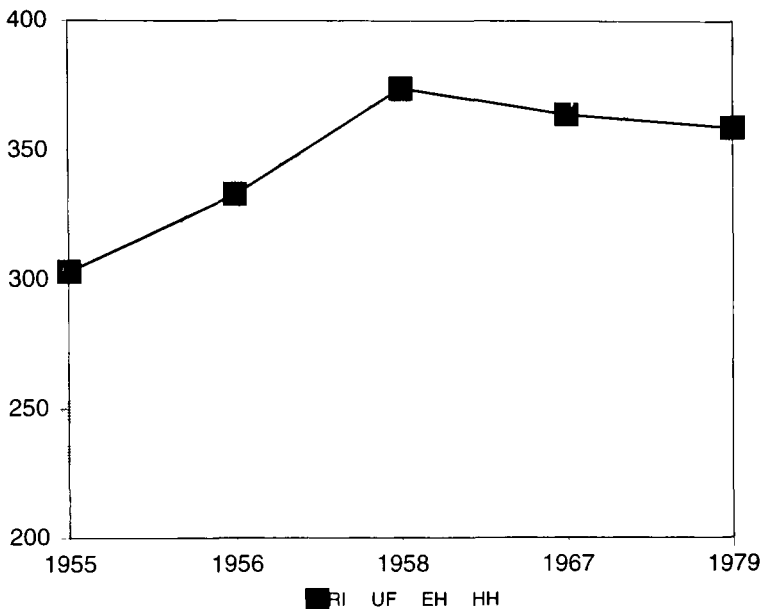


Figure 5. Cell lumen area, latewood (CAL, lw) averages for site and year.

during that year. Thus a CAL lw reduction would still indicate drought stress but not necessarily exclude other concurrent stresses.

Finally, it should be pointed out that this kind of analysis is very labor intensive initially, but as key sensitive morphometric features are identified and the methods of analysis refined, the time constraints are reduced. Furthermore, once this stage has been reached, a shift to an automatic image analyzer may be possible for certain morphometric features (such as cell lumen area), which would further reduce analysis time and hence morphometric analysis would have more practical value.

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