Effect of Leaf Aging on Water Deficit–Water Potential Relationships of Dogwood Leaves Growing in Two Environments

By

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Abstract

Water deficit–water potential relationships were determined at approximately monthly intervals from May to August on leaves collected from dogwood trees growing in two environments. The relationships were not the same for leaves of different ages or for leaves of the same age, but growing in the different environments. With aging of the leaves, the relationships shifted to progressively lower water potentials for a given water deficit. Increased leaf dry weight, decreased cell wall elasticity, and decreased osmotic potentials accompanied leaf aging. These changes and the shifts in the relationships were greatest for leaves growing under high light intensity and dry environmental conditions. The lack of constancy in the relationships reduces the usefulness of water deficit or relative turgidity as an estimator of water potential. For the purposes of some workers, however, the relationships may be sufficiently constant for mature leaves of a given species growing in a relatively constant environment.

Introduction

Water potential generally is regarded by plant physiologists as the most meaningful measure of the plant water status, but water deficits or relative turgidities are considerably easier to measure. Weatherley and Slatyer (1957) correlated relative turgidities with leaf water potentials and suggested that the former could be used to predict the latter. Since that time numerous workers have determined the relative turgidity–water potential relationships for various species (Slatyer 1960, Carr and Gaff 1961, Todd et al. 1962, Whiteman and Wilson 1963, Jarvis and Jarvis 1963 a, b, Ehlig and Gardner 1964, Lemée and Gonzalez 1965). Even though most curves relating relative

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turgidities or water deficits to water potentials possess the same general features, it appears that there is a unique relationship for leaves of a given species and age growing in a given environment (Jarvis and Jarvis 1963 b, Gardner 1965). The objective of this study was to examine systematically the effects of leaf aging on water deficit–water potential relationships of dogwood leaves developing and growing in different environments.

Material and Methods

Two mature dogwood trees, *Cornus florida* L., growing in a forest at Durham, N. C. were selected for study. One tree was growing near a stream in the shade, the other on a ridge exposed to direct sunlight. Hereafter these trees will be referred to as stream dogwood and ridge dogwood. The leaves growing on these trees were characteristic of shade and sun leaves respectively. Water deficit–water potential relationships were determined on leaves from each tree at approximately 5 week intervals beginning May 1 and ending August 26 during the 1965 growing season. Cut branches were taken to the laboratory, and simultaneous measurements of water deficits and water potentials were made as the branches progressively dried.

Water deficits were measured on whole leaves (Hewlett and Kramer 1963) that were cut transversely with a razor about 1 cm above the leaf base. Fresh weights were determined on a precision torque balance sensitive to 0.001 g, and the leaves were placed in a pint Mason jar with the cut bases immersed in about 1 cm distilled water. The jars were stored at about 5°C to minimize leaf dry weight losses during water uptake. After 5 to 10 hours, the leaves were blotted dry between layers of Kleenex tissue and reweighed to obtain the turgid weight. The leaves were then ovendried at 110°C for a minimum of 8 hours. Water deficits were measured on three leaves at each sampling time. Water deficits (WD) were calculated according to the equation of Stocker (1929):

$$WD = \frac{\text{Turgid weight} - \text{Fresh weight}}{\text{Turgid weight} - \text{Oven dry weight}} \times 100$$

Water deficit is the complement of the expression relative turgidity (Weatherley 1950) — or relative water content (Ehlig and Gardner 1964) — the two values adding up to 100 % for a given set of weight determinations.

Leaf water potentials were measured with an isopiestic modification (Boyer and Knipling 1965) of the Richards and Ogata (1958) thermocouple psychrometer. This technique determines the potential of the solution which would result in zero output if the solution were placed on the thermocouple junction. This solution is interpreted as having a potential equal to that of the leaf tissue, and the measurement is free of the leaf diffusive resistance error (Rawlins 1964). The temperature of the psychrometer chamber was measured with a dry thermocouple junction in order to evaluate the leaf heat of respiration error (Barrs 1965).

During each sampling period the average leaf dry weight as a percentage of the turgid leaf weight was calculated, and osmotic potentials of sap expressed from turgid leaves were measured with the thermocouple psychrometer (Boyer 1965).

To obtain an indication of the severity of the natural plant water stress regime of each tree, daily extremes of leaf water potential were measured at 6 am and 2 pm

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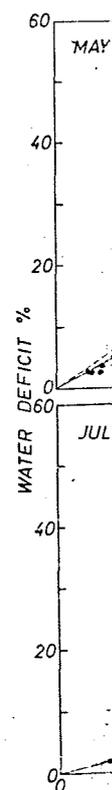

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over a three-day period during each of the months of May, June, and July. Atmometer water loss was recorded at each site during the June and July sampling periods. A reference atmometer was maintained nearby in full sunlight.

Results

The periodic determinations of the water deficit–water potential relationships of stream and ridge dogwood are presented in Figure 1. All of the curves possess the same general features, which are also characteristic of the relationships for other species (Gardner 1965). Initially, there is a relatively small change in WD per unit change in water potential, about 0.5 to 1.5 % bar^{-1}. At water potentials of about –10 to –15 bars, there is an abrupt increase in the slope of the curves and a greater change in WD per unit change in potential, 3.0 to 4.0 % bar^{-1}. At about 50 % WD, the slopes of some of the curves become less steep and appear to approach infinitely low water potentials as water deficits asymptotically approach 100 %.
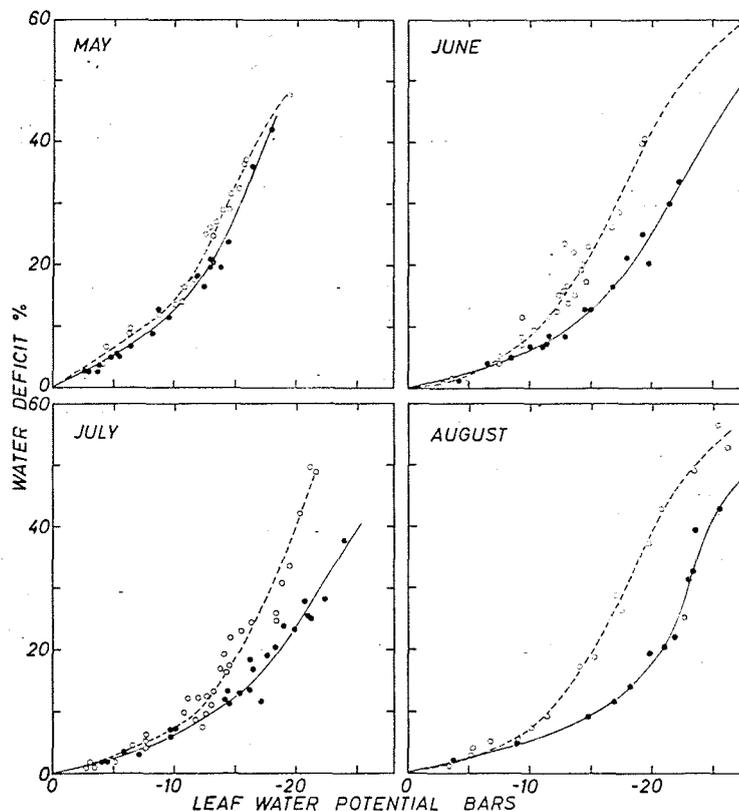

Figure 1. *Comparisons of the water deficit–water potential relationships for stream dogwood* (○) *and ridge dogwood* (●) *leaves during May, June, July, and August.*
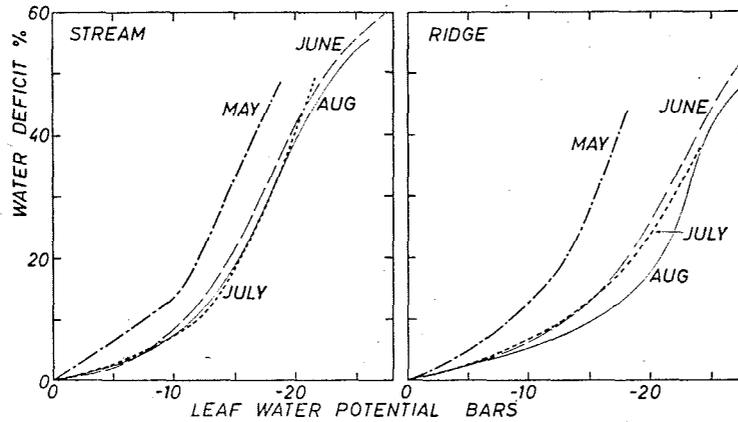
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Figure 2. *Comparisons of the water deficit–water potential relationships at different leaf ages for stream dogwood and for ridge dogwood.*

The curves of Figure 1 show that the water deficit–water potential relationships are not constant for dogwood leaves growing in different environments. For a given WD, the ridge dogwood curve in May was at about a 1 bar lower potential (more negative) than was the stream dogwood curve. In June and July, the ridge dogwood curves were at 3 to 4 bars lower potentials than were the stream dogwood curves. And in August, the deviation between the stream and ridge curves for a given WD were 5 to 6 bars.

Figure 2 shows that with aging of the leaf tissue the curves for each tree shifted to progressively lower potentials for a given WD. The greatest change was between May and June, about 2 bars for stream dogwood and about 5 bars for ridge dogwood. The July and August stream dogwood curves are shifted slightly from the June curve, but the less than 1 bar difference between the three curves probably is not significant. The June and July curves are about the same for ridge dogwood but show an additional 1 to 3 bar shift in August.

Table 1 shows that changes in the dry matter and osmotic potentials of turgid leaves paralleled the shifts in the water deficit–water potential curves.

Table 1. *Changes in dry weight and osmotic potential of turgid leaves of stream and ridge dogwood from May to August.*

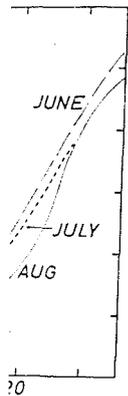| Month	Dry weight, %		Osmotic potential, bars	
	Stream	Ridge	Stream	Ridge
May ...	26.0	24.8	− 9.5	− 10.5
June ...	30.8	34.4	− 11.9	− 16.8
July ...:	31.6	35.3	− 12.5	− 16.9
August .	31.8	36.0	− 13.5	− 16.8

Figure 3. *Diurnal tr(dogwood leaf water atmometer water l △-full sunlight (atm*

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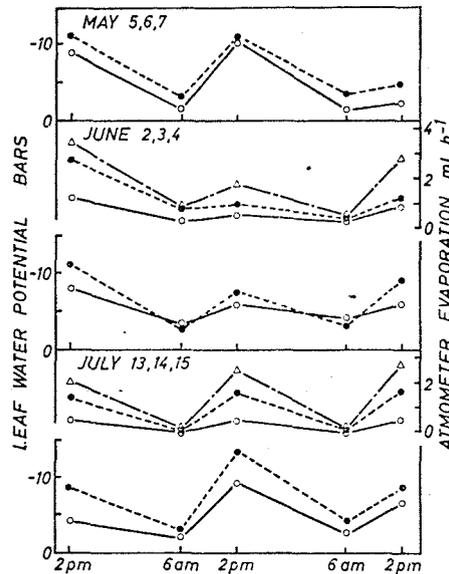potential curves.*

f stream and ridge

Figure 3. *Diurnal trends in stream and ridge dogwood leaf water potentials as related to atmometer water loss.* O-stream, ●-ridge, △-full sunlight (atmometer).

From May to August, the percentage leaf dry weight increased from 26.0 to 31.8 for stream dogwood and from 24.8 to 36.0 for ridge dogwood. Leaf osmotic potentials decreased from −9.5 to −13.5 bars for stream dogwood and from −10.5 to −16.9 bars for ridge dogwood. The greatest changes occurred between May and June for leaves from each tree. The changes for the ridge tree were greater than for the stream tree.

The daily trends in natural leaf water potentials during three different sampling periods are given in Figure 3. The ridge dogwood tree definitely was subjected to greater plant water stresses than was the stream tree. Ridge leaves at 2 pm generally had potentials 2 to 4 bars lower than stream leaves, and at 6 am, 1 to 2 bars lower than stream leaves. The daily course in water potentials follows closely the relative evaporative demands at the two sites as measured by atmometer water loss. Availability of soil moisture probably was not a factor in the plant water stresses at either site because of unusually heavy and frequent spring and early summer rains.

Discussion

The association of the changing leaf dry weights and osmotic potentials with the shifting water deficit—water potential relationships suggests that leaf aging and environmental conditions affect the relationships through changes in internal leaf structure and osmotic potentials. In addition to the general observation that the leaves progressively became more rigid as they developed and matured, the measured increases in leaf dry matter suggest that the elasticity of cell walls decreased with leaf aging. The elasticity

affects the amount of change in leaf pressure potential for a given unit of dehydration, and thus, determines the slope of the water deficit–water potential curve at the low water deficits or high water potentials (Gardner and Ehlig 1965). For a given percentage loss of water from a turgid cell, a thin-walled, elastic cell will tend to decrease in volume, maintaining pressure on the cell contents. However, a thicker-walled, inelastic cell will tend to remain about the same size and have a relatively greater reduction in pressure potential. It is evident from Figure 2 that the slopes of the water deficit–water potential curves at the low water deficits became less steep as the leaf tissues aged from May to August. The greatest decrease in slope of the curves, and hence the greatest decrease in cell wall elasticity, occurred between May and June, the same period in which the largest increases in leaf dry weight occurred.

The dogwood leaves were immature and still expanding when sampled in May. Catsky (1959) points out that during the saturation period for WD determinations young leaf tissues with elastic cells take up water in excess of that needed to satisfy the passive water deficit because of extension growth of the cells. This may have contributed to the higher water deficits in May than in later months for the same water potentials. Catsky (1962) emphasizes, however, that the extension growth represents a real physiological requirement for water by young leaf tissues and is not a limitation of the water deficit technique.

The abrupt change in slope of the water deficit–water potential curves at −10 to −15 bars water potential corresponds to an abrupt change in cell wall elasticity and to a pressure potential of 2 to 3 bars (Gardner and Ehlig 1965). Since the total water potential of a leaf generally is regarded as the sum of two components, pressure potential and osmotic potential, the water potentials beyond the point at which pressure potential is reduced to zero should be equal to the osmotic potential of the leaf. Thus, changes in the internal leaf osmotic potentials would be expected to result in shifts of the water deficit–water potential curves. The dogwood data in this study show that the relationships do change according to the decreases in osmotic potentials. These changes are particularly well correlated from May to June when both the leaf osmotic potential and the curves shifted by approximately the same amount, 2 to 3 bars for stream dogwood and 5 to 6 bars for ridge dogwood. The increases in dry matter as the leaves aged also may have contributed to the shifts in the water deficit–water potential relationships if adsorption forces in the cell wall material contributed a matric potential component to the total water potentials. Slatyer (1960) found possible evidence for a matric potential component in *Acacia phyllodes*.

The results of other workers are in general agreement with the findings of this study. Slatyer (1960) and Gardner and Ehlig (1965) found decreasing water potentials of various species at high water deficits to be approximately equal to decreasing osmotic potentials. Jarvis and Jarvis (1963 a, b) demonstrated that lupine and birch seedlings grown in culture solutions of different osmotic potentials had different leaf relative turgidity–water potential relationships, presumably because of different leaf osmotic potentials. Jarvis and Jarvis (1963 b) also found differences in the relationships for seedlings and mature forest trees growing in different environments, and they showed

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the relationships for leaves from aspen seedling to shift following severe soil watering regimes. The relationships did not change for birch however. Slatyer (1960) found no difference in the relationships for well-watered and droughted Acacia, but in this case the phyllodes were fully developed prior to the treatment period. Whiteman and Wilson (1963) observed a shifting of the relative turgidity–water potential relationships with aging of Sorghum levaes. However, Slatyer (1960) found no difference in the relationships for immature and mature Acacia. In this case, however, immature and mature referred to the size of the trees and not to the age of the phyllodes. Jarvis and Jarvis (1963 b) interestingly interpret the position of relative turgidity–water potential curves as reflecting the degree of leaf tissue hardening to drought.

There is little doubt that the position of water deficit (or relative turgidity)–water potential curves for various species is dependent on the elasticity of cell walls, the amount of cell wall material, and the cell osmotic potential. All of these features change as leaf tissues age. The greatest changes occur in leaf tissues growing under high light intensity and dry environmental conditions. The lack of constancy in the relationships reduces the usefulness of water deficit or relative turgidity as a method for estimating water potential. For the purposes of some workers, however, the relationships may be sufficiently constant for fully expanded and mature leaves of a given species growing in a relatively constant environment.

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