Drought Avoidance in Katsura by Drought-induced Leaf Abscission and Rapid Refoliation

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Abstract. The limited use of the katsura tree (*Cercidiphyllum japonicum* Sieb. & Zucc.) in the landscape may be due to its reputed, but uncharacterized, intolerance of drought. We examined the responses of katsura trees subjected to episodes of drought. Container-grown trees in a greenhouse were subjected to one of three irrigation treatments, each composed of four irrigation phases. Control plants were maintained under well-hydrated conditions in each phase. Plants in the multiple-drought treatment were subjected to two drought phases, each followed by a hydration phase. Plants in the single-drought treatment were exposed to an initial drought phase followed by three hydration phases. Trees avoided drought stress by drought-induced leaf abscission. Plants in the multiple- and single-drought treatments underwent a 63% and 34% reduction in leaf dry weight and a 60% and 31% reduction in leaf surface area, respectively. After leaf abscission, trees in the single-drought treatment recovered 112% of the lost leaf dry weight within 24 days. Leaf abscission and subsequent refoliation resulted in a temporary reduction in the leaf surface area : root dry weight ratio. After relief from drought, net assimilation rate and relative growth rate were maintained at least at the rates associated with plants in the control treatment. We conclude that katsura is a drought avoider that abscises leaves to reduce transpirational water loss. Although plants are capable of refoliation after water becomes available, to maintain the greatest ornamental value in the landscape, siting of katsura should be limited to areas not prone to drought.

The genus *Cercidiphyllum* is composed of two species native to eastern Asia. The common katsura (*C. japonicum*) is endemic to Japan and China, although its native range in China has diminished to the degree that it is now classified as uncommon (Chien, 1992). As a landscape plant, the katsura is valued for its brilliant autumnal leaf color, picturesque form, slightly shaggy bark, and disease and pest resistance. The species recently gained celebrity by being named the Tree of the Year for 1997 by the International Dendrology Society (Andrews, 1998).

Despite these attributes, use of katsura in the landscape is rare. The reputation of katsura as a drought-intolerant tree may play a role in its limited usage. While experimental evidence pertaining to the drought intolerance of katsura is lacking, anecdotal references are common. Flint (1997) discusses the necessity for maintaining adequate soil moisture, as do others (Dirr, 1998; Wyman, 1971; Yiesla and Giles, 1992). Leaves on trees subjected to drought stress often become scorched and

after prolonged periods may senesce and abscise (personal observations). While drought may induce a significant amount of leaf abscission, refoliation after water becomes available has been observed, but not quantified (Kjelgren, 1994).

Soil moisture contents may vary considerably in natural and maintained landscapes as

soils go through successive wet and dry cycles (Mazzoleni and Dickmann, 1988). Experiments simulating these conditions have been used to examine the response of trees subjected to cycles of drought (Liu and Dickmann, 1992; Mazzoleni and Dickmann, 1988). The objectives of our study were to examine the growth and morphological responses of katsura trees subjected to periods of drought and well-hydrated conditions. We quantified the degree of drought-induced leaf abscission and determined the refoliation capacity of trees after drought ended.

Materials and Methods

Plant material. On 4 Apr. 1997, 132, 2-year-old, dormant, bare-root seedlings of katsura (Lawyer Nurseries, Plains, Mont.) were planted singly into 45-dm³ Classic 816 (Nursery Supplies, Chambersburg, Pa.) nursery containers filled with Metro-Mix 700 (Scotts, Marietta, Ga.). We placed pieces of wire screen inside containers to prevent the loss of medium through drainage holes and put containers on a greenhouse bench under natural photoperiod (lat. 42°N). Containers were irrigated with tap water (pH of 8.74, EC of 0.45 mS·cm⁻¹) as needed to keep the surface of the medium moist, and fertilized weekly with N at 155 mg·L⁻¹ from Peters Excel all-purpose 21N–2.2P–16.6K fertilizer (Scotts, Marietta, Ga.) until treatments began.

Irrigation treatments. The study consisted of three irrigation treatments applied over four consecutive phases that simulated either drought or well-hydrated conditions (Fig. 1). In the control treatment, all phases were well-hydrated. The multiple-drought treatment consisted of drought in phases one (two cycles) and three (one cycle), and hydration in phases two and four. Plants in the single-drought

Fig. 1. Schematic of experimental protocol. Katsura trees assigned to control, single-drought, or multiple-drought treatments were subjected to hydrated and/or drought conditions over four consecutive phases. Destructive harvests were conducted on the first day treatments began and at the conclusion of each phase. The entire experiment was conducted three times.

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treatment were subjected to drought in phase one (two cycles), and hydrated conditions in phases two through four. For all treatments, phases one and three were considered complete when water was resupplied at the conclusion of a drought cycle, and lasted from 6 to 11 d and 4 to 6 d, respectively. Phases two and four were arbitrarily assigned a duration of 9 d. Destructive harvests were conducted on the first day treatments began and at the conclusion of each phase. For harvests where plants had been subjected to the same cumulative irrigation regimen, treatments were combined.

On 4 June 1997, 44 plants were selected for uniformity, randomly arranged on greenhouse benches and randomly assigned to one of the three treatments. There were 16, 12, and 12 plants assigned to the control, multiple- and single-drought treatments, respectively. The following day, phase one began and the first destructive harvest (of the remaining four plants) occurred. Stem length from the stem base to the shoot apex of each plant was measured. All plants were fertilized at the beginning of each phase with N at 155 mg·L⁻¹ from Peters Excel all-purpose 21N-2.2P-16.6K fertilizer (Scotts). Drought was imposed by withholding irrigation for the remainder of each drought cycle. A drought cycle was defined as complete when 50% of the plants subjected to drought wilted during either midday (1300 to 1500 HR) or morning (0600 to 0900 HR) hours in phases one and three, respectively. Phase one consisted of two drought cycles. When the first drought cycle was complete, containers were brought to container capacity with tap water and the second drought cycle began. Phase three consisted of one drought cycle. During hydration phases, plants were irrigated daily with tap water with the amount of water lost the previous 24 h due to evapotranspiration, as determined gravimetrically. Volumetric soil moisture content of the medium of each container was determined daily, before irrigation, with a Theta Probe (meter type HH1, sensor type ML1; Delta-T Devices Ltd., Cambridge, U.K.) soil moisture sensor at 6 cm below the soil surface.

Growth and leaf water potential. At each destructive harvest, we identified the youngest, fully expanded pair of leaves on each plant to be harvested. One of these leaves was used to determine the predawn (0300 to 0500 HR) leaf water potential (ψ_{pd}), measured with a pressure chamber (PMS Instruments, Corvallis, Ore.). The relationship between soil moisture content and y_{pd} was described by using Deltagraph® 4.0 (DeltaPoint, Monterey, Calif.) as the equation: $-MPa = (\text{soil moisture content}^{-0.8976})(0.09255)$; $R^2 = 0.645$.

Stem diameter at 2.5 cm above the soil surface and stem length from the stem base to the shoot apex of each plant were measured. Internode length was determined by measuring the length between the node of the identified pair of leaves and the node immediately below it. From the remaining identified leaf, a 0.5-cm² disc was removed from the interveinal region of the basal half of the blade and dried at 67 °C for 2 to 3 d. Specific leaf weight was calculated by dividing the dry weight of each

disk by its area. Because the drought treatments resulted in leaf desiccation and/or abscission, leaves (including petioles) were removed from the plants and designated as either viable or nonviable. Individual leaves that had not abscised and had $\approx 50\%$ or more of their tissue undamaged were considered viable. The remaining leaves were classified as nonviable. All leaf data reported were obtained from viable leaves. Leaf surface area of viable leaves was measured by using an area meter (LI-3100; LI-COR, Lincoln, Nebr.). Roots were separated from their growth medium by hand in tap water. Dry weight of leaves, stems, and roots was determined after the material was dried for 2 to 3 d at 67 °C. The ratio of viable leaf surface area : root dry weight was calculated. Net assimilation rate and relative growth rate were determined for each treatment during each phase (Harper, 1977).

Experimental design and analysis of data. There were four single-plant replications (experimental units) within each harvest $\times$ treatment combination. The experiment was conducted three times, with the second and third experiments over time starting on 31 July 1997 and 6 Sept. 1997, respectively. Based upon a completely randomized design, data were analyzed by using the Statistical Analysis System (SAS Institute, Cary, N.C.). Within each harvest group, analyses of variance were performed by using the General Linear Model (PROC GLM), and treatment means that differed were separated according to the LSD test ($P \leq 0.05$). Single-plant replicates one and two, and replicates three and four were combined and the averages used for statistical analysis of net assimilation rate and relative growth rate.

Results and Discussion

At soil moisture contents of 0.16 m³·m⁻³ or higher, leaves did not abscise, but as moisture content decreased below 0.16 m³·m⁻³, percentage leaf abscission increased linearly [percentage leaf abscission = $0.802 - 4.35$ (soil moisture content); $R^2 = 0.488$; $P = 0.0115$]. As drought severity increased, abscission of leaves progressed acropetally along shoots. During each drought phase, leaf dry weight and leaf surface area were reduced (Table 1). At the second harvest, leaf dry weight of plants in the drought treatments was 34% lower than that of control plants. Following drought in the third phase, leaf dry weight of plants in the multiple drought treatment was 63% lower than that of control plants. Leaf surface area of drought-stressed treatments was reduced by 31% and 60% following phases one and three, respectively. Soil matric potentials of less than -1.0 MPa induced leaf abscission and reduced total leaf area by 10% in two cultivars of hybrid poplar (*Populus L.*) (Mazzoleni and Dickmann, 1988), and black walnut trees (*Juglans nigra L.*) subjected to ψ_{pd} of -1 and -2 MPa abscised $\approx 35\%$ and $\approx 62\%$ of their leaves, respectively (Pallardy and Rhoads, 1993). Yet, while soil moisture content values of 0.16 m³·m⁻³ induced leaf abscission in our study, values as

low as 0.02 m³·m⁻³ did not induce leaf abscission in cultivars of Freeman maple (*Acer $\times$ freemanii* E. Murray) (Zwack et al., 1998). Plant response, however, could have been influenced by differences in container media.

Abscission is a principal defense against drought (Addicott, 1982), and plants that shed leaves to avoid water deficits during water shortages have dehydration-sensitive tissues (Ludlow, 1989). Leaf loss abruptly decreases the evaporative surface and lowers transpirational water loss. Abscission of dehydration-sensitive leaves obviously decreased the katsura tree's demand for water and increased its internal water content. After drought-induced leaf abscission, soil water content in the drought treatments at the conclusion of non-drought phases was higher than in the controls (Table 1). At the conclusion of the study, drought treatments had higher (less negative) values of ψ_{pd} than did controls (Table 1). Similarly, Ginter-Whitehouse et al. (1983) determined that drought-induced leaf abscission in black walnut resulted in a conservation of water and an increased supply of water to the remaining leaves.

After drought ended, trees refoliated and leaf dry weight and leaf surface area increased (Table 1). At harvest five (22 to 24 d after rewatering), plants in the single-drought treatment had recovered 104% of their initial leaf dry weight and 96% of their initial leaf surface area. Black walnut also refoliated after drought-induced leaf abscission, but the amount of new foliage never exceeded 5% of the original leaf area (Parker and Pallardy, 1985). While Pallardy and Rhoads (1993) observed refoilation after abscission in black walnut and sugar maple (*Acer saccharum* Marsh.), they found that the amount of new leaf area was inadequate to compensate for that lost. Based upon our observations, the high degree of refoilation found in katsura was probably associated with the rapid increase in lateral branch development, although we did not quantify this. Defoliation stimulates the development of lateral branches in other trees; a 2-fold increase in lateral branches was observed in hybrid poplar (*Populus $\times$ euramericana* (Dode) Guinier 'Negrito de Granada') (Bassman and Dickmann, 1982). Katsura is dimorphic, producing both long and short shoots. Apical dominance of the terminal long shoots inhibits the growth and development of the mature lateral branches below, maintaining them as short-shoot spurs. Titman and Wetmore (1955) found that removal of the auxin source, via decapitation of the terminal long shoot, resulted in the extension of the short-shoot spurs into juvenile long shoots. During our study, the inhibition of auxin transport associated with drought stress (Levitt, 1980) may have initiated the extension of the lateral spurs into juvenile long shoots, thus enabling plants to recover leaf area freely.

Drought reduced root dry weight of plants at the fourth and fifth harvests (Table 1). At harvest five, root dry weight of plants in the multiple- and single-drought treatments was 41% and 23% lower than that of control plants, respectively. Reduction in stem dry weight

Table 1. Soil moisture content, predawn leaf water potential, dry matter partitioning, leaf surface area (LSA), and LSA : root dry weight ratio of katsura trees before treatment (harvest 1) and after being subjected to one of three irrigation treatments (control, multiple-drought, and single-drought), each composed of four phases of either hydrated or drought conditions. In harvests where the irrigation regimen of plants in multiple- and single-drought treatments did not differ, they are indicated as having been subjected to drought. Values are the means of 12 replicate trees obtained during three experiments.

Treatment	Irrigation phase	Soil moisture content (m ³ ·m ⁻³)	Predawn leaf water potential (–MPa)	Dry wt (g)			LSA (m ²)	LSA : root dry wt ratio (cm ² ·g ⁻¹)
				Leaf	Root	Stem		
All	Hydrated	0.31	0.29	34.2	31.0	58.6	0.84	345
<i>Harvest 1—before treatments</i>								
<i>Harvest 2—after phase one</i>								
Control	Hydrated	0.27 a ²	0.33 a	36.1 a	30.1 a	64.8 a	0.81 a	381 a
Drought	Droughted	0.11 b	0.88 b	23.7 b	30.1 a	53.5 b	0.56 b	278 b
<i>Harvest 3—after phase two</i>								
Control	Hydrated	0.25 b	0.32 a	36.1 a	37.2 a	69.4 a	0.89 a	418 a
Drought	Hydrated	0.29 a	0.32 a	26.4 b	29.2 a	62.3 a	0.61 b	358 a
<i>Harvest 4—after phase three</i>								
Control	Hydrated	0.20 b	0.33 a	42.4 a	40.8 a	75.4 a	0.90 a	328 a
Multiple drought	Droughted	0.09 c	1.50 b	15.6 c	28.9 b	65.1 a	0.36 c	213 b
Single drought	Hydrated	0.24 a	0.29 a	32.8 b	34.2 ab	69.0 a	0.72 b	295 a
<i>Harvest 5—after phase four</i>								
Control	Hydrated	0.16 c	0.47 b	49.0 a	46.3 a	98.5 a	1.10 a	273 a
Multiple drought	Hydrated	0.30 a	0.32 a	20.8 c	27.3 c	68.8 b	0.48 c	252 a
Single drought	Hydrated	0.20 b	0.38 a	35.5 b	35.5 b	81.2 b	0.81 b	309 a

²Mean separation within columns and harvests by analysis of variance and LSD, $P \leq 0.05$.

also was observed (Table 1). At the final harvest, stem dry weight of multiple- and single-drought treatments was reduced by 30% and 18%, respectively. Drought reduced root elongation in white oak (*Quercus alba* L.) and post oak (*Quercus stellata* Wangenh.), and root elongation and stem dry weight in black walnut and red oak (*Quercus rubra* L.) (Pallardy and Rhoads, 1993). Manual defoliation also reduced root and stem dry weight in tuliptree (*Liriodendron tulipifera* L.) (Madgwick, 1975). The reduction in root and stem dry weight in katsura may have resulted from the inhibition of growth associated with a limited supply of water and decreased photosynthate due to leaf abscission, and depleted root and stem reserves associated with refoleation.

Because of leaf abscission, the ratio of leaf surface area : root dry weight in plants completing a drought cycle was lower than that in plants subjected to well-hydrated conditions at harvests two and four (Table 1). However, after droughted plants had refoleated during a 9-d hydration phase, ratios were similar in all treatments. The temporary reduction in leaf surface area : root dry weight ratio resulted in a more favorable balance between the water-absorbing (roots) and water-losing (leaves) tissues. This change in the ratio suggests that once drought ends, katsura allocates more carbon to the production of new leaves than to production of new root and stem tissue.

During drought phases, net assimilation rate and relative growth rate of drought treatments were negative (Table 2), probably because of leaf abscission. During phases two and four, net assimilation rates were positive in all treatments and did not differ, indicating that trees that had previously been subjected to drought could assimilate carbon at the same rate as controls. In phase three, plants in the single-drought treatment had a higher net assimilation rate than did control plants, indicating that during recovery, the former were

temporarily more efficient at assimilating carbon than were the latter. Relative growth rate of plants in all treatments differed only if they were irrigated differently during that phase (Table 2). While net assimilation rate in the single-drought treatment increased temporarily during phase three, the relative growth rate did not. Although the values remained positive, net assimilation rate and relative growth rate also decreased in red maple (*Acer rubrum* L.), pawpaw [*Asimina triloba* (L.) Dunal], black tupelo (*Nyssa sylvatica* Marsh.), and bald cypress [*Taxodium distichum* (L.) Rich.] subjected to drought (Nash and Graves, 1993). Paralleling our observations of katsura trees recovering from defoliation, Madgwick (1975) found that both the photosynthetic efficiency of tuliptree leaves, expressed as unit leaf rate, and the rate of leaf production increased with severity of defoliation.

Drought decreased stem diameter and stem elongation, although plants in the single- and

multiple-drought treatments did not differ from one another. At the conclusion of the study, stem diameter was reduced by 16.4% and 15.7% in the multiple- and single-drought treatments, respectively. Control treatments grew an additional 43 cm, whereas single- and multiple-drought treatments grew only 29 and 28 cm, respectively; drought reduced stem elongation ≈34%. After 3 weeks of severe drought, stem elongation of eastern cottonwood (*Populus deltoides* Marsh.) seedlings was reduced by ≈13% (Kelliher et al., 1980). Mazzoleni and Dickmann (1988) found that, while drought reduced height growth in 'Eugenei' hybrid poplar by ≈17 cm, 10 d of irrigation at the conclusion of the study led to a flush in height growth of ≈12 cm. In our study, 22 to 24 d of irrigation following drought in a single-drought treatment, resulted in an increase in height growth of only 1 cm. No differences among treatments were observed in internode length and specific leaf weight.

Table 2. Net assimilation rate (NAR) and relative growth rate (RGR) of katsura trees subjected to one of three irrigation treatments (control, multiple-drought, and single-drought), each composed of four irrigation phases that simulated either hydrated or drought conditions. In phases where the irrigation regimen of plants in multiple- and single-drought treatments did not differ, they are indicated as having been subjected to drought. Values are the means of six replicate trees obtained during three experiments.

Treatment	Irrigation phase	NAR ($\mu\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$)	RGR ($\text{mg}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$)
Phase one			
Control	Hydrated	60 a ^z	5.6 a
Drought	Droughted	−97 b	−2.3 b
Phase two			
Control	Hydrated	82 a	9.7 a
Drought	Hydrated	62 a	3.1 a
Phase three			
Control	Hydrated	143 b	13.1 a
Multiple drought	Droughted	−144 c	−1.7 b
Single drought	Hydrated	257 a	18.7 a
Phase four			
Control	Hydrated	198 a	13.7 a
Multiple drought	Hydrated	63 a	7.6 a
Single drought	Hydrated	115 a	10.1 a

²Mean separation within columns and phases by analysis of variance and LSD, $P \leq 0.05$.

Ludlow (1989) stated that drought-induced leaf abscission reduces photosynthesis and leads to a slow recovery once stress is relieved. While leaf shedding probably reduced photosynthate production, we found that net assimilation rate and relative growth rate were maintained and net assimilation rate temporarily increased after drought ended. Katsura also appears to have a heightened capacity for refoliation, perhaps contributing to an enhanced recovery, because we found that trees replaced 112% of the leaf dry weight lost within 24 d.

As a means of avoiding drought stress, katsura abruptly reduces transpirational water loss by shedding leaves of lower photosynthetic activity. This leads to the conservation of water for the whole tree and an increased supply of water to the remaining leaves. While katsura may postpone damage associated with drought on a short-term basis, the long-term costs of repeated drought stress and droughts of longer duration are likely to be severe. In addition to the loss of photosynthate associated with leaf abscission, additional reductions in root dry weight, stem diameter and stem elongation may occur. The elongation of short-shoot spurs into juvenile long shoots may temporarily decrease the sexual reproductive capacity of established trees, since flowers are produced only on mature spur branches. The variability in growth habit (single stem versus multistem) of katsura trees has been associated with provenance and gender, although only anecdotally. This variability may be equally explained by the interplay of dimorphism and auxin-regulation (perhaps due to drought) in young trees. Because our conclusions are based only on the response of young plants, further study of the effects of drought on mature trees is warranted. To date,

no genotypes of katsura have been selected for resistance to drought or other forms of environmental stress. The identification and selection of genotypes that tolerate drought by means other than leaf abscission would strengthen the appeal of this ornamental landscape tree.

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