EVALUATING STREET TREES FOR DROUGHT TOLERANCE

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ABSTRACT.--The structure of the urban environment frequently exacerbates the problem of drought stress in street trees, creating the need for a method to evaluate trees for their relative drought resistances. Drought-stressed and well-watered *Cornus* species were evaluated using several parameters. Compared by growth measurements alone, *C. florida* was more sensitive to drought than *C. kousa* and *C. racemosa*. However, the latter two species displayed differing strategies for coping with drought when evaluated by transpiration rates and membrane permeability.

INTRODUCTION

The urban environment imposes many restrictions on the normal growth of trees planted on its streets. Elements such as air pollution, deicing salts, soil compaction, limited rooting space, poor soil structure and chemical makeup, frequent mechanical injury, inadequate light due to shading by tall buildings, and the physical structure of the city itself with its heat-modifying properties interact in various ways to produce heterogeneous microclimates for urban vegetation (Bernatzky, 1978).

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Several of these elements frequently combine to impose drought conditions on street trees even when there would have been adequate precipitation had the trees been growing in a forested or rural site. Drought conditions impose water stress within a tree by either restricting the supply of water to plant roots or by increasing the demand for water by the transpiring leaves. Within the urban environment, both supply and demand may be limited simultaneously. There are several possible ways in which rainfall is prevented from reaching a tree's root system: impervious surfaces such as asphalt, concrete, or highly compacted soil can restrict water ingress into the root zone; confined rooting space caused by containerized plantings, underground structures or compacted soil can limit both the potential reservoir of soil water and root growth, per se; runoff is often channelled away from the root zone into sewers; the small soil surface around the street tree is frequently inadequate for rainfall interception; discontinuity of the street tree pit with ground water supplies can eliminate another source of water; and high levels of soil salts or other contaminants in the planting area can reduce the availability of soil water or kill roots outright thus eliminating root surface area for water absorption.

Above the ground, street tree leaves can experience atmospheric conditions which increase their rate of water loss. Trees in a forest stand are mutually shaded thus reducing the amount of direct solar radiation affecting leaves. Typically, street trees are planted singly so that more of the tree's canopy directly intercepts solar radiation. Building materials, asphalt, concrete, and car tops can build up heat during the day and then reradiate that heat to the street tree microclimate after incoming solar radiation has ceased, thus increasing air and leaf temperature while reducing relative humidity (Bassuk and Whitlow, unpublished data; Bernatzky, 1978). Urban wind tunnels caused by wind being compressed between buildings may also affect water loss from leaves by replacing the humid boundary layer of air around leaves with drier air (Halverson and Potts, 1980). All these factors combine to increase the vapor pressure deficit between leaves and the air causing in turn, an increased transpiration rate and demand for more and more water.

Water deficits in plants cause numerous responses some of which are temporary, reverting to normal after the stress is relieved. Others are of longer duration and some are irreversible. The nature of plant responses depends on the severity and duration of the water deficit as well as the developmental stage of the plant in question.

At very mild levels of stress, cell expansion is inhibited, followed shortly by an inhibition of cell wall synthesis. At increasingly negative water potentials, protein synthesis is impaired by stomatal closure, and respiration is affected. At still lower water potentials, proline is accumulated in plant tissues (Hsiao, 1973).

Outward signs of the effects of water stress in trees can be the cessation of growth, reduced leaf size, premature autumn coloration through the loss of chlorophyll, marginal browning, early leaf abscission and finally, stem dieback and tree death (Parker, 1969; Hinckley, et al., 1979). Water stress has been shown to predispose certain trees to disease and insect attack (Schoeneweiss, 1981; Kramer and Kozlowski, 1979).

The desirability of having drought resistant trees for urban landscapes is clear. Little progress has been made, however, in objectively identifying and developing drought resistant material. There are numerous lists which rate trees according to their ability to tolerate various urban stresses. While experimental evidence buttresses such ratings for some species in relation to some stresses (especially pollution and deicing salts), most ratings are not based on experimentation and are thus relatively crude. While conventional wisdom is a good base for launching a rigorous inquiry, it is counterproductive to regard any of the numerous lists as "the last word." Useful as they are, two shortcomings compromise the value of existing lists. First, no uniformity of stress severity can be inferred from casual observations. It is difficult enough to arrive at an operational definition of water stress under experimental conditions, much less in a variety of uncontrolled field sites observed by many different people. Second, the unit of analysis, supposedly the species, lacks adequate definition in these schemes. For example, Acer rubrum, a species well known for its broad ecological amplitude, is generally treated as the species, despite the existence of 23 cultivars readily available in the nursery trade (Berrang and Karnosky, 1983). Are we to assume all cultivars are equally tolerant of drought? These cultivars have been developed to achieve desirable size, form, leaf shape, and color. Ironically, this intraspecific variation which has been exploited so deftly to achieve visual effects has been largely neglected with respect to drought tolerance. It is highly likely that some cultivars are more suited to urban drought than others and indeed, that even more tolerant potential cultivars exist in the native germ plasm (Townsend and Roberts, 1973). The task of quantifying the genotypic variation in tolerance to urban drought within even a wide species is imposing. Extended to a broad palette of plant material and an array of interacting stresses, the task becomes overwhelming. Yet this kind of investigation is required if we hope to develop improved plant material for urban areas.

Models for this approach exist in forestry where provenance gardens are used to identify genotypes best adapted to a local or regional environment, and in agronomy where genetically diverse experimental populations are challenged with a specific stress to identify parents for crop improvement programs. Simple selection for superior genotypes will undoubtedly yield improved material for street use.

To arrive at this stage of initial selection, a screening protocol is required. Characteristics of a good screening procedure include the ability to: be used on a wide variety of species; measure tolerance to nonlethal stress levels; encompass the variables of timing, duration and intensity of stress; measure plastic plant characteristics (acclimation); and point to underlying physiological mechanisms. These last two points are especially important for two reasons. First, because many popular street trees are native to moist habitats, pressures of natural selection may not have produced adaptations to drought which are always apparent. It may not be possible to select traits which constitute a preadaptation to drought (small leaf size or thick cuticle, for example) because these traits may develop only under drought conditions. In this respect, selection for drought tolerance differs from selection for growth habit in that the latter should be relatively constant regardless of environmental conditions. As emphasized in a recent review of drought resistance in crop plants, a definition of drought conditions must precede a selection program (Turner, 1977).

The second point, dealing with underlying physiological mechanisms, is not only of basic scientific interest but is important, too, from the standpoint of efficiency. The ultimate goal of many selection/breeding programs in agriculture and forestry is improved yield. However "yield" is defined, it is time consuming to quantify in a perennial plant. At least two years of growth measurements are required to estimate an average yield and more than this minimum number of observations is highly desirable. Long term experiments with trees necessarily mean field experiments, which in the eastern United States preclude precise control of drought stress. Rather than screening initially on the level of whole, mature trees, it may be more efficient to identify the most promising populations and individuals on the basis of a physiological trait before investing in field trials. The utility of this approach is illustrated by Boyer's work with soybean cultivars where he found that increased cultivar yeild paralleled less negative afternoon water potentials (Boyer, 1982). Screening for such traits requires a much shorter period of time than whole plant yeild studies. Only superior material would be selected for subsequent field trials.

It is apparent to us that only a multi-tiered screening procedure will possess the necessary characteristics. By multi-tiered we mean a protocol which examines a plant at several different levels of integration. At the whole plant level, the kinds of data which we think are most important are growth (diameter, shoot, leaf area), water balance (transpiration rate, water potential), and carbon balance (carbon dioxide uptake rates, carbohydrate partitioning). At the level of plant organ, leaf size is both plastic and accessible and thus avails itself as a response indicator. Roots are difficult to study so that they are not conveniently included in an initial screening.

Finally, at the level of tissues and cells there are myriad physiological characteristics which have been linked to drought tolerance. It is important to keep the goal of screening plant material paramount and avoid the seduction of pursuing all available lines of inquiry. We have selected membrane permeability as an important trait. It has proved useful in separating a variety of crop cultivars according to tolerance to drought, heat, and chilling stress (Blum and Ebercom, 1981; Yadova and Doud, 1978). Further, since all metabolic processes are mediated by membranes, any impairment of membrane function could logically be expected to affect a wide range of plant processes.

The remainder of the paper will discuss a multi-tiered screening of three _Cornus_ species and permit an evaluation of its efficiency.

EXPERIMENTAL PROCEDURE

Methods

Cornus florida L., flowering dogwood, _Cornus racemosa_ Lam., _grey dogwood_, and _Cornus kousa_ Hance, _Chinese dogwood_, were chosen as our _test species_ because they are commonly used, congeneric, small trees with purported differences in drought resistance. _Cornus florida_ is thought to be intolerant of drought while _C. racemosa_ and _C. kousa_ have been variously reported as being drought tolerant (Wittick, 1983).

Twelve three-year-old, well-branched trees of each species were potted in 38 liter containers in a peat-perlite-soil mix (1-1-1 by volume) and allowed to establish under optimal water and fertilization regimes for one year. During the next growing season, half of all the trees underwent repeated drying cycles by having water withheld until the permanent wilting point was reached after which time they were rewatered for a week to allow recovery before the imposition of next drying cycle. Control plants were watered to field capacity every two to four days. Several growth and water status measurements were taken including stem diameters, water potentials before sunrise, diurnal transpiration rates and membrane permeability differences.

Water potentials were taken using a _Soil Moisture_ pressure bomb. Transpiration rates were measured on a _Li-Cor_ 1600 diffusion porometer.

A detailed account of our technique for determining membrane permeability and recovery indices may be found elsewhere (Whitlow and Bassuk, manuscript in preparation). Briefly, we quantified differences in membrane permeability between species, between drought treatment, and over the course of a growing season. Appropriate leaf material was removed from the trees and washed to remove surface electrolyte. One cm diameter punches were taken from the leaves and brought to full hydration in glass distilled water. The leaf discs were subsequently dried to 55% of their fresh weight. Electrolyte leakage (as electroconductivity of the bathing medium) was then monitored during a one hour rehydration period in glass distilled water. Data are expressed as a Recovery Index, representing the change in electrolyte efflux into the rehydration vial from the initial rate. This effectively portrays the rate at which membrane semipermeability is regained after injury.

Results and Discussion

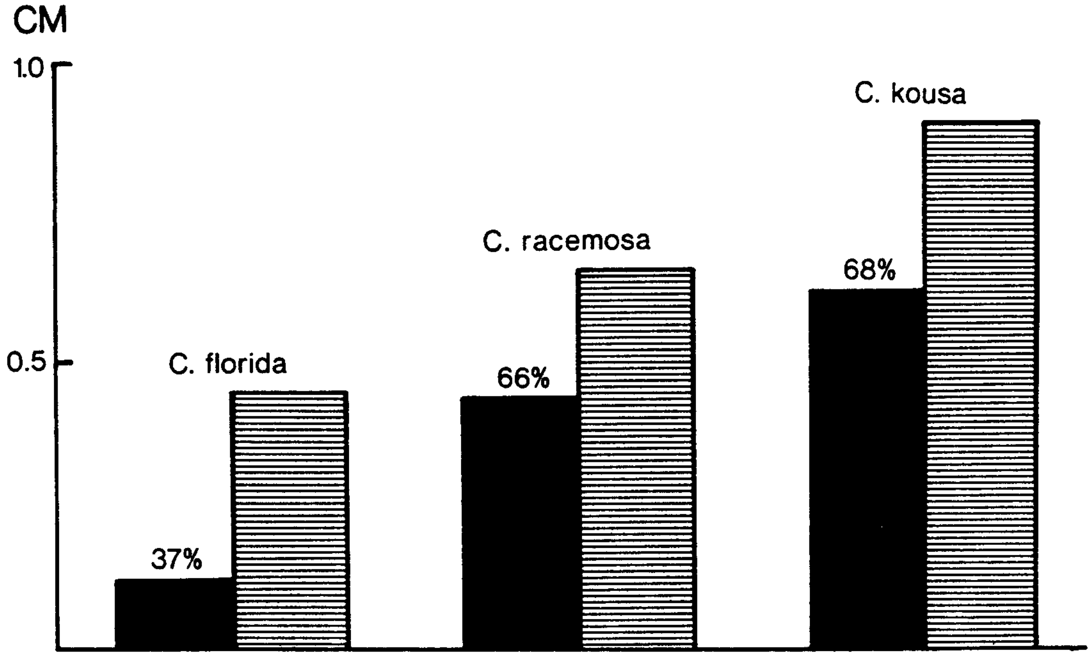

Figure 1. Growth of trunk diameters for drought-stressed and well-watered Cornus species. Percentages refer to stressed trees' growth as a percent of the well-watered trees' growth.

Figure 1 shows stem diameter measurements for both stressed and well-watered plants of all three *Cornus* species. Stressed *C. florida* plants increased in diameter only 37% as much as the well-watered controls, while *C. racemosa* and *C. kousa* showed similar responses of 66% and 68% respectively compared to their control plants. Based only on stem diameter as a mode of comparison, the conclusion can be drawn that while *C. kousa* and *C. racemosa* show nearly equal drought resistances, *C. florida* is considerably more sensitive to drought conditions.

To further examine whether or not *C. kousa* and *C. racemosa* are truly equal in drought resistance, a comparison was made of their diurnal transpiration rates for both control and stressed plants early in the summer (July 12th or 14th) and later in the summer (August 26th), (Figures 2 and 3). It is important to note that immediately prior to these measurements all plants were well watered so that any differences would reflect the treatment history of that plant and not its current water status. In Figure 2, well-watered control *C. racemosa* plants showed high rates of water loss compared to prestressed plants. The July 12th measurement occurred after only two drying cycles and shows considerable acclimation by the prestressed plants in that they have become much more conserving of water. The August 26th reading (after four drying cycles) shows a continuation of that trend with greater water conservation in the prestressed plants in the face of continuing 'nonthrifty' transpiration in the well-watered controls.

Cornus kousa exhibits a markedly different pattern of water use (Figure 3). Even at the early July 14th measurement, well-watered control plants are nearly as conserving of water as are the prestressed, acclimated plants. Later in the year (August 26th), there is no difference between well-watered and prestressed plants, both showing the same water conserving pattern. This comparison of transpiration rates in *C. racemosa* and *C. kousa* does not lend itself to a simple ranking of drought resistance, yet it elucidates different strategies for acclimation to drought conditions; one responsive to environmental cues, in the case of *C. racemosa*, and one predetermined, in the case of *C. kousa*.

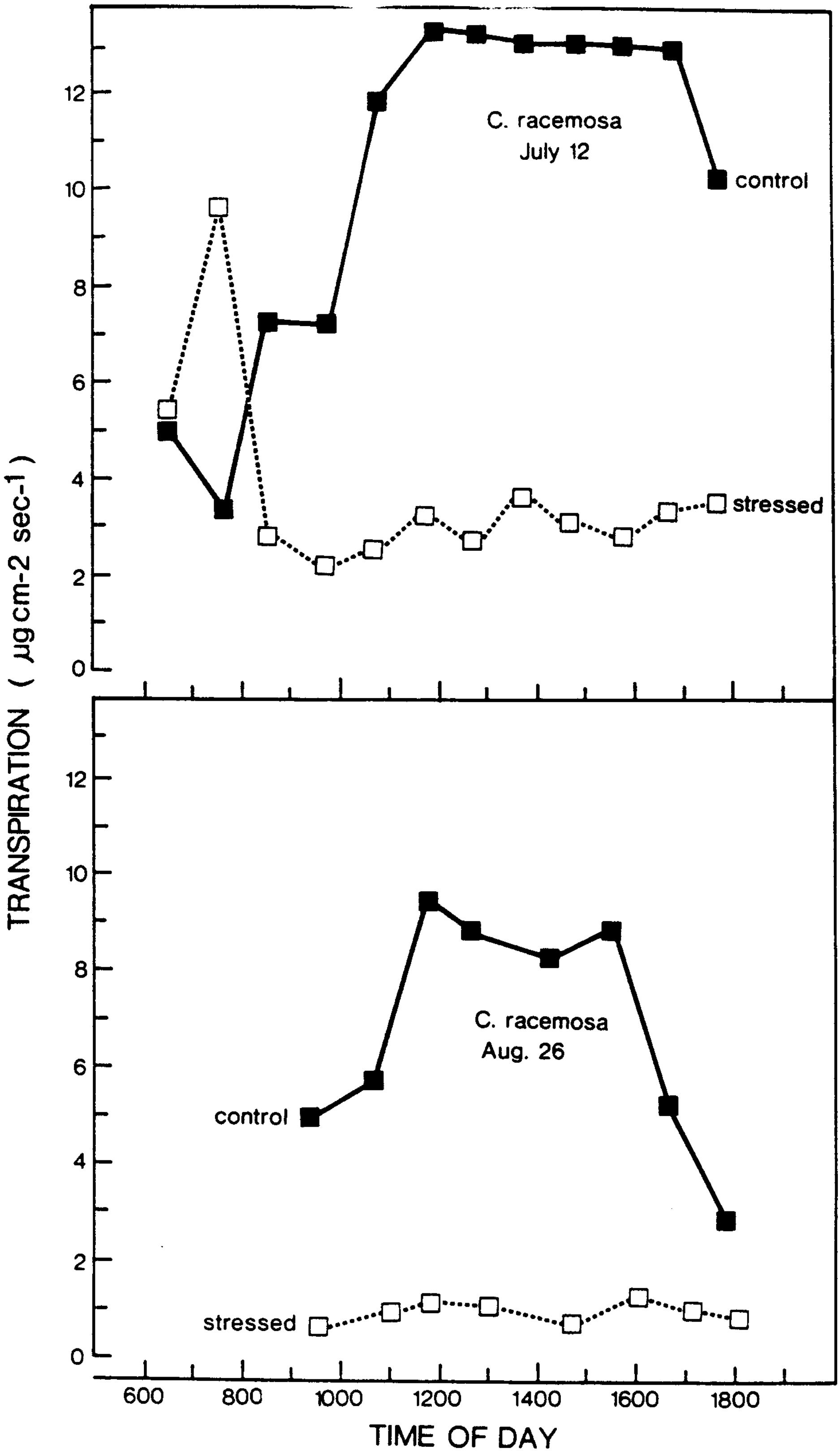

Figure 2. Diurnal transpiration rates for drought-stressed and control *Cornus racemosa* trees on July 12th and August 26th.

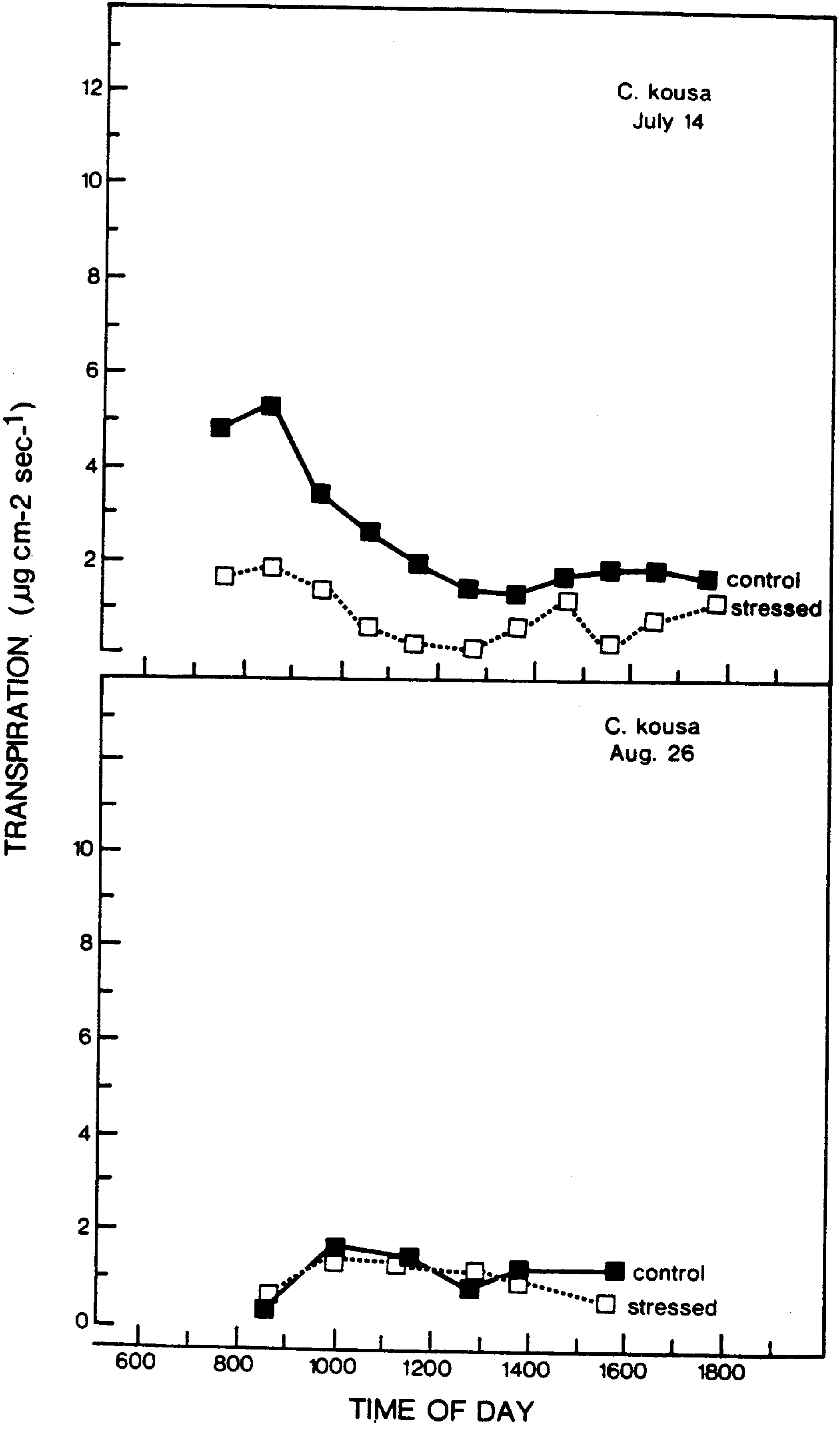

Figure 3. Diurnal transpiration rates for drought-stressed and control <u>Cornus kousa</u> trees on July 14th and August 26th.

Figure 4 shows the recovery indices for *Cornus kousa* and *C. racemosa* control (well-watered) and acclimated (drought-stressed) plants at various times over the 1982 growing season. *Cornus kousa* shows no difference between treatments at any measurement point, though variation over the growing season is apparent. Seasonal trends indicate the effect of leaf age. Phenologically, leaves appear to gain in their capacity to recover from an injury up to a point. Late season decreases in recovery probably indicate senescence. (Please note that negative values represent increasing injury during the rehydration period. This would be analogous to a human patient who was bleeding faster after first aid than before.)

Cornus racemosa presents a very different picture than *Cornus kousa*. Initial treatment differences are quite apparent, with the drought-acclimated trees showing recovery indices of 50 while well-watered controls show indices of less thazero. This apparent acclimation to dehydration on the level of leaf membranes is induced by withholding water from the entire plant. The advantage imparted by withholding water early in the season disappears later in the season when there are virtually no differences between treatment and control. There are two components, then, to change in membrane permeability: a treatment or pre-history component and a leaf age or phenological component. The two interact in *Cornus racemosa* but not in *Cornus kousa*.

It should be emphasized that we cannot state simply on the basis of these data which species is more drought tolerant. Rather, the species have different strategies for coping with drought. *Cornus kousa* appears to be preadapted to water conservation on a *whole* plant level. This could effectively protect leaf membranes from transient dehydration events and thus eliminate the need for protection at the membrane level. *Cornus racemosa*, in contrast, uses water more freely but acclimates to water shortages in a variety of ways, including altering the permeability characteristics of leaf membranes. Only by examining the plants at several different levels and by knowing their experimental histories can we arrive at a clear understanding of drought tolerance syndromes.

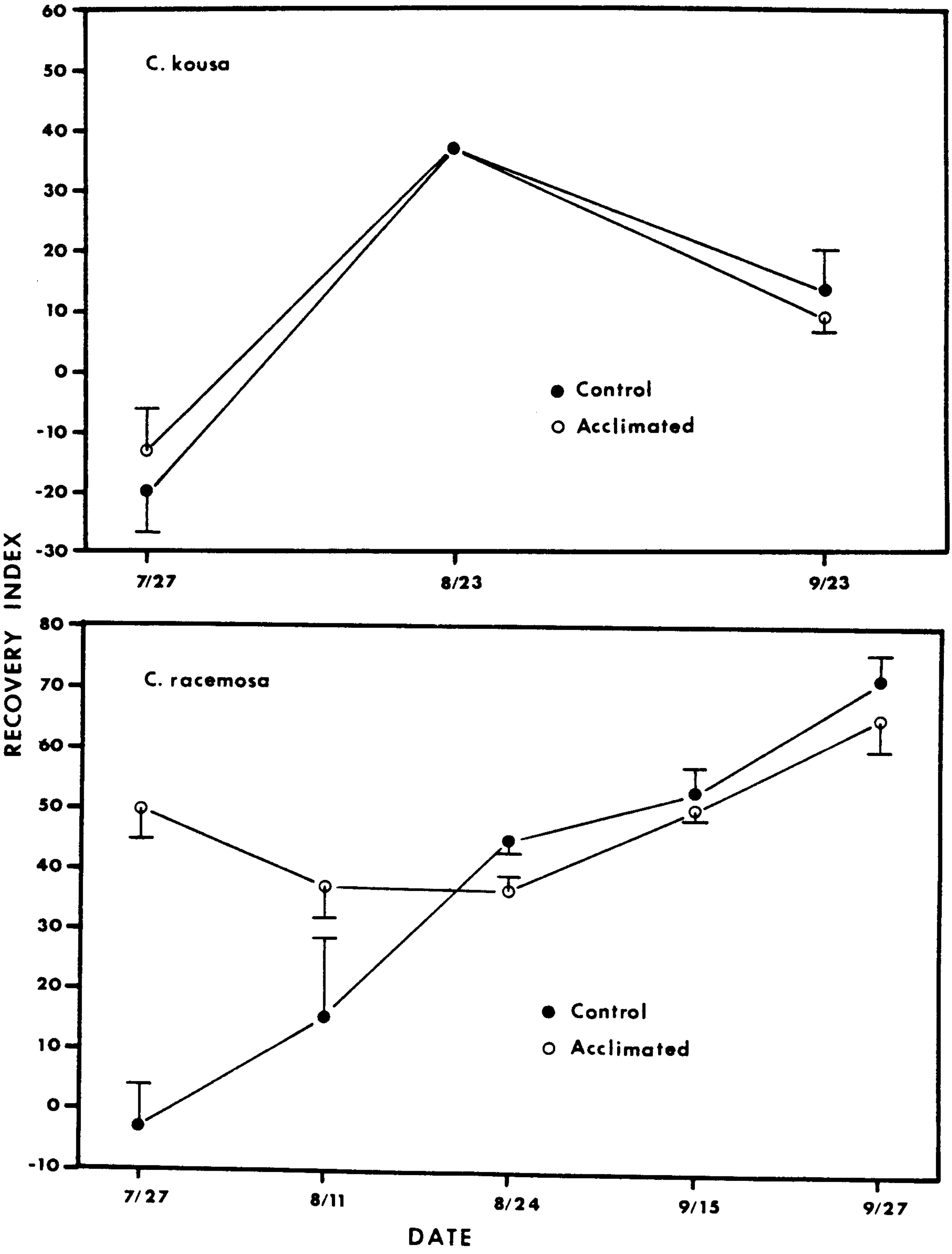

Figure 4. Seasonal changes in the recovery of cell membrane semi-permeability in control (well-watered) and acclimated (prestressed) *Cornus kousa* and *Cornus racemosa* plants.

CONCLUSIONS

We initiated this study with three questions in mind: 1) What are the drought tolerances of *Cornus florida*, *C. racemosa*, and *C. kousa*? 2) What are some of the mechanisms of drought tolerance and how are they differentially expressed among the species? 3) Can an effective screening protocol be assembled to evaluate drought tolerance in trees?

We have partial answers to questions one and two. *Cornus florida* is less drought tolerant than *C. kousa* or *C. racemosa* based on observations of growth characteristics. Logistics prevented rigorous comparisons on other bases, but our observations are consistent with prevailing opinion. This question may not be meaningful when applied to *C. kousa* and *C. racemosa*. Each is adapted to drought, with *C. kousa* being nonplastic but preadapted, with good stomatal control and water conservation at the expense of growth. *C. racemosa* is not initially drought adapted but shows an ability to acclimate while continuing to grow. This difference in phenotypic plasticity between the two species is manifest in terms of growth, water balance, and membrane permeability. Yet these differences illustrate different solutions to the same problem rather than absolute tolerance differences. We draw two conclusions from this apparent dilemma. First, the nature of the drought we expect plants to withstand must be carefully specified, especially with respect to time of occurrence and events. Second, we must realistically evaluate the role we expect individual trees to perform in the landscape and then evaluate drought responses in terms of fulfilling that function. Leaf loss is an excellent mechanism for reducing water loss and thus insuring survival. Survival during an especially dry year may well be an acceptable trade-off against visual effect in the short run. If reliable shade is needed for a sidewalk cafe, leaf loss may not be acceptable.

The answer to question three is a qualified "yes." Yes, it is possible to objectively evaluate plant performance at several levels. If we are dealing with interspecific comparisons, however, we should not expect an unambiguous evaluation to emerge. Differences will emerge which do not necessarily imply that one is better than another. This should not be viewed as a shortcoming; rather, by conveying a fuller understanding of how a plant functions under stress, we are in a better position to use that plant intelligently.

An exciting answer to a question which we did not ever ask involves the potential for management strategies timed to individual species' needs. For example, *Cornus racemosa* would probably benefit from the imposition of a controlled drought early in the growing season. This would facilitate acclimation and could result in better late season performance. With *C. kousa*, such a strategy would probably not have any effect.

Can we realistically expect to rank trees according to tolerance to a stress? We have found this task to be difficult, even with three congeneric species. A subjective ranking, based on plant function in a particular landscape, is possible. Objective rankings, based on the response of a particular set of characters, is most feasible on the intraspecific level. If our goal is tree improvement, this is not a problem because implicit in this process is the manipulation of within-species variation. A multi-tiered approach to screening should be considered as a first step toward this goal.

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