Leaf Curl and Water Relations of Kousa Dogwoods Showing Resistance to Summer Stress[1]

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Abstract

Kousa dogwood (*Cornus kousa* Hans.) trees often develop unattractive leaf curling throughout canopies during hot and/or dry weather. Aesthetically superior trees were compared to control trees for their ability to tolerate summer stress, in an established kousa dogwood plantation in 2000 and 2001. An index of leaf curl revealed that superior trees showed less curling than controls during June, July and August of 2000 and 2001. Superior trees often had higher stomatal conductance than trees in both control groups during both years, with seasonal averages 16 to 40% higher in superior than in control trees. Leaf water status, characterized by leaf osmotic potential, remained similar in superior trees and control trees throughout the 2000 summer season. Leaf temperatures were similar between groups during each summer. We confirmed that trees initially selected as having superior visual appearance had measurable differences in foliar characteristics compared to control trees, and that these trees better tolerated summer stress.

Index words: Chinese dogwood, *Cornus kousa*, drought stress, heat stress, leaf curl, ornamental tree, osmotic potential, stomatal conductance.

Significance to the Nursery Industry

Kousa dogwood is a popular landscape tree with natural resistance to dogwood anthracnose (*Discula destructiva* Redlin) and powdery mildew (*Microsphaera pulchra* Cooke and Peck). When located in full or afternoon sun exposures, foliage of kousa dogwoods in the southern United States often develops an unsightly curl, diminishing the aesthetic appeal of the tree during summer months. In 1998 and 1999 we identified several individual trees in a plantation of kousa dogwoods in Tennessee that had both a superior growth habit and minimal leaf curl in June, July and August. During the 2000 and 2001 summer seasons, superior selections were compared with average and above-average control trees. Leaves on the superior selections curled less and maintained higher stomatal opening than leaves on trees from either control group throughout both summer seasons. If plants propagated from the parent trees consistently retain the resistance, the best among them can be developed as kousa dogwood cultivars that offer improved appearance in southern states, potentially expanding the use of this tree in landscapes of USDA hardiness zones 8 and 9.

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Introduction

The kousa dogwood is native to the temperate areas of China, Japan and Korea. Since its introduction in 1875, kousa dogwood has become a popular ornamental tree in the United States. Part of the kousa dogwood's popularity is due to its resistance to dogwood anthracnose and powdery mildew. This species is being recommended as a replacement for native flowering dogwoods (*Cornus florida* L.) that have been decimated by dogwood anthracnose (4).

Although kousa dogwood is listed as adapted for USDA hardiness zones 4 to 8 and some trees have fared well in southern environments (5), the foliage of many kousa dogwoods located in full sun or afternoon sun exposures loses its aesthetic appeal during hot summer months in many southern landscapes. During periods of hot, dry weather, the foliage often develops an unattractive leaf curling and may scorch. Although the trees survive and may even grow well over time, unsightly summer foliage is a concern for a landscape specimen.

We observed several individual trees in a plantation of kousa dogwoods that had both a superior growth habit and minimal leaf curl during sustained July and August drought and heat in Tennessee. To further characterize these trees and quantify their resistance to summer stress, we monitored leaf curl, stomatal behavior, leaf osmotic potential (Ψ_π) and leaf temperature in the plantation during two seasons. Our hypothesis was that superior and control trees would differ in one or more of these parameters. We compared the superior trees with a group of control trees that in April 2000 were of the same size and similar overall appearance, with similar foliar characteristics. We compared superior and control trees again in 2001, adding a second control group which represented 'average' kousa dogwoods.

Materials and Methods

Plant materials and experimental site. In 1989, seeds of several cultivars of kousa dogwood were provided by Polly Hill from the private arboretum at Barnard's Inn Farm, Vineyard Haven, MA. Seeds were cleaned and stratified in 1989 and germinated in 1990. Seedlings were planted in a standard pinebark nursery mix in copper-treated 5 cm × 5 cm (2 in × 2 in) tubes and subsequently transplanted into 4 liter (#1), then 8 liter (#2), then 16 liter (#4) containers to accommodate growth outdoors at the research nursery at The University of Tennessee (UT). In 1994, representative lots of seedlings were moved to the Great Smoky Mountains National Park and tested for susceptibility to dogwood anthracnose.

In June 1996, the highest quality trees surviving the anthracnose test were planted at the UT Forestry Experiment Station and Arboretum (USDA hardiness zone 7a; 36°1' N and 84°13' W) in Oak Ridge, TN. The plantation is located on a ridgetop location in full sun and covers 1.2 ha (3 A). Trees were spaced at 3.1 to 3.7 m (10 to 12 ft). Long-term mean annual precipitation (30 yr normals, 1967–96) at the arboretum was 1385 mm (54.5 in), and mean temperature was 14.0C (57F). Soil at the site is a strongly acidic, moderately permeable forest soil classified as Fullerton cherty silt loam, in the taxonomic class of Clayey, kaolinitic, thermic Typic Paleudults. Paternal parents of the trees were 'Julian', 'Steeple', 'Big Apple' and an unnamed tree. Maternal parents included 'Steeple', 'Big Apple', 'Snowbird' and the unnamed tree. Tree growth and foliar quality were highly variable after planting. By summer 2001, 43 of the original 383 trees died or were removed because of disease problems, and some of the smaller surviving trees were only about 1.4 m (4.5 ft) high. Some trees began blooming in 1998, and the majority bloomed in 1999.

In both 1998 and 1999, 15 trees showed very little leaf curl following sustained drought and heat. These trees contrasted markedly with the majority of trees, which responded to the summer stresses with moderate to severe leaf curling.

Data collection and analysis. In April 2000, after leaves were fully expanded, 12 of the 15 superior trees were tagged for subsequent measurement of seasonal water relations and leaf curl. These trees were scattered throughout the plantation, located in five different north-south rows and seven different east-west rows. Among the remaining trees in the plantation, the highest quality trees were selected as a control group; these trees were visually indistinguishable from the superior trees at that point in the season (before heat or drought stress had occurred) in terms of both foliar characteristics and overall tree size and quality. To minimize both above- and belowground environmental variation, each superior tree was paired with the nearest control tree of the same size and quality, in all cases from 3.0 to 4.3 m (10 to 14 ft) away. In April 2001, we selected from each group for further study eight trees that showed the least leaf curl in 2000. We also identified and added to the experiment a second group of control trees. These were representative of average trees in the plantation (within the middle third in terms of overall quality) — smaller trees with less appealing habit than superior or above-average 2000 controls. Each superior tree/above-average tree pair was matched with the nearest average control tree, resulting in matched sets of three trees in 2001.

Stomatal conductance (g_s), leaf temperature, leaf Ψ_π (year 2000 only) and leaf curl of four leaves (subsamples) of each tree (replicate) from each treatment group were measured every two to three weeks during the summers of 2000 and 2001, between 11:00 a.m. and 1:00 p.m. Preliminary measurements showed that g_s tended to be highest during this time of day. Three or four workers typically gathered data each day to reduce total measurement time and thereby minimize diurnal variation. Both trees (superior tree and control tree) in a matched set (block) were measured before moving to the next set. The two experimental groups of trees had similar leaf Ψ_π during 2000, and Ψ_π measurements were discontinued for 2001.

To get a reasonable representation of trees, we sampled leaves for all parameters from the terminal ends of shoots on the north, south, east and west sides of each tree's canopy on each measurement day. Leaves from the east, west and south sides of each tree were selected from unshaded shoots, and leaves from the north side of each tree were selected from shaded shoots. Abaxial g_s of recently expanded, relatively undamaged leaves was measured using diffusion porometry (AP4, Delta-T Devices, Cambridge, UK), parallel to the midvein and in the center of leaves. Two porometers were used in 2000, and equal numbers of superior and control trees were measured with each porometer on each date. Porometer was recorded with each measurement and included in the statistical model. Ambient irradiance on leaves was determined with each measurement of g_s, with the porometer's quantum sensor (accuracy confirmed with a recently calibrated quantum sensor prior to starting measurements; LI-190SA, LiCor, Lincoln, NE). Leaf temperatures were measured with the porometer during each g_s measurement.

Leaves of similar quality and orientation to those used for g_s measurements (four leaves per tree) were also selected for measurement of Ψ_π and leaf curl. For analysis of Ψ_π, leaves were excised from the tree, immediately sealed in a syringe and frozen in liquid nitrogen. Samples were stored in an ultra-low freezer (–80C), pending later analysis using a vapor pressure osmometer (Model 5500 XR, Wescor Inc., Logan, UT). Syringes were removed from the freezer and allowed to thaw until no longer cold to the touch (10–15 min) before measuring Ψ_π of mixed symplastic and apoplastic water fractions. The osmometer was calibrated with graded NaCl solutions with each use.

Leaf curl was assessed as a ratio: distance between the left and right edges of the leaf (in its natural, curled state) divided by leaf width (actual width of flattened leaf). Widths were measured 2 cm (0.8 in) distally from the base of the leaf blade. Many trees had foliage whose edges undulated on the distal (tip) half of the leaf, edges that curled markedly and irregularly toward and away from midveins. Because of the inconsistent curl on the distal portion of leaves, leaf curl was measured on the basal half of the leaf. The much more consistent curl of the basal portion of leaves tended to reflect the overall curliness of the distal portion, providing in essence an integrated indication of the irregular curl on the distal portion. Distal portions of leaves typically curled much more than basal portions, and so the measured ratio was a conservative estimate of curl.

The data were analyzed using mixed model ANOVA (SAS, Cary, NC). The experimental design was a randomized block design, blocked on sets as described above: each block (matched set) contained one replicate of each tree group, resulting in two trees per block in 2000 and three trees per block in 2001. Years were analyzed separately, and the model included repeated measures over the growing season. Independence of the data was assured by the random locations of selected trees. Other assumptions of ANOVA such as normality and homogeneity of variance were tested. Least-square

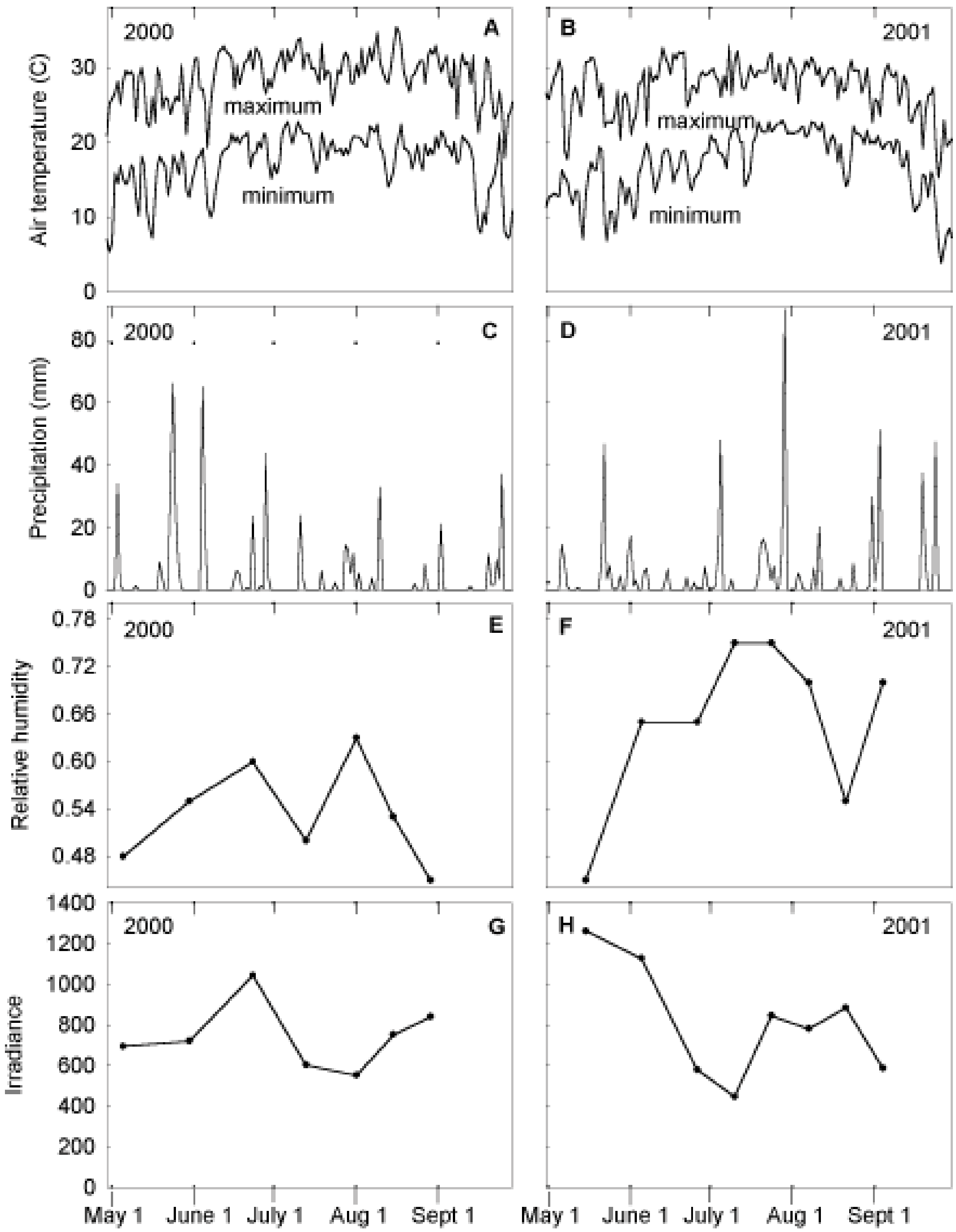

Fig. 1. **Maximum and minimum daily air temperatures (A, B); daily precipitation (C, D); and relative humidity (E, F; n = 1) and irradiance (G, H; n = 96) at the time of leaf curl, g_s and Ψ_π measurements, during the summers of 2000 and 2001. Symbols for irradiance represent the average of all light measurements made at the moment of recording each g_s measurement.**

means were compared with Fisher's Protected LSD ($P = 0.05$). Correlation analysis was performed by calculating Pearson correlation coefficients. Pooled standard errors of the means were calculated by dividing square roots of the error mean squares by the square root of the number of observations in a mean.

Results and Discussion

The summers of 2000 and 2001 offered typical environmental challenges for trees in the plantation. They were not extreme years, but each had both dry and hot periods. Air temperatures reached 34C (93F) in July and 35C (96F) in August of 2000 (Fig. 1A) and 33C (91F) in July and 31C (88F) in August of 2001 (Fig. 1B). Rainfall ranged from 53 to 183 mm (2.1 to 7.2 in) per month during the growing season in 2000 (Fig. 1C) and from 61 mm to 234 mm (2.4 to 9.4 in) per month in 2001 (Fig. 1D). Cumulative rainfall from May through September was 582 mm (22.9 in) in 2000 and 656 mm (25.8 in) in 2001. Relative humidity at time of g_s measurements ranged from 45 to 75% during the two seasons (Fig. 1E and 1F). Typical kousa trees in the plantation and in nearby urban and rural locales were visibly stressed during each summer. Trees contracting powdery mildew were removed from the plantation in 1998, and no trees in the plantation have since shown any symptoms of powdery mildew or dogwood anthracnose. At the end of the summer 2001 season, average tree heights (mean ± SE) were 4.9 ± 0.2 m (15.9 ± 0.6 ft) for superior trees, 4.9 ± 0.2 m (16.0 ± 0.8 ft) for the above-average control trees and 4.7 ± 0.1 m (15.6 ± 0.4 ft) for average control trees. Average axial areas at 15.2 cm (6 in) above the soil level were 343 ± 18 cm^2 (53 ± 3 in^2) for superior trees, 314 ± 12 cm^2 (49 ± 2 in^2) for the above-average control trees and 236 ± 11 cm^2 (37 ± 2 in^2) for average control trees.

Flowering dogwoods tend to drop their leaves in response to drought, whereas leaves of kousa dogwoods remain on the tree but curl with drought and heat, exposing the lighter, somewhat muddy-colored abaxial surface (Windham, Witte, personal observations). Individual kousa trees vary greatly in form and foliar characteristics, and many individuals show considerable leaf curl as soon as leaves mature in the spring, regardless of air temperatures or soil moisture conditions. We avoided those trees for this study. Degree of leaf curl was similar in the superior and above-average control trees at the start of the 2000 season, just after foliage had emerged and matured (Fig. 2A). By May 30, 2000, the two groups differed, and the superior selections had less leaf curl on six of the seven measurement days subsequent to the initial day. The quantitative differences in the index between groups were visually apparent; a tree with a value of 0.80 has leaves that are noticeably more curled than trees with leaves of an index of 0.88. Superior trees again had similar leaf curl as the above-average control group at the start of the 2001 season (May 15, 2001) but less curl than the average control group (Fig. 2B). By the next measurement day at the beginning of June, superior trees had less leaf curl than either control group. Superior trees had less leaf curl than above-average control trees on half of the measurement days of the 2001 season. Superior trees had less leaf curl than average control trees on all measurement days of the 2001 season. Seasonal averages in 2000 were 0.85 for superior trees and 0.79 for trees in the above-average control groups. Seasonal averages in 2001 were 0.90 for superior trees, 0.81 for the above-average control trees and 0.81 for the average control trees. Shaded leaves on the north side of trees had less leaf curl (mean over both years = 0.92) than exposed leaves on the other three sides of trees throughout both seasons (mean = 0.81). Leaf curl was negatively correlated with irradiance for both 2000 (P = 0.0001) and 2001 (P = 0.0001).

We did not systematically measure the smaller and more curled trees in the plantation — those representing roughly the lower 50% of trees in terms of quality — but the leaf curl index in some trees was 0.50 or lower. On severely curled leaves, the curl ratio of the distal half oscillated widely, sometimes back and forth from negative to positive numbers (negative numbers when leaf edges curl over one another). Under severe heat conditions kousa foliage can scorch (Windham,

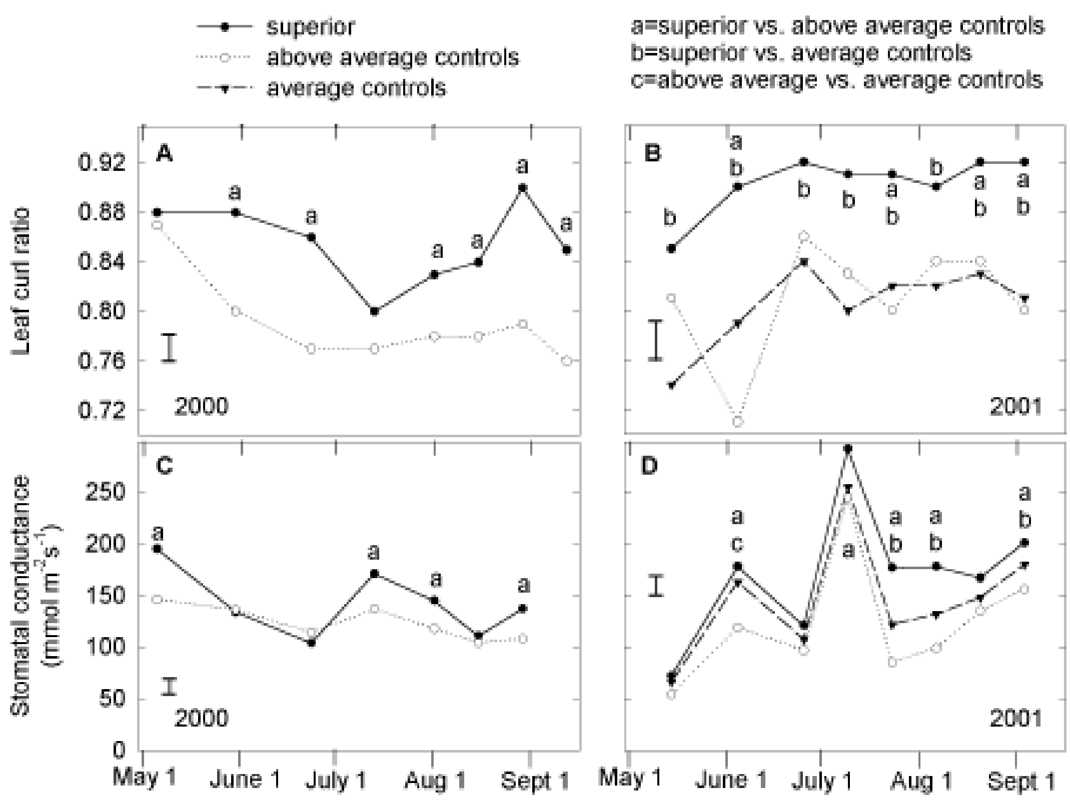

Fig. 2. Leaf curl ratio (A, B; the smaller the number, the greater the curl) and stomatal conductance (g_s; C, D) during the summer months of 2000 and 2001. Superior trees were compared with one control group (above-average control trees) in 2000. Superior trees were compared with two control groups (above-average and average control trees) in 2001. Symbols represent daily averages of 12 replicates per tree group in 2000 and 8 replicates per tree group in 2001, and four measurements for each replicate: one leaf from the north, south, east and west sides of the canopy. Significant differences between daily means were determined by Fisher's Protected LSD and are represented as a, b or c above symbols for each day.

Witte, personal observations). Scorch was not observed in either superior or control trees during 2000 or 2001.

Stomatal conductance, a measure of bulk stomatal openness, provides an indicator of overall physiological state of a leaf or tree (9). Stomatal behavior is very responsive to changes in environmental conditions such as soil moisture, light, relative humidity (vapor pressure deficit of air), wind and other abiotic and biotic factors (9). Within a group of plants of a species growing in a similar, stressful environment, higher g_s in some plants often signifies that those individuals are more resilient to stress. In the absence of stress, higher constitutive g_s may indicate greater plant health or vigor and be associated with higher rates of photosynthesis (9). Superior trees had higher g_s than above-average control trees on four of the seven 2000 measurement days and five of the eight 2001 measurement days (Fig. 2C and 2D). Superior trees had higher g_s than average control trees on three of the eight 2001 measurement days (Fig. 2D). Stomatal conductance of the two control groups differed only once during the season. Seasonal averages in 2000 were 142 for superior trees and 123 mmol m^{-2} s^{-1} for the above-average control trees. Seasonal averages in 2001 were 173 for superior trees, 124 for the above-average control trees and 147 mmol m^{-2} s^{-1} for the average control trees.

We have observed that g_s is typically relatively low in kousa and flowering dogwoods compared to g_s of other temperate, deciduous tree species (3). Absolute values of g_s of the kousa dogwoods reported here were similar to those observed before in flowering dogwoods in this region. Stomatal conductance of exposed, unshaded foliage of native flowering dogwoods at the UT arboretum remained mostly below 150 mmol m^{-2} s^{-1} (1) and did not exceed 200 mmol m^{-2} s^{-1} in the canopies of mature trees on the UT campus during the 1997 season (7). At the nearby Walker Branch Watershed in Oak Ridge, TN, g_s of naturally growing flowering dogwoods in the understory exceeded 150 mmol m^{-2} s^{-1} in 1996 only when provided with above ambient soil moisture (2). Stomatal conductance of the kousa dogwoods in our current study was not related to irradiance at the time of measurement, which we have also observed for flowering dogwood (1). Stomatal conductance was often as high or higher on cloudy days than on sunny days. Stomatal conductance was negatively correlated with leaf temperature for 2000 ($P = 0.0001$) and 2001 ($P = 0.0001$).

Leaf temperatures were similar in superior trees and both groups of control trees during the two summer seasons, with daily averages ranging from 27 to 35C during 2000 and from 25 to 34C in 2001. Therefore, the lower degree of leaf curl in superior trees was evidently unrelated to ability to reduce leaf temperature, possibly via increased transpiration rates. Across all replicates of all groups, leaf curl ratio was negatively correlated with leaf temperature for both 2000 ($P = 0.02$) and 2001 ($P = 0.001$).

Leaf Ψ_π has been used as a sensitive indicator of plant drought stress, to track changes in soil and plant water status (e.g., 6, 8). Osmotic potential was measured in the first year of the study to determine if water status of superior and control trees responded differently during the season to environmental changes. Leaf Ψ_π was similar in superior and control trees on all measurement days. Leaf Ψ_π declined during the season, from about –1.33 MPa in the beginning of May to about –1.6 MPa at the end of August (pooled SE of the means = 0.03 MPa). Soil moisture was not measured in this study, but we assured that replicates of each group were exposed to similar soil conditions by carefully matching superior tree replicates with nearby control replicates, and by studying trees throughout the plantation. We do not believe that the possibility of deeper or more extensive root systems of superior trees, providing greater access to soil moisture, explains the more stress-free nature of superior trees, as water status was similar in superior and control trees in 2000, the drier year of the two years.

Trees selected as superior by visual observation in 1998 and 1999 had less leaf curl and maintained higher stomatal opening during the 2000 and 2001 seasons than other kousa dogwoods in the plantation, even other trees of similar size and high springtime foliar quality (hypothesis proved true). Based on casual observations, superior trees maintained good foliar color, typically appearing a deeper, more healthy green than that of the average kousa on the plantation and maintained further into the autumn. The superior trees also showed other desirable horticultural features. They were among the largest trees on the plantation, generally having a pleasing overall shape and average or above average spring bloom. Superior trees are currently being propagated by cuttings and will be further tested for aesthetic performance in USDA plant hardiness zones 7–9. Should clones prove to be as resistant to summer stress as parent material, we anticipate releasing stress-resistant kousa cultivars.

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