WATER STRESS AND GROWTH OF COTTONWOOD SAPLINGS

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Abstract.--Morphometric and ecophysiological methods to measure seasonal growth and water stress in several groups of cottonwood (*Populus deltoides*) growing at a rolling prairie site in NE Kansas were developed. Resolution of morphometric measurements was significantly increased by determining number and length or diameter of the trees' lateral branches in addition to the conventional measures of height and stem diameter. Combined measurements of evaporation, daily stem shrinkage (with a manometric dendrometer proposed by Alvim, 1975), and soil moisture revealed significant differences in seasonal water stress between experimental groups, which were well correlated with observed differences in seasonal growth during 2 consecutive seasons. Differences in water stress resulted from (1) relative position of trees along a slight slope, which provided trees at the lower site with additional water from run-off, (2) differences in planting density, and (3) position of trees at the edge of or within a stand.

Additional keywords: Morphometry, dendrometer, ecophysiology, density effects, site effects, *Populus deltoides*.

During the past decade field methods for the assessment of plant water relations have been markedly improved, and daily and seasonal changes in tree water relations have been studied intensively (Hinckley et al. 1978). Because of the considerable effort involved in the complete analysis of the soil-plant-atmosphere continuum for a single day, such studies have been mostly limited to the analysis of one or a few trees and a few "representative" days (e.g., Hinckley and Bruckerhoff 1975, Hinckley et al. 1978; Pereira and Kozlowski 1978). Comparisons of water relations between tree groups subject to different sets of environmental conditions and integration of single-day analyses into an assessment of a tree's seasonal water economy have been rarely attempted. However, such integration is needed if our understanding of the effect of tree water relations on seasonal tree growth is to progress beyond the establishment of correlations between the seasonal time course of major climatic variables and annual production of biomass.

In this study, growth of cottonwood saplings (*Populus deltoides*) was measured at an upland site in eastern Kansas during 4 growing seasons. The observed differences in annual growth increments between several groups of trees were found to be highly correlated with differences in water stress resulting from variations in site factors, interaction between trees, and climate.

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MATERIALS AND METHODS

As part of a study to compare biomass production in several tree species at the Sunflower Research Area near Lawrence, Kansas (Naughton & Geyer 1979), 1-year-old cottonwood seedlings (*Populus deltoides*) cut to a uniform length of 80 cm, were planted in Spring 1976 in a plantation of 4.3 ha sloping from S to N at 3 - 8%, as follows (Fig. 1, top): (1) plot N contained 210 trees arranged in a cartwheel design of 17 m radius with 30 spokes of 7 trees each. This plot was located at the northern edge and the lowest point of the plantation and was traversed by a draught carrying, after heavy rains, run-off water from the remainder of the plantation; (2) Plot C, containing 1400 trees spaced 1.3 x 1.3 m in 10 E-W rows of 140 trees each, was located immediately S of plot N; (3) Plot S, identical in tree number and layout with plot N, was situated at the southern edge of the plantation about 100 m S of and approx. 4 m higher than plot N. Immediately N of plot S there was a row planting of silver maple (*Acer saccharinum*) identical to plot C.

Based on differences in tree size visible at the end of the first growing season, experimental groups of 10 trees each were selected for morphometric analysis and later ecophysiological studies as described in Table 1 and Figure 1.

TABLE 1.-- Location and planting density of experimental groups of cottonwood at Sunflower Research Area. LD = low density; HD = high density (Compare Figure 1 top).

Group #	Location	Spacing in m	Density
G1	Plot C, 45 m W of G3	1.3	HD
G2	Plot C, 30 m W of G3	1.3	HD
G3	In plot C, directly S of and adjacent to G5	1.3	HD
G4	N side of plot N, 5 trees each on 2 outermost circles of wheel	3.6	LD
G5	S side of plot N, 5 trees each on 2 outermost circles of wheel	3.6	LD
G6	S half of plot N, between center of wheel and G5. 5 trees each on 2 adjacent circles.	1.25	HD
G7	S side of plot S, as G5	3.6	LD
G8	Within plot S, as G6	1.25	HD
G9	N side of plot S, as G5	3.6	LD

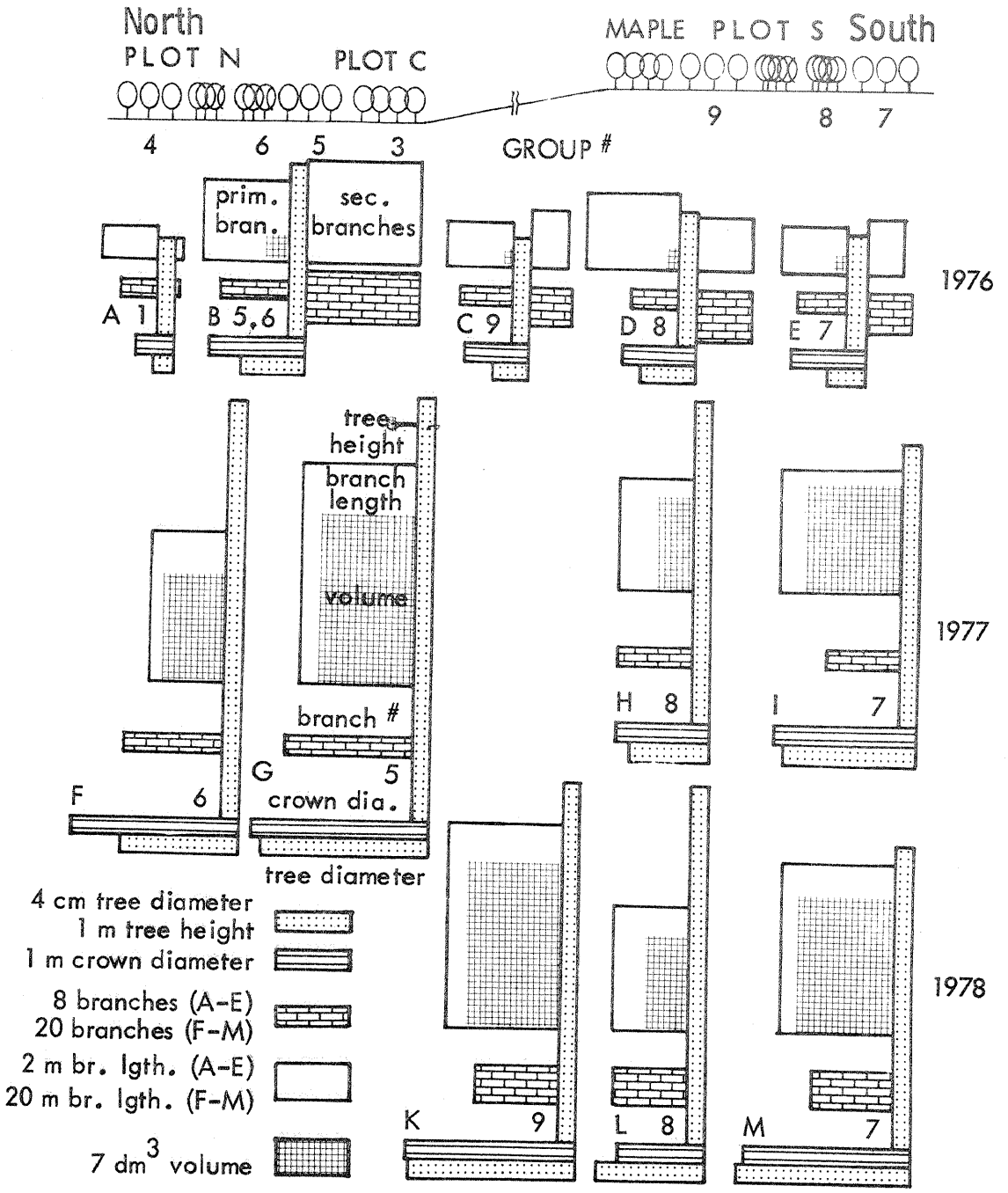

Fig. 1. Top. Schematic N-S section through experimental plots showing relative position of experimental groups of cottonwood trees. For actual dimensions and description of groups see text and Table 1. Lower Half (A-M): Size and complexity of cottonwood trees as measured at the end of the growing season in 1976 (A-E), 1977 (F-I), and 1978 (K-M). For each group (number in lower right corner) of 10 trees the means of tree height, crown and stem diameter, branch number and length, and volume are represented in a diagram. Number and total length are given separately for primary and secondary branches in 1976, but for branches inserted on main stem only in 1977 and 1978. For explanation of diagrams see B and G. Note change in scale for branch numbers and length between 1976 and 1977.

Morphometry

At the end of the first growing season the following variables were measured in all 10 trees of the various experimental groups: tree height, diameter of the tree crown, stem diameter 10 cm above ground, number and length of all primary and secondary (proleptic) branches formed during the season, and height of insertion of all primary branches on the main trunk. Measurement of branch length became impractical during consecutive years and was replaced by measurement of branch diameters 1 cm from their insertion at the trunk. Because branch diameters (d_b) were found to be highly correlated with the total length of the branch system (l_b) they support ($r = .95$ in 1976; $r = .90$ in 1977/78), the latter could be calculated from measured branch diameters by the formula $\log l_b = 1.86 \cdot \log d_b + 2.27$.

By means of a computer program written in FORTRAN, number, mean, maximum and total length of primary and secondary branches were calculated for each tree and experimental group and printed together with the measured variables. The Biomedical Statistical Package from UCLA (BMPD) was used for statistical evaluation of the data. Analysis with BMDP2D showed that data for the second and later years tend to be normally distributed, while about half of the variables for the first growing season were positively skewed. This was to be expected, since trees began branching during this year and many values were small but could not be less than zero. Principal Components Analysis and Discriminant Function Analysis were carried out using statistics packages BMDP4M and BMDP7M, respectively.

Based on the assumption that both main stem and branches are cone-shaped, the trees' total volume was calculated to obtain a crude estimate of relative changes in "biomass".

$$V = \frac{1}{3} \cdot r^2 \cdot h \cdot \pi + \sum_{b=1}^{b=n} \frac{1}{3} \cdot r_b^{\,2} \cdot l_b \cdot \pi$$

where r and h are radius and height of a tree,
r_b and l_b are radius and lenght of a branch, and
V is the tree's volume.

Morphometric data for group 9 were not collected in 1977, because differences between groups 7 and 9 were not yet apparent. Data for groups 5 and 6 were not taken after 1977, because tree exceeded manageable size.

Ecophysiological Measurements

For each working day, the following environmental variables were measured with the frequency and by means of the instruments given in parenthesis: temperature and relative humidity (sling psychrometer, all experimental groups every 3 h), rainfall (rain gauge, twice weekly), soil moisture (Bouyoucous soil moisture meter, weekly within each group at one site at 30 and 90 cm depth), evaporation (7-day recording evaporimeter).

Stem shrinkage was measured with manometric dendrometers made according to Alvim (1975) from 40 ml flat polyethylene bottles with dropper caps, into which 1.50 m of 2 mm OD/1 mm ID Tygon tubing had been glued as a manometer tube (glass capillary tubing is more expensive and easily breaks when trees are bent by strong winds). Dendrometers were filled with colored ethyleneglycol and attached to trees with adjustable hose clamps. Manometer tubes were extended by tying their upper end around a branch. On measurement days the height of the manometer fluid was at 7:00 h set to a marker by means

of the adjusting screw of the hose clamp, and rise or fall of the liquid was measured with a ruler at 16.00 h. Beginning at 6:00 and 7:00 h respectively, xylem pressure potential and stomatal resistance were measured in 1979 every 3 h in 4 to 6 fully exposed leaves per group with a pressure chamber and LI-COR autoporometer, respectively.

Measurement of all experimental groups at the same day was impossible. Data on the N and S plots were therefore collected on 2 consecutive days, once or twice weekly. During continuing dry spells day-to day variation was small and data of the N and S plots are comparable (most data of 1978), but rainfall on one of the 2 measurement days, as it occurred several times during the wet summer of 1979, rendered data of the 2 plots incomparable.

RESULTS AND DISCUSSION

Morphometry

To reliably assess relatively small differences in tree size as may result from slight variations in site factors or microclimate during one growing season, the traditional measurement of tree height and stem diameter is not sufficient. Statistical analysis of the data indicated that determinations of branch number and length, introduced as additional variables to characterize tree complexity and size, respectively, notably improved the quantification of tree structure. Principal Components Analysis demonstrated a high degree of covariation among most of the variables in 1976 (squared multiple correlations (SMC) near 0.9), and slightly lower covariation (SMC = 0.8) thereafter. The first 3 axes explained 89% of total variance in 1976 and 81% in later years. Variation could be ascribed mainly to size differences (67%, 57%), short trees with many short branches vs. tall trees with few long branches (12.7%, 23.6%), and varying ratios of primary to secondary branches (9%, 0). By means of Discriminate Function Analysis all experimental groups were clearly separated from each other by various combinations of variables (primarily branch length in 1976, height, crown, and stem diameter thereafter), and at least 7 or 8 out of 10 trees in each group were correctly identified in all cases.

Morphometric data collected from 1976 to 1978 are summarized in Fig. 1 and show the following:

(1) Throughout the observation period from 1976 to 1978 group G5 in plot N clearly outgrew all others (Fig. 1, B, G). As trees of this group were spaced widely and rooted in deep (> 1m) sandy loam, provided with ample moisture by run-off from surrounding slopes, growth data of the first season suggested that suboptimal growth of other experimental groups might be primarily the consequence of water stress suffered by the trees.

(2) Along the row planting of plot C there was a marked decline in growth vigor in experimental groups growing at increasing distance from the bottom of the draught (G3 > G2 > G1; Fig. 1, B vs. A; for location of groups see Table 1), which was well correlated with a decline in depth of soil from more than 100 cm in G6 to about 30 cm in G1.

(3) Throughout the study, trees in all groups of plot N grew more than trees in the corresponding groups of plot S: G5 > G7, G4 > G9, G6 > G8 (Fig. 1; B, G > E, I; B, F > D, H). In 1977, i.e. in its second year of growth, G5 had attained the size and volume which was reached by G9, the most vigorous group in plot S, only one year later (Fig.1: G vs. K).

(4) In 1976, no significant differences were found between groups G3, G4, G5, and G6 of plot N (data not shown), i.e., an effect of planting density was not apparent, while in plot S the high density group G8 grew significantly more than its low density neighbors G7 and G9 (Fig. 2: D vs. C, E). During the

following years, however, growth in high density groups in both the N and S plots increasingly fell behind that of their low-density neighbors: G6 < G5,G4 and G8 < G7,G9 (Fig. 1: F < G; H < I; L < K, M).
(5) As trees increased in size, those of the low density group G9 on the north side of plot S became notably larger than those of its counterpart at the South side of this plot (G7). We tentatively ascribed this difference between the 2 groups to differences in water stress resulting from full exposure of G7 to prevailing hot, southerly winds and sheltering of G9 from these winds by 18 rows of trees of plot S and from northerly winds by row plantings of silver maple, which by 1979 constituted a 6 m tall, dense windbreak.
(6) Seasonal increments in all experimental groups varied strongly from year to year. In both relative and absolute terms, size and volume of trees increased dramatically during 1977 (Figure 1). For instance, in 1977 calculated tree volume, an indicator of the trees' increase in biomass, rose from 1.0 to 41.4 dm^3 in G5, and from 0.2 to 25.3 dm^3 in G7. Increases in all variables were modest during the relatively dry summer of 1978 (Figure 1: H to L and I to M), but again large in the wet summer of 1979 (data not shown).

Ecophysiological studies

The purpose of ecophysiological studies was (a) to examine the suitability of simple dendrometers as proposed by Alvim (1975) for comparing water status in several groups of trees, and (b) to establish correlations between tree growth and water stress as postulated above. Stem shrinkage experienced by a tree during the day reflects an excess of transpirational water loss over water absorption from the soil, i.e., a tree water deficit, and has been found to be strongly correlated with the daily decline in xylem water potential (Hinckley et al. 1978). Preliminary testing of dendrometers during 1977 showed that use of 4 dendrometers per group of 10 trees consistently gave significant differences between trees of the N and S plot, as well as between trees within the same plot planted at high and low density.

Four dendrometers per experimental group were therefore used in all later studies. The standard error of measurements is very high (Fig. 2, C), and we have not determined so far whether the observed variation in daily measurements reflects variation between trees or variation in sensitivity of individual dendrometers. However, as changes in stem shrinkage from week to week exceed in most cases variation in measurements at a given day and all dendrometers of a group, including the "outliers", usually change in the same sense (Fig. 2, C), we consider the dendrometers as suitable indicators of seasonal changes in water stress in different groups of experimental trees, if used in conjunction with measurements of soil moisture and atmospheric evaporative demand.

Data of evaporation, stem shrinkage, and soil moisture for 8 of 12 observation weeks in Summer 1978 are summarized in Fig. 2 and show the following:
(1) Evaporation, as measured in the center of plot N, is low after rainfalls and increases steadily during rainless periods (Fig. 2A);
(2) Soil moisture at both 30 cm and 90 cm depth reaches values of < 10% earlier in plot S than plot N. The rapid recharging of the soil down to 90 cm in plot S but not plot N after the rainfall in Week 5 suggests that the soil is more permeable in the S plot, but soil samples taken during the installation of soil moisture blocks appeared rather similar in both plots.
(3) Stem shrinkage and evaporation were generally well correlated in trees well supplied with water, but stem shrinkage was relatively low when soils were dry. For instance,

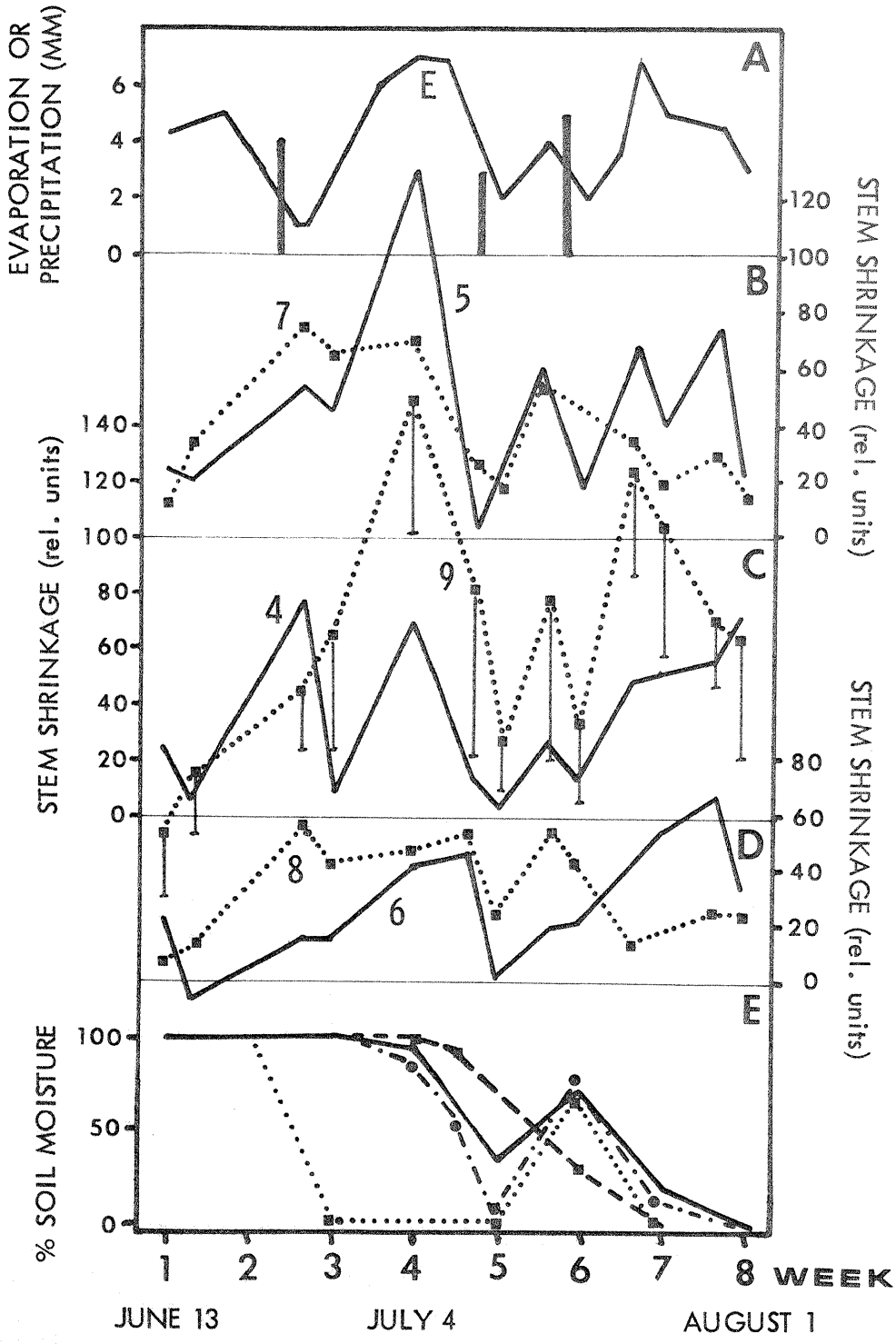

Fig. 2. Seasonal variation in stem shrinkage and relevant environmental variables during summer 1978. A. Evaporation and rainfall as measured in center of plot N. B-D: Stem shrinkage in low density groups at S edge (B:G5,G7) and N edge (C:G4,G9) and in high-density groups (D:G6,G8) of plot N (——) and plot S (·····). Standard errors given for group 9. E: Soil moisture measured in high density groups in plot N (at 30 cm depth: ———; at 90 cm: ----) and plot S (at 30 cm: ·····; at 90 cm: -·-·-·).

(4) As compared to G5, stem shrinkage in G7 was high during the first weeks, but when both evaporation and stem shrinkage of G5 peaked in Week 4, shrinkage of G7 was low, reflecting the reduced soil moisture availability in this group and - implicitly increased stomatal resistance (Fig. 2, A, B, E).
(5) A comparison between the 2 groups at the N side of plots N and S shows that stem shrinkage in G9 is considerably higher than in G4 and well correlated with evaporation (Fig. 2, A, C).
(6) The seasonal pattern of stem shrinkage of G9 is remarkably similar to that of G5, suggesting that evapotranspiration stress and soil moisture supply were similar in these groups, which were well sheltered within the plantation. Furthermore,
(7) when soil moisture at 90 cm in G7 and G8 approached the wilting point during Week 4, these groups, but not G9 and trees in the N plot, started shedding their leaves and subsequently shrank less (Fig. 2, B, D: weeks 6 to 8).
(8) Throughout the season trees planted at high density in the interior of plots N and S (G6, G8) shrank less than their low density neighbors to the S (Fig. 2, D vs. B), but G8 always suffered greater water deficits than G6 as long as it retained its leaves.

In sum, the data reflect not only significant differences in water stress between the N and S plots, but also between trees inside or at the edge of each plot.

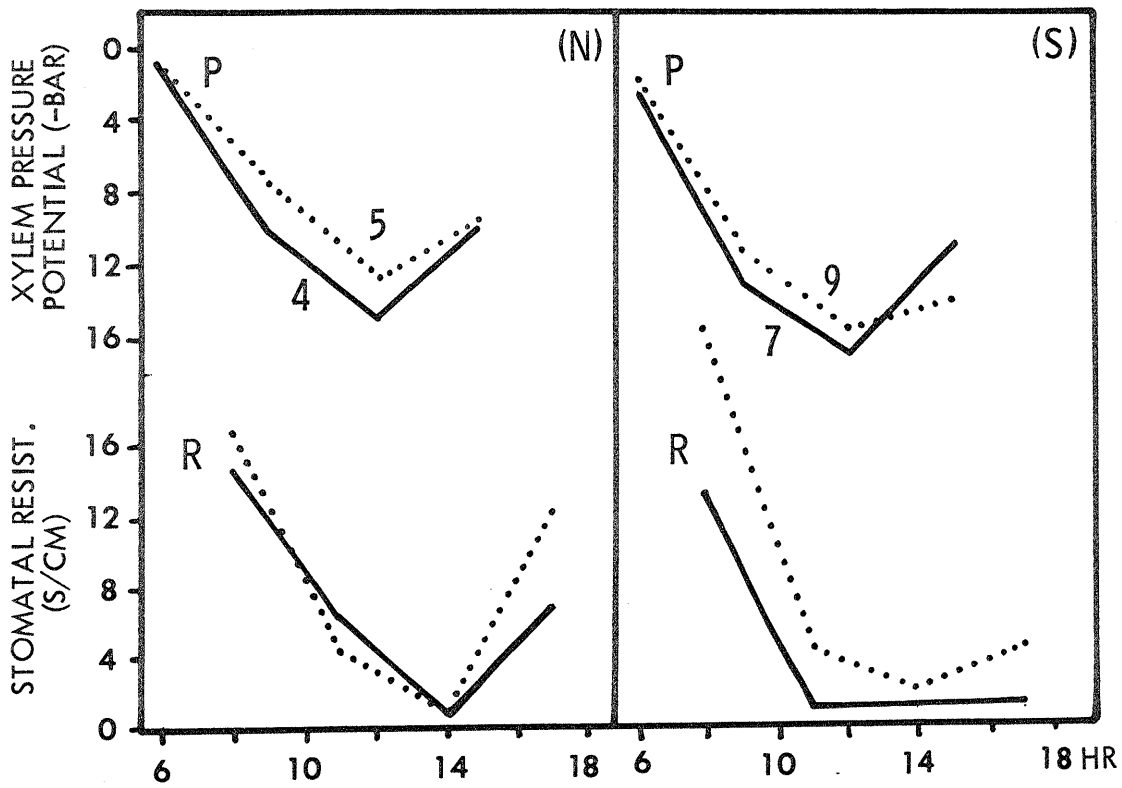

Fig. 3. Daily variation in xylem water potential (P, top) and leaf resistance (R, bottom) in exposed (G4, G7: ———) and sheltered (G5, G9: ·····) groups on plot N (left) and plot S (right) on July 2 and 3, 1979.

In summer 1979, the ecophysiological study of the experimental trees was repeated and expanded to include measurements of xylem water potential (P) and stomatal resistence (R). In comparison to 1978, this summer was unusually wet, as reflected in the following observations: (1) Precipitation was rather frequent, and (2) daily maximum temperature was on the average about 5 C lower than in 1978. (3) Evaporation was usually low (1 to 3 mm/day) and never exceeded 4 mm/day, while it had reached values of 7 mm/day in 1978. (4) The lowest soil moisture (SM) measured during the 12 week observation period was 40%, as observed only once in plot S. In 1978 SM had declined to < 10% several times (Fig. 2E). (5) predawn (base) water potentials (BP) below -5 bar were measured only on 4 and below -8 bar on one of the 24 measurement days. (6) While elongation of main shoots had ceased around July 10 in 1978, it continued until August 15 in 1979, and (7) biomass increments of trees were higher than in 1978.

Because of rain at one of the 2 measurement days per week, ecophysiological measurements obtained in the N and S plots on consecutive days were not comparable several times (e.g., weeks 2, 6, 8, 10 in Fig. 4).

Early in the summer, trees showed a daily decline in P and R during the morning followed by an increase in both values during late afternoon (Fig. 3), as characteristic of trees well supplied with water (Hinckley et al. 1978). Later in the season, on most days neither P nor R rose before 17.00 h. Throughout the season, values of P and R in plot S were somewhat lower at most observation times than those of the N plot (compare Fig. 3, 4), and trees exposed at the edge of each plot (G4, G7) suffered greater water stress than those sheltered by other trees (G5, G9), but seasonal data of R did not correlate well with either Pmin or stem shrinkage.

Data on seasonal variation in daily stem shrinkage (Fig. 4A) confirm the observations of 1978: with the exception of one week (W7), in all weeks for which comparable data were obtained, 2 or 3 of the groups in plot N showed less stem shrinkage and a higher daily minimum water potential (Pmin) than groups in plot S (Fig. 4 A,B). In contrast to groups in plot S (and to all groups in 1978), growth in girth ("negative stem shrinkage") during the day was observed several times in G4 or G5 until late July 1979 (Fig. 4A). In both plots the amount of daily stem shrinkage increased as the season advanced.

Data of week 7 illustrate the problems associated with carrying out measurements in plots N and S on consecutive days, but also show that different variables of the set of measurements can be checked against each other for consistency: On July 22 SM had reached its lowest value in both plots (Fig. 4C). Because of a SM of only 40% at 30 cm depth - and in spite of 90% SM at 90 cm depth - BP in G5 and G6 had declined to -6.6 bar and by 9.00 h P was - 15 bar in both groups. Rain started falling before noon, P rose to -8 and -10 bar, respectively, by 15.00 h, and daily stem shrinkage was low. Because of the rain, by July 23 soil moisture at 30 cm - but not at 90 cm - had risen to 90% in plot S, BP was -2.9 in G7 and G8, and stem shrinkage was high on the hot (Tmax = 31.5 C) day. The data suggest that both BP and stem shrinkage - reflecting transpiration - are strongly determined by SM in the upper, but not lower layers of the soil.

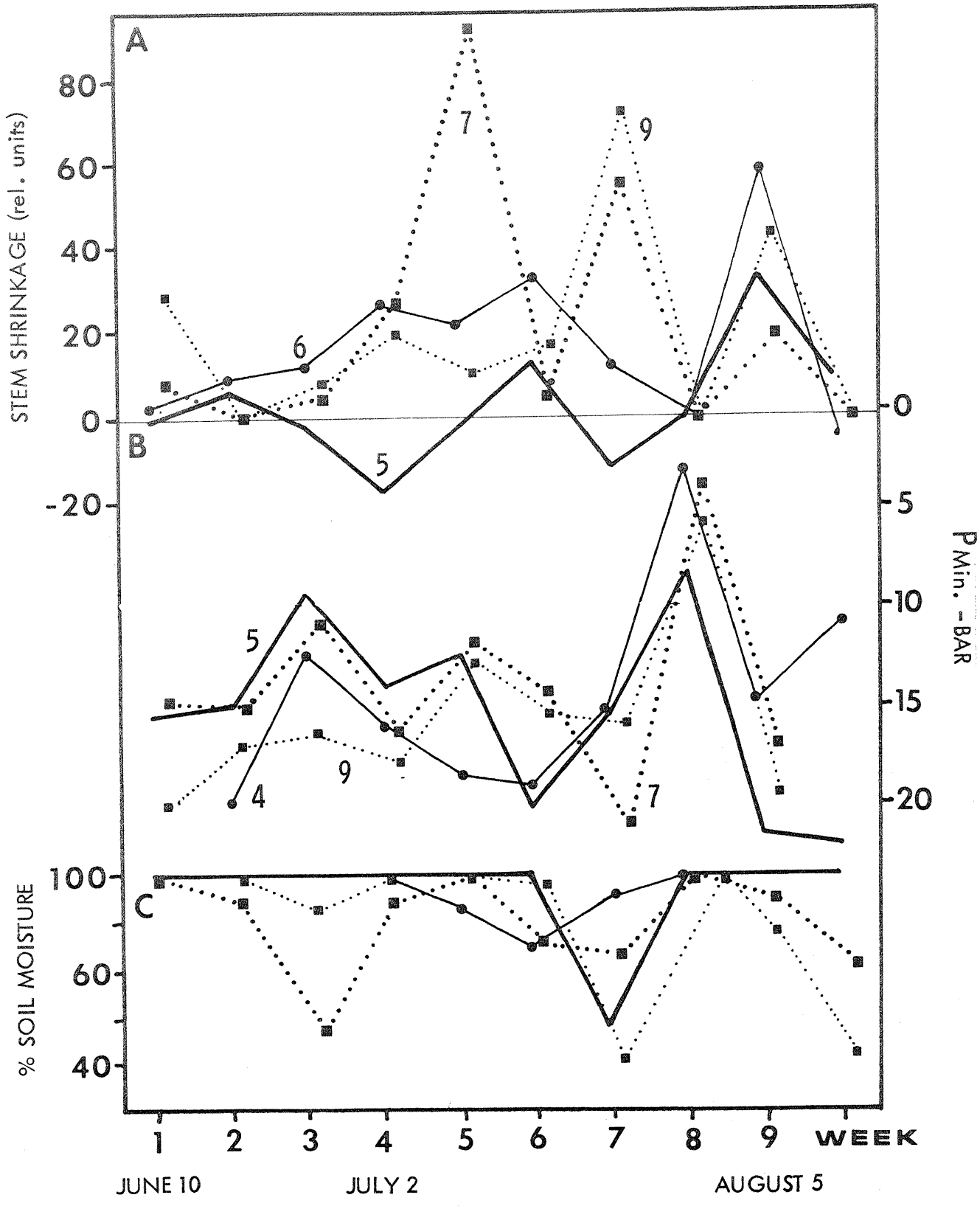

Fig. 4. Seasonal variation in stem shrinkage (A), daily minimum xylem water potential (B) and soil moisture (C) as observed in plot N (continuous lines) and pot S (dotted lines) in summer 1979. Experimental groups are identified by numbers on curves.

Within both plots stem shrinkage was markedly lower and Pmin higher in the sheltered, low density groups (G5, G9) than in the low density groups exposed at the N (G4) or S (G7) edge of plots N and S, respectively. A difference in tree water deficit resulting from previous differential water stress is well illustrated in week 7 (Fig. 4): Both Pmin and stem shrinkage of G7, exposed at the edge of plot S, were lower than in G9 indicating that a relatively low SM in G7 caused a low Pmin and hence reduced transpiration and stem shrinkage.

While Pmin in high density groups (G6, G8) was not significantly different from the other groups in their plots, in many weeks trees in these groups shrank markedly more than others in the same plot, indicating the effect of root competition for soil moisture in high density plantings (e.g., G6 vs. G5 in Fig. 4A).

CONCLUSIONS

The past decade has seen a notable rise of interest in the dynamics of shoot growth in trees and their "adaptive geometry", but morphometric methods for the quantification of tree size and complexity providing adequate results with a reasonable input of effort are not available. A computer-aided method developed earlier to evaluate the dynamics of tree growth (Borchert 1976) is unsuited for use with trees beyond the seedling stage. The determination of branching ratios, a method increasingly used during the past years (e.g., Steingraeber et al. 1979) is of questionable value in characterizing tree geometry (Borchert, unpublished) and cannot be used to quantify tree size and complexity. Because of the good correlation between the diameter of a tree's individual branches and their total length (and possibly leaf area; Shinozaki et al. 1964), measurement of the diameter of all branches along a tree's main stem, feasible in trees of up to about 6 m height, appears to constitute a reasonable way of measuring a tree's branch system. While the reliability of such measurements will require further verification, the present study shows that such measurements do improve the quantification of tree size and complexity to such an extent that even rather small differences in seasonal growth of several groups of trees can be assessed with a degree of confidence impossible to obtain with the traditional measurements of tree height and diameter.

Ecophysiological work was based on the hypothesis, that the observed growth differences between groups of cottonwoods growing within the same plantation and rather close to each other were the cumulative result of differences in water stress experienced during the relatively dry and hot growing season in Kansas. Measurement of stem shrinkage was chosen as the method to assess differences in water stress between experimental groups, because (1) the amount of daily stem shrinkage is an integrated measure of the tree's changing water balance during the day as it results from changes in the soil-tree-atmosphere continuum; (2) dendrometers proposed by Alvim (1975) cost little and can be easily attached to a large number of trees; and (3) the effort required to monitor stem shrinkage in numerous trees is rather modest. Because of the direct relationship between measured evaporation and potential evapotranspiration (PE) and between daily stem shrinkage and transpiration (T), measurements of evaporation and stem shrinkage permit assessment of the ratio T/PE. This ratio couples atmospheric evaporative demand with the plant's ability to respond and, therefore, constitutes an excellent indicator of water stress experienced by trees (Reed and Waring 1974). The data

presented here show that this method is suitable to detect relatively small differences in water stress between several groups of trees even in a rather wet season. The good correlation of Pmin with stem shrinkage, as observed earlier by others (Hinckley et al. 1978) validates the dendrometer measurements.

As changes of R observed in the field are not clearly related to any single variable in the plant or its environment (Hinckley et al. 1978, Pallardy and Kozlowski 1979), the lack of correlations between measurements of R and seasonal trends of water stress in experimental trees was to be expected. It thus appears that measurements of daily evaporation and stem shrinkage combined with determinations of predawn (base) water potential throughout a season permit - with a rather modest input of work - assessment of changes in relative water stress experienced in groups of small trees throughout the growing season as well as comparisons of water stress suffered by comparable trees growing at different sites or belonging to different species.

Like other pioneer species (Tobiesson & Kana 1974), cottonwood, a tree occurring naturally in moist river bottoms of the US-Midwest, showed little control of water loss throughout the season. Within the range of observed Pmin (to -21 bar), midday closing of stomata was never observed, soil moisture was rapidly depleted during rainless periods, and leaf shedding occurred during severe drought. This behavior was in marked contrast to silver maple (*Acer saccharinum*) growing at the same site: throughout the season P never fell below -13 bar, and stomatal closing often occurred when P was approx. -11 bar (Borchert, unpublished observ.).

To fully realize its growth potential, cottonwood apparently must be well supplied with water throughout the season. Because of its inadequate control of water loss and rapid depletion of soil moisture reserves, differences in soil water supply and evapotranspiration stress, as they existed within the study area, markedly affected the water economy of cottonwood and hence seasonal growth.

While some of the differences between experimental groups were inherent in the experimental site (good water supply in plot N, exposure to southerly winds in plot S), others resulted from interaction between trees and, because of the rapid growth of cottonwood, changed markedly during the observation period. In 1976 high-density trees in plot S apparently profited from being sheltered by their neighbors and grew faster than these, but in later years they suffered greater water stress and grew less than their low density neighbors. In 1976, all low density groups at the perimeter of plots N and S were apparently exposed to similar conditions and grew at the same rate within each plot. As groups 5 and 9 became increasingly more sheltered by adjacent row plantings of trees, they suffered less water stress and grew more than their counterparts at the edges of the plantation. Similar differences in water stress and growth of trees at the N vs. S periphery or inside of a stand of *Populus nigra* have been described by Polster (1963).

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