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An examination of drought-stress avoidance and germinability of katsura tree

by

Michael Sean Dosmann

A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of
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This is to certify that the Master's thesis of
Michael Sean Dosmann
has met the thesis requirements of Iowa State University

Signatures have been redacted for privacy

For the Graduate College
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CHAPTER 1. GENERAL INTRODUCTION

Introduction

This thesis and the studies described herein evolved quite rapidly after I arrived in the Department of Horticulture at Iowa State University. I was given the opportunity to explore my own interests in woody landscape plants and encouraged to design a study with relevance to this area. Before I settled on a project, I recalled the advice of a professor at Purdue University, Robert Joly. He told me that research involves filling in the holes; but before you can begin researching, you have to know enough about something to know where the holes lie. Following his advice, I made a list of woody plants that had piqued my curiosity over the years. I examined this list, compared a few notes, and selected a tree that had several holes in our basic understanding that needed filling.

I chose the katsura tree, *Cercidiphyllum japonicum* (Sieb. and Zucc.). Horticultural academics have applauded this tree since its introduction to cultivation in the latter part of the 19th century. One of them, Michael Dirr (1990, p. 198), states, “If I could use only one tree this would be my first tree.” Recently katsura achieved additional celebrity by being named the 1997 Tree of the Year by the International Dendrology Society (Andrews, 1998). Yet despite these and other accolades, *Cercidiphyllum* is labeled rare and unusual in the nursery trade. The relative obscurity of this high-quality landscape plant was puzzling; I wanted to find out why.

General encyclopedic entries pertaining to katsura allude to its inability to withstand drought (Dirr, 1990; Flint, 1997; Wyman, 1971). However, an examination of the primary literature revealed that there had not been any research conducted on the drought response of katsura. I decided that an examination of the effect of drought on the species not only would fill a gap in the literature, but would complement current research in the department. As the study progressed, I found a need to germinate seeds of katsura. I consulted scientific references on the germination of katsura tree seed, but again, found little published
information. Seeing an opportunity to fill yet another hole, I set out to study the germinability of katsura seed.

By conducting research in these two areas, my objectives were to answer questions relevant to the nursery and landscape industries and contribute to the scientific literature. Furthermore, my goal was to learn as much about this particular tree as possible, including its history, landscape usage, taxonomy, and physiology. Perhaps as a 'katsura ambassador' I could promote its usage in the ornamental horticulture industries.

**Thesis Organization**

The remaining portion of this chapter is a review of the literature. Included are an overview of the genus and reviews of information relevant to my drought-stress and germination studies. The second chapter is a manuscript to be submitted to *HortScience* that summarizes my experiment on the response of katsura to drought stress. The third chapter is also in the format of a manuscript submitted to *HortScience*, and reports the findings of my study on the effect of stratification and irradiance on the germination of the two species of katsura. The final chapter is a brief discussion of my general conclusions based upon the projects and experimental research.

**Literature Review**

*Cercidiphyllum*

Dignified. Elegant. Exotic. These adjectives appropriately describe one of the most ornamental genera of trees to be introduced from Asia, *Cercidiphyllum*. The name *Cercidiphyllum* is derived from *Cercis*, the genus of redbud, and *phyllon*, the Greek word for leaf. It refers to the cordate shape of the mature, short-shoot leaves, which resemble those of redbud (*Cercis canadensis* L.). I was enthralled by the taxon after seeing my first katsura tree a decade ago at Fernwood Botanic Garden in Niles, Mich., where a stately specimen graces the
North Vista. Little then did I know that I would come to learn much more about this genus in the future.

The taxonomic placement of katsura has been questioned ever since the genus was first described by physician and plant collector Philipp von Siebold and his colleague J. G. Zuccarini in 1846. *Cercidiphyllum* was originally assigned to the Magnoliaceae, later placed in the Trochodendraceae, and then reorganized into its own, single-genus family by the German botanist Heinrich Engler in 1909 (Hutchinson, 1964). The relationship of Cercidiphylaceae to other families of flowering plants has been, and continues to be, a subject of discussion. The primary difficulty in assigning this isolated family to a particular order is that it shares characteristics with both the Magnoliaceae and Hamamelidales. The family has been placed within the Hamamelidales by Cronquist (1988) and Thorne (1983), and research by Manos et al. (1993) confirms the close relationship between Cercidiphylaceae and Hamamelidaeae. Endress (1986) placed the katsura family within the Trochodendrales, an order intermediate the Magnoliales and Hamamelidales, although he later (Endress, 1993) declined to place it in either Hamamelidales or Trochodendrales, stating only that it has affinities with both. Takhtajan (1997) maintains that the family is distinct enough to be placed within its own order, a belief supported by Mohana Rao (1986). While taxonomists disagree about the ordinal placement of the family, all agree that Cercidiphylaceae stands, isolated, either among the Hamamelidales or intermediate between the Hamamelidales and Magnoliales.

*Cercidiphyllum* comprises two extant species, both endemic to eastern Asia. At least five additional species of *Cercidiphyllum* have been identified in fossil records from the upper Cretaceous through the Tertiary in the north temperate zones of North America, Europe, and Asia (Brown, 1939). Currently, however, the genus is found only in Japan and portions of central and eastern China. The range continues to shrink, and the common species, *C. japonicum*, has been classified as rare in China (Chien, 1992). The second species,
Cercidiphyllum magnificum (Nakai) Nakai has a native range limited to isolated sub-alpine regions of Honshu, Japan.

Cercidiphyllum japonicum

This species was described in 1852. As the specific epithet suggests, the species is native to the Japanese islands where it is most abundant in northern Honshu. It also is encountered in Hokkaido, Shikoku, and Kyushu (Fig. 1). It grows at sea level in Hokkaido (Spongberg, 1979), and at 1,800 meters in Shikoku (Fanta, 1969). The native range also encompasses portions of central and eastern China from western Zhejiang to northeastern Guizhou, north to southeastern Gansu, southern Shanxi, and western Henan (Fig. 1) at 400 to 2,700 meters (Chien, 1992). In China, loss of habitat, low fertility, logging, and apparent pest problems threaten the survival of this species (Chien, 1992), and evidently, the most desirable lowland forest habitats are being destroyed to make room for farming and homes (R. Lewandowski, personal communication). Throughout its range, katsura inhabits mountainous areas where the soil is moist and high in organic matter. Associated species of C. japonicum include Dipteronia sinensis Oliv., Emmenopterys henryi Oliv., Kalopanax septemlobus (Thunb. ex A. Murray) Koidz., Quercus mongolica var. grosseserrata (Bl.) Rehd. and Wils., Tilia japonica (Miq.) Simonkai, and species of Abies Mill., Fagus L., and Picea A. Dietr. (Chien, 1992; Lindquist, 1954).

The ultimate size of this species varies. Heights typically range from 9 to 24.5 meters, although some trees have been found to grow much larger. In the forested areas of Yezo, Japan, Charles S. Sargent (1893, p. 52), found that trees reached very large dimensions, “often rising to the height of a hundred feet (30.5 meters), and developing a cluster of stems eight or ten feet (2.5 to 3.1 meters) through.” Sargent reported one tree near Sapporo that girted 6.6 meters at 0.9 meters above the ground. In China, katsura reaches even greater heights of up to 40 meters (Chien, 1992). E. H. Wilson (In: Rehder and Wilson, 1913,
Figure 1. Distribution of *Cercidiphyllum japonicum* in eastern Asia. Adapted from Chien (1992) and Spongberg (1979).
p. 317) believed that katsura “both in height and girth . . . exceeds all other broad-leaved deciduous trees known from China.” Trees also can reach impressive size in cultivation. A male tree located on the grounds of the Morris Arboretum in Philadelphia has a circumference of 6.7 meters at 46 centimeters above the ground; a height of 20.7 meters; and an average spread of 30.8 meters, with a maximum spread of 35.1 meters (R. Lewandowski, personal communication).

Single- to multitrunked, *C. japonicum* varies in form and habit, ranging from pyramidal and upright to broadly spreading, the width sometimes surpassing the height as in the Morris Arboretum tree. In wide-spreading trees, limbs tend to branch low to the ground. A tree of unknown age and origin at Dumbarton Oaks, Washington, D.C., exemplifies this trait, with massive lower limbs hovering above the ground, one stretching outwards for over 13.7 meters (G. Griffin, personal communication). The bark of the katsura is grayish-brown, becoming slightly furrowed and twisting with age, somewhat resembling that of ironwood [*Ostrya virginiana* (Mill.) K. Kock].

The slender, graceful twigs are reddish-brown in color and become gray with age. Branches lack true terminal buds, having instead a solitary bud or, typically, two opposite pseudoterminal buds that resemble the hooves of a deer. The acute, appressed buds are covered by two outer scales that are red, contrasting with the gray color of older branches.

Katsura is dimorphic, producing distinct juvenile and mature leaf forms on long- and short shoots, respectively (Fig. 2). The terms long- and short shoot refer to the relative lengths of the branches. Both types are sympodial, a condition where the terminal bud(s) die at the end of each growing season and subsequent growth continues the following year from axillary buds. The juvenile long shoots arise from the axillary bud of a short-shoot branch and have leaves arranged oppositely or suboppositely (occasionally in whorls of three). In the second year of growth, most of the long-shoot axillary buds begin to develop into the mature, short shoots. Instead of elongating into a branch with many leaves, each year the short shoot
C. japonicum

C. magnificum

Figure 2. Morphology of *C. japonicum* (left) and *C. magnificum* (right).
produces but a single leaf, and after several years takes on a spur-like appearance (much like *Ginkgo* L. and *Larix* Mill.). The spurs also are the site of the inflorescences. In *C. japonicum*, the spurs remain small, growing up to 6 mm in length. After individual trees are physiologically mature (15 - 20 years old) most of the shoots are of the short-shoot type, with long shoots found only on the terminal portions of branches (Titman and Wetmore, 1955). The phenomenon of dimorphism in katsura is controlled by apical dominance. Titman and Wetmore (1955) found that auxin produced in the terminal leaves of the long shoots inhibited the growth and development of the buds below, suppressing their growth and creating the short-shoot spurs. When the auxin source was removed by decapitating the terminal portion of the long-shoot branch, short-shoot spurs developed and elongated into juvenile long-shoot branches.

Long-shoot leaves, up to 4.5 cm long and 3.2 cm wide, are broadly ovate to elliptic with rounded to truncated bases and entire to finely serrated margins (Fig. 2). Stipules associated with this leaf type are narrowly lanceolate and 8 to 9 mm long, abscising after the leaf blades have expanded. Short-shoot leaves are cordate with crenated margins and may grow 9 cm long and wide. Stipules of the short-shoot leaves are lanceolate, 5 to 6 mm long, and, like those of long shoots, are caducous. The two leaf types also differ in venation; long-shoot leaves have palmate to pinnate veins, while short-shoot leaves are palmately veined.

The emerging leaves, coincident with or shortly after flowering, are burgundy to mauve, progressing in color to light green and eventually bluish-green at maturity. The foliage is crisp and densely arranged on the branch ends, giving the tree a fine-textured appearance. Fall color can be brilliant, yet often unpredictable. Leaves are typically apricot-yellow, but may become shades of red, yellow, pink, and mauve. It has been suggested that variability in autumnal leaf pigment may be linked to soil moisture, fertility (Flint, 1997), and pH (Dirr, 1990).
In addition to the kaleidoscope of color, senescing leaves produce a sweet, pungent aroma. Depending upon the nose, it is reminiscent of crushed strawberries, cotton candy, or burnt brown sugar. The aroma, alluded to in the German common name *Kuchenbaum* (cake tree) is associated with maltol, a compound used in the food industry as a flavor enhancer. Tiefel and Berger (1993) found that the concentration of maltol in the leaves varied throughout the year, but peaked during senescence. Another compound, cercidin, is derived from the leaves and has antimicrobial properties. It is thought to play a role in the plant's self-defense system and has potential for use as a food preservative (Tada and Sakurai, 1991).

Katsura is dioecious, and the flowers of both male and female trees are produced in March or April. They are arranged in inconspicuous, dense racemes arising from short-shoot spurs. The perianth is absent in both male and female flowers. Staminate flowers are comprised of many (up to 35) stamens =1 cm long with slender, pendulous filaments and reddish anthers. Individual male flowers are difficult to differentiate from one another due to the compactness of the inflorescence. Female inflorescences are composed of two to eight unicarpellate flowers with slender reddish styles up to 14 mm long. Cylindrical follicles =15 mm long become purplish brown as they ripen in early autumn. The slightly curved fruits contain numerous (15 to 30) seeds, 5 mm long (Fig. 2). Tan in color and winged on the proximal end, the seeds are dispersed by the wind in late autumn through winter. Apparently, monoecious *Cercidiphyllum* have been found (Endress, 1993), but it is not known if these plants are self-compatible or whether they require fertilization from another tree.

Over the years, some have considered *C. japonicum* indigenous to China to be a separate and distinct variety. The Chinese type, designated *C. japonicum* var. *sinense* by Rehder and Wilson (1913), is thought to differ from the Japanese type in that it is single stemmed and pubescent on the follicles and veins of the underside of the leaves. Spongberg (1979), however, found these features to be inconsistent in geographical distribution and frequency, and concluded that those plants showing pubescence should be recognized as *C.
japonicum f. miquelianum Inokuma, a form occurring in both China and Japan. He also considered the single-stemmed habit of trees from China to be taxonomically insignificant. Chun (1921, p. 136) found that there was no botanical difference between the Chinese and Japanese types and noted that "the varietal name is useless except as it may designate a geographic region."

The tan, straight-grained wood is light, soft, and easily worked. In China, the wood is used to make furniture, wood carvings, sketching boards and utensils (Chun, 1921), while in Japan, where it is still highly regarded as a timber tree (P. del Tredici, personal communication), it is used in the construction of packing cases and the interior finishings of inexpensive houses (Sargent, 1893). Sargent also noted that the Ainus of Japan hollowed out huge trunks for use as canoes and constructed mortars from the leftover wood.

As a landscape plant, *C. japonicum* functions best when planted in open areas that accommodate its potential size and allow its attractive form and character to be appreciated fully. It is cold hardy from USDA hardiness zones 5a to 9a, however, a few specimens have been found growing without injury well into zone 4, including a mature tree located in Logan, Utah, where temperatures have reached −30°Fahrenheit (Kjelgren, 1994). Because of the considerable genetic variation among trees available in the trade, and because selections for cold hardiness do not yet exist, in regions where cold hardiness is a concern, plants should be obtained from sources identified as cold hardy.

In nativity, *C. japonicum* thrives in areas where soils are high in organic matter and drought is uncommon. Therefore, it is important to supply ample moisture after transplanting until the tree has become established, especially during dry periods (Dirr, 1990; Flint, 1997; Wyman, 1971). For this reason, caution is needed when planting katsura in areas prone to drought. During drought, katsura has been observed to abscise its leaves, only to refoliate once water is available again (Kjelgren, 1994).
C. japonicum grows best when planted in full sun, although it will tolerate partial shade, and Flint (1997) suggests that some shade may be necessary in southern regions of the United States (USDA hardiness zones 8 and 9). Sunscald may damage young trees, especially if they have been limbed-up. Leaving lower branches on young, newly planted trees may help prevent sunscald by shading the bark during sunny winter days. Tolerant of low to neutral pH and lacking any serious pest or pathogen problems, the tree, once established, is fairly easy to maintain.

*Cercidiphyllum magnificum*

*Cercidiphyllum magnificum*, the broad-leafed katsura, was initially described by the Japanese botanist Takenoshin Nakai in 1919 as a variety of *C. japonicum*, but was given species status the following year. Despite this formal recognition, *C. magnificum* has been virtually ignored and is sometimes not even recognized as a legitimate taxon. Rehder did not mention the tree in either his Bibliography of Cultivated Trees and Shrubs (1949) or Manual of Cultivated Trees and Shrubs (1940). Bean (1970) and Flint (1997) recognize its existence but treat it as a variety. Dirr (1990) also describes the tree, yet acknowledges the taxonomic confusion by giving both variety and species distinctions. Krüssmann (1965) accepts the tree as a second species, as does Spongberg (1979) in his comprehensive review of the genus. Several other fine commentaries (Haag, 1982; Lindquist, 1954), all making cases for a distinct and separate species, have been published on *C. magnificum*, including a recent piece written by Roy Lancaster (1997).

The native range of *C. magnificum* is restricted to the main island of Japan and includes sub-alpine regions of the Japanese Alps west of Tokyo and a small, isolated locale on Mt. Hiyachine in northeastern Honshu (Fig. 3). *C. japonicum* also is native to these regions, but the two taxa are seldom sympatric because *C. magnificum* is found at higher elevations, from 1,000 m to 2,900 m (Andrews, 1998). Like *C. japonicum*, *C. magnificum* inhabits moist
Figure 3. Distribution of *Cercidiphyllum magnificum*. Adapted from Lindquist (1954).
areas where the soil is rich in organic matter. It is often found growing with *Prunus grayana* Maxim., *Acer japonicum* Thunb., and *Acer shirasawanum* Koidz. (Lindquist, 1954).

*C. magnificum* has many of the same attributes of *C. japonicum*, although there are some differences. Trees have narrower crowns and are smaller (up to 10 m tall, some reaching over 15 m in cultivation) than is *C. japonicum*. While the trunk of the common katsura develops a ropy, fissured bark early on in life, the trunk of *C. magnificum* remains smooth, becoming textured only with age. Like the other species, trees are single- to multistemmed. The graceful and picturesque habit is similar to that of *C. japonicum*, the autumn leaf color as beautiful, and some (Krüssmann, 1965) find *C. magnificum* the more appealing of the two. While the developing leaves of *C. japonicum* are purplish-red, the leaves of this species are reddish-orange (Brotzman, 1998; M. Vehr, personal communication)

The long-shoot leaves of *C. magnificum* are larger than those of *C. japonicum*, expanding to 8.3 cm long and 5.8 cm wide, with a broader apex (Fig 2). The short shoots are more pronounced than those of *C. japonicum*, extending up to 18 mm long. The short-shoot leaves are often broader than they are long, up to 7.7 cm wide and 7.1 cm long, orbicular to ovate with strongly cordate, overlapping bases. The margins of both leaf types are strongly crenate to serrate. The stipules of the long- and short-shoot leaves are ≈1 and ≈3 mm long, respectively, and are oblong to ovate in shape. Unlike the common katsura, the stipules of *C. magnificum* are persistent. The follicles of *C. magnificum* are somewhat larger and longer, 12 to 20 mm in length, and have a recurved apex (Fig 2). The seeds of the two species also show marked differences. Those of *C. magnificum* are larger, up to 7 mm long, yellowish in color, and have two distinct wings.

As a smaller version of the common katsura, *C. magnificum* may find its niche as an understory tree and in areas where space is limited. Like *C. japonicum*, it also may require careful siting in regions prone to drought. It has been observed that while *C. magnificum* shows more tolerance of flooding than *C. japonicum*, it also is more demanding of moisture
(R. Haag, personal communication). *C. magnificum* also may be more sensitive to sunscald, due to its smoother, thinner bark.

Established trees of *C. magnificum* are virtually unknown in the United States. The University of Washington Arboretum acquired seeds of this species from the Botanic Garden at Göteborg, Sweden, in 1946 (Mulligan, 1982). One of these trees currently measures 15.6 m in height and 51.3 cm in girth (R. Hitchin, personal communication). Very few nurseries in the United States market this plant; two that do are Heronswood Nursery and Trees, both in the state of Washington.

Evaluation programs on both sides of the Atlantic ocean are beginning to fill in the gaps with regard to our knowledge of the species. British plant collector Roy Lancaster has distributed wild-collected seed of *C. magnificum* in Britain and Ireland for germination and further examination. Another evaluation is being supported by the USDA-ARS, North Central Regional Plant Introduction Station in Ames, Iowa. Seedlings will be distributed through the NC-7 Regional Ornamental Trials for evaluation of performance including climatic adaptability and landscape value.

Propagation of katsura

Commercial propagation of katsura is typically dependent upon seed germination, although vegetative propagation is also an option. In reviewing the literature relevant to the propagation of these species, I was somewhat surprised to find little substantiated information pertaining to either sexual or asexual methods. Because germination of katsura seed was a sizable component of my thesis, I have reviewed that literature below in a separate section.

*C. japonicum* can be propagated with softwood cuttings, with and without supplying additional auxin in the form of indolebutaric acid (IBA). Dirr (1977) notes that cuttings taken from mature wood in June, treated with 20,000 ppm IBA, and placed under mist failed to callus and root, although 90% of the cuttings taken from young seedlings rooted when treated
with 10,000 ppm IBA. Chong et al. (1992) found that when dissolved in a solution of 45% propylene glycol, 10,000 ppm IBA was effective in rooting ≈70% of softwood cuttings.

Treating cuttings with synthetic auxin is not necessary, though. Halward (1956) demonstrated that within 9 weeks, 100% and 76% of softwood cuttings taken in late June had calloused and rooted, respectively, despite not being treated with any hormones.

The few clonal selections of katsura must be propagated by asexual means. 'Heronwood Globe', the round-headed cultivar of *C. japonicum*, is successfully propagated by softwood cuttings treated with 5000 ppm IBA (D. Hinkley, personal communication).

While Dirr and Heuser (1987) state that the weeping clones of katsura are either chip budded or wedge or cleft grafted onto upright understocks, pendulous forms have been shown to root. Barnes (1989) was able to root 60% of the softwood cuttings of *C. magnificum* 'Pendulum' by using 1500 ppm dissolved in a 50% propylene glycol solution.

Drought-induced Leaf Abscission

Water is fundamental to the growth and survival of plants. As Kramer and Boyer (1995, p.18) state, "Almost every plant process is affected directly or indirectly by the water supply." The effects of drought on plants has been an important subject of research, especially in crop plants. Thousands of scientific papers, in addition to scores of reviews and books, have been written on the subject.

As biological organisms, different plants respond variably to drought. However, in general, when water content within a plant progressively decreases, cell turgor is lost, cell enlargement (and thus growth) ceases, stomata close, photosynthesis is reduced, and processes such as protein synthesis and enzyme activity are altered. Eventually, if drought stress persists, cell and organismal death can occur (Hsiao, 1973; Kramer and Boyer, 1995; Levitt, 1980). In trees, water deficits have been shown to reduce the amount of shoot growth, root elongation, radial growth, and the number, rate of expansion, and final size of leaves. Studies
documenting these and other effects of drought on trees are numerous and have been summarized quite well in several reviews (Kozlowski, 1987; Kramer, 1987; Zahner, 1968). Because my research was the first of its kind to examine the effects of drought in katsura, a review of previous literature on the effects of drought on katsura would be brief, indeed. In this review, I have decided to examine the particular phenomenon of drought-induced leaf abscission and its role in drought avoidance.

Strategies of plants for resisting the negative effects of drought are discussed in detail elsewhere (Levitt, 1980; Ludlow, 1989; Parker, 1968; Parsons, 1979). The term drought resistance refers to both avoidance and tolerance of drought. Mechanisms of drought avoidance allow a plant to resist drought stress by maintaining optimal tissue-water contents during low levels of water availability and high levels of atmospheric evaporative demand. Drought-tolerance mechanisms, on the other hand, permit a plant to function even though tissue water contents are suboptimal. While plants may both avoid and tolerate drought, a particular species will rely on one strategy more than the other (Levitt, 1980).

Plants that avoid drought have dehydration-sensitive tissues and higher lethal leaf water potentials than plants that tolerate or escape drought (Ludlow, 1989). For this reason, these plants must minimize water loss and maximize water uptake to maintain a water content above levels that might result in injury or death. The conservation of water by these methods is largely morphological-anatomical in nature (Levitt, 1980).

Drought-induced leaf abscission is one of the principal defenses a plant has against the injury of water deficiency (Addicott, 1982). The shedding of leaves during drought abruptly decreases the evaporative surface and reduces transpirational water loss, preventing the dehydration of plants to lethal levels (Kozlowski, 1973; Kramer, 1987). Leaf abscission during drought generally begins with older leaves of lower photosynthetic activity and progresses acropetally to the youngest leaves (Ludlow, 1989; Mazzoleni and Dickmann, 1988;
Prior to being shed, water is typically translocated from older leaves to younger leaves (Kozlowski, 1973).

Higher proportions of water-absorbing organs (roots) and lower proportions of water-losing organs (leaves) have long been associated with the maintenance of a more favorable water balance in plants. Parsons (1979) states that the shedding of leaves is a major way of reducing water loss and increasing the root:shoot ratio. High root:shoot ratios indicate a higher capacity for absorption of water and lower capacity for transpirational water loss; factors important for growth and survival of trees during drought conditions (Kozlowski, 1987).

Leaf shedding in response to drought has been observed and studied in many desert and semi-desert plants (Harrison et al., 1971; Orshan, 1954; Runyon, 1934). Among deciduous trees of temperate climates, this response has been observed in red maple (Acer rubrum L. 'Franksred') (Nash and Graves, 1993), sugar maple (Acer saccharum Marsh.) (Pallardy and Rhoads, 1993), eastern cottonwood (Populus deltoides Bartr.) (Kelliher et al., 1980), clones of poplar (Populus) (Mazzoleni and Dickmann, 1988), and black walnut (Juglans nigra L.) (Ginter-Whitehouse et al., 1983; Lucier and Hinckly, 1982; Pallardy and Rhoads, 1993; Parker and Pallardy, 1985).

Compared to other deciduous tree species native to the eastern United States, black walnut shows an accentuated propensity for leaf abscission. At predawn leaf water potential values of -1 to -3 MPa, leaf shedding was significantly greater than that of sugar maple, post oak (Quercus stellata Wangenh.), and white oak (Quercus alba L.) (Pallardy and Rhoads, 1993). As predawn leaf water potential decreased from -1.5 to -3.5 MPa., Parker and Pallardy (1985) found that the percentage of black walnut seedlings exhibiting leaf abscission increased almost linearly. At predawn leaf water potential values of -3.5 MPa or less, the authors observed total leaf abscission in almost all seedlings. Abscission of 60% of the leaves in one-year-old black walnut seedlings increased the root:shoot ratio and improved the water balance (Carpenter and Hanover, 1977). The conservation of water and increased water supply to
remaining leaves also has been observed following leaf abscission (Ginter-Whitehouse et al., 1983; Parker and Pallardy, 1985). Parker and Pallardy (1985, p. 820) maintain that the "shedding of foliage of lower photosynthetic activity and the presence of an expansive . . . root system result in a reduction in whole-plant water use, while high rates of CO₂ uptake per unit leaf area are maintained."

As Ludlow (1989) stresses, the shedding of leaves, while a good short-term survival mechanism, does have both short- and long-term costs. The loss of the photosynthetic apparatus curtails carbon acquisition, and recovery may be slow, because new leaves must be formed. Also, avoidance mechanisms do not prevent dehydration of sensitive tissues, and if drought is not relieved, these tissues, and subsequently the plants, will die. Orshan (1954) notes that many desert plants avoid lethal desiccation during periods of severe drought by abscising leaves, only to refoliate once adequate water is available again. While droughted black walnut maintained higher leaf water potentials at predawn and solar noon than white oak and red cedar (Juniperus virginiana L.) due to abscission (Ginter-Whitehouse et al., 1983), it has little capacity to refoliate once drought is removed. Parker and Pallardy (1985) found that the regrowth of foliage after abscission never exceeded 5% of the original leaf area, and Pallardy and Rhoads (1993) observed that the amount of refoliation was inadequate to compensate for the leaf area that was lost.

Mazzoleni and Dickmann (1988) found that drought-stressed hybrid poplar [Populus ×euroamericana (Dode) Guinier 'Eugenei'] abscised 10% of its leaf area. Yet, once drought was removed, the trees refoliated and increased leaf expansion, resulting in a total leaf area that was no different from non-stressed trees. Manual defoliation of tuliptree (Liriodendron tulipifera L.) (Madgwick, 1975) increased the rate of carbon assimilation per leaf and enhanced the production of new leaves. Following mechanical defoliation, higher rates of photosynthesis have been found in leaves of hybrid poplar [Populus ×euroamericana (Dode) Guinier 'Negrito de Granada'] (Bassman and Dickmann, 1982), red oak (Quercus rubra L.)
Dormancy Removal in Seeds

In the process of developing my project on *Cercidiphyllum*, I had the opportunity to communicate with professionals in the North American nursery industry. In speaking with propagators from six nurseries, I found that all of them produced non-clonal katsura by germinating seeds. While all of the nurseries reported successful germination, I was surprised to find that some of their methods differed considerably. Helen Kunkel (personal communication), propagator at J. Frank Schmidt & Son Co. in Boring, Ore., informed me that she achieves maximal germination of *C. japonicum* after stratifying seeds for approximately 60 days. Dan Hinkley (personal communication), owner of Heronswood Nursery in Kingston, Wash., doesn't give seeds a controlled stratification treatment, but sows seed of both species of katsura outdoors immediately after ripening in the fall. After overwintering, the seeds germinate near capacity the following spring. At Carlton Nurseries in Dayton Ore., Mike Anderson reports high germination percentages of *C. japonicum* without giving the seed any form of stratification and sowing the seed directly outdoors in the spring (personal communication).

Many published reports on germination of katsura seed (*C. japonicum* in all references) found relatively low levels of germinability. In trials, Krüssmann (1964) found that only between 15% and 20% of seed germinated, while Fanta (1969) reported germination of 58% of seed. Another study by Rohde (1977) determined the optimum air temperature for germination was between 21 and 25 °C. At 21 and 25 °C, 40.3% and 49.0% of the seeds germinated in 10 and 8.4 d, respectively. In the reports stated above, additional information on environmental conditions were not given. Because stratification was not mentioned, I assume that seeds had...
not been chilled prior to germination, and I wondered if the lower percentage germination values listed above were due to the lack of stratification. Dirr and Heuser (1987) state stratification is not required and that seed germinates within 7 to 14 d. Likewise, Dirr (1977) reported that 90% of seed collected in April germinated within 2 weeks. I wondered if this higher germination percentage in Dirr's trial [compared to the results of others (Fanta, 1969; Krüssmann, 1964; Rohde, 1977)] was because the seed had been collected in the spring, when any dormancy requirements the seeds may have had could have been removed over the winter months.

The effect of photosynthetically active radiation (PAR) on germination of katsura seed has also never been examined. Light, both the wavelength and the photoperiod, can be a factor in controlling germination of many species and is of substantial ecological importance. Typically, seeds requiring irradiance to germinate are small in size and depend upon a shallow depth of planting for survival (Hartmann et al., 1990).

Most of the responses associated with light-sensitivity in seeds are linked to the activity of the phytochrome pigment system located in the seed coat and endosperm. In their pioneering work with the germination of lettuce seeds (*Lactuca sativa* L. 'Grand Rapids'), Borthwick et al. (1954) first described the phytochrome system. In imbibed seeds exposed to wavelengths of light in the range of 660 to 760 nm (red light), the red form of phytochrome (Pr) changes to the far-red form (Pfr) and germination is promoted. When seeds are exposed to far-red light (760 to 800 nm), Pfr changes to Pr and germination is inhibited. This reversion also slowly occurs when seeds are placed in darkness.

Hartmann et al. (1990, p. 127) state, "Temperature is, perhaps, the most important environmental factor that regulates the timing of germination." The practice of stratification, whereby seeds are exposed to moisture and chilling temperatures prior to germination, has been used to remove embryo- and coat-imposed dormancy in seeds for years. Under natural conditions, a low-temperature requirement may prevent seeds from germinating during
unseasonably warm periods in the autumn or winter, ensuring that germination occurs at the optimal time.

While the mechanism by which irradiance controls the release of dormancy is fairly well understood, a similar mechanism (or mechanisms) controlled by low temperature is still elusive. Several hypotheses have been proposed including the degradation of inhibitors and accumulation of promoters within the embryo. Levels of inhibitors have been found to decrease in embryos exposed to low temperatures, as was reported with levels of abscisic acid in acorns of red oak (Vogt, 1974). In embryonic axes of hazelnut (Corylus avellana L.), levels of giberellin, a promoter, have been found to increase following stratification (Arias et al., 1976). Yet, Bewley and Black (1982) contend that a causal relationship between dormancy removal and inhibitor depletion or the promoter accumulation remains to be established.

In most species, the optimal temperature for prechilling is approximately 5 °C, although the duration of the exposure may vary considerably from several days to several months (Bewley and Black, 1982). Within a species, the optimal temperature and duration of the chilling period also may vary with provenance. The most consistent finding has been that seeds from northern geographic origins require longer periods of chilling than do seeds of the same species from southern sources (Flint, 1974).

The interaction of light and low temperatures in the removal of dormancy is exhibited in many species. In monarch birch (Betula maximowicziana Reg.), dormancy can be removed only if the seeds have been stratified and exposed to light (Nagata and Black, 1977). In other species, however, the light requirement for germination can be removed by stratification. Black and Wareing (1955) found that stratified seeds of downy birch (Betula pubescens Ehrh.) germinated equally (95%) under complete darkness and a photoperiod of 8 hr. In seeds that had not been stratified, 0% and 16% germinated in the dark and light, respectively. A similar response was observed in empress tree [Paulownia tomentosa (Thunb.) Steud.] (Carpenter and Smith, 1981), where stratification removed any of the seeds' light requirements, as
germination was 98% in complete darkness and under a photoperiod of 12 h. Unstratified seed germinated at 11% and 50% in the dark and light, respectively.

Literature Cited


CHAPTER 2. KATSURA TREE REFOLIATES AFTER DROUGHT-INDUCED LEAF ABSCISSION

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Abstract. The limited use of 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. Containerized 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 the mechanism of drought-induced leaf abscission. Due to drought, plants in the multiple- and single-drought treatments underwent a 63% and 34% reduction in lamina dry mass and a 60% and 31% reduction in leaf surface area, respectively. After abscission, trees in the single-drought treatment recovered 112% of the lost leaf dry mass within 24 days. Leaf abscission and subsequent refoliation resulted in a temporary reduction in the leaf surface area : root dry mass ratio. After relief from drought, net assimilation rate and relative growth rate of plants in drought treatments 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 is available, to
maintain the greatest ornamental value in the landscape, siting of katsura should be limited to areas not prone to drought.

**Introduction**

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 rare (Chien, 1992). As a landscape plant, the katsura tree 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 uncommon. 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, 1990; 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 cycles of wet and dry conditions (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 a series 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**

On 4 April 1997, 132, two-year-old dormant, bare-root seedlings of katsura (Lawyer Nurseries, Plains, Mont.) were planted singly into 45-dm$^3$ 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.

The study consisted of three irrigation treatments applied over four consecutive phases that simulated either drought or well-hydrated conditions. In the control treatment, all phases were well-hydrated. The multiple-drought treatment consisted of drought in phases one and three, and hydration in phases two and four. Plants in the single-drought treatment were subjected to drought in phase one, and hydrated conditions in phases two through four. For all treatments, phases one and three were complete when drought cycles in the drought treatments had ended, 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, Marietta, Ga.). Drought was imposed by withholding irrigation for the remainder of each drought cycle. A drought cycle was 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 began the second drought cycle. 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, 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, United Kingdom) soil moisture sensor at 6 cm below the soil surface.

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 \( \Psi_{\text{pd}} \) of each plant, measured with a pressure chamber (PMS Instruments, Corvallis, Ore.). 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 mass was calculated by dividing the dry mass of each disk by the disk area. Because the drought treatments resulted in leaf desiccation and/or abscission, leaves (including
petioles) were removed from the plants and arbitrarily designated as viable or nonviable. Individual leaves that had not abscised and had 50% or more of their tissue undamaged were considered viable. The remaining leaves were classified as nonviable. 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 mass of viable leaves, stems, and roots was determined after the material was dried for 2 to 3 d at 67 °C. The ratio of leaf surface area : root dry mass was calculated. Net assimilation rate and relative growth rate were determined for each treatment during each phase (Harper, 1977).

There were four single-plant replications (experimental units) within each harvest × 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 differences between treatment means at \( P < 0.05 \) were considered significant. 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**

Katsura trees avoid drought stress by the mechanism of drought-induced leaf abscission. The relationship between soil moisture content and \( \psi_{pd} \) was described by using DeltaGraph® 4.0 (DeltaPoint, Inc., Monterey, Calif.) as the equation: \( \psi_{pd} = (\text{soil moisture content}^{8976})(0.09255) \); \( R^2 = 0.645 \). At soil moisture contents of 0.16 m\(^3\)·m\(^{-3}\) or higher, leaves did not abscise, but as soil moisture content decreased below 0.16 m\(^3\)·m\(^{-3}\), percentage leaf abscission increased linearly [percentage leaf abscission = 0.802 - 4.35(soil moisture content)].
As drought severity increased, abscission of leaves progressed acropetally along shoots. During each drought phase, leaf dry mass and leaf surface area were reduced (Table 1). At the second harvest, leaf dry mass of plants in the drought treatments was 34% lower than among control plants. Following drought in the third phase, leaf dry mass of plants in the multiple drought treatment was 63% lower than among 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 hybrid poplar (Mazzoleni and Dickmann, 1988), and it was found that black walnut trees subjected to $\psi_{FD}$ of -1 and -2 MPa abscised ~35% and ~62% of their leaves, respectively (Pallardy and Rhoads, 1993). However, while soil moisture content values of .16 m$^3$·m$^{-3}$ induced leaf abscission in our study, values as low as 0.02 m$^3$·m$^{-3}$ did not induce leaf abscission in cultivars of Freeman maple (Acer xfreemanii E. Murray) (Zwack et al., 1998). Abscission is a principal defense a plant has 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. It is evident that abscission of dehydration-sensitive leaves decreased katsura tree's demand for water and increased the internal water content. After drought-induced leaf abscission, plants in the drought treatments at the conclusion of non-drought phases had higher values of soil moisture content than did the controls (Table 1). At the conclusion of the study, drought treatments had higher (less negative) $\psi_{FD}$ than controls (Table 1). Similarly, Ginter-Whitehouse and others (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 in the drought treatments, trees refoliated and leaf dry mass and leaf surface area increased (Table 1). At harvest five (22 to 24 d after removal from drought),
plants in the single-drought treatment had recovered 104% of their initial leaf dry mass and 96% of their initial leaf surface area. Black walnut also has been observed to refoliate 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 refoliation after abscission in black walnut and sugar maple, they found that the amount of new leaf area was inadequate to compensate for the amount of leaf area lost. Based upon our observations, the high degree of refoliation found in katsura was likely associated with the rapid increase in lateral branch development, although we did not quantify this. Defoliation has been found to stimulate the development of lateral branches in other trees, including a twofold increase in hybrid poplar (Populus × euroamericana '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 mass of plants in the drought treatments at the fourth and fifth harvests (Table 1). At harvest five, root dry mass of plants in the multiple- and single-drought treatments was 41% and 23% lower than control plants, respectively. Reduction in stem dry mass was observed in drought treatments (Table 1). At the final harvest, stem dry mass of multiple- and single-drought treatments was reduced by 30% and 17%, respectively. Drought reduced root elongation in white oak (Quercus alba L.) and post oak (Quercus stellata Wangenh.), and root elongation and stem dry mass in black walnut and red oak (Quercus rubra
Defoliation reduced root and stem dry mass in tuliptree (*Liriodendron tulipifera* L.) (Madgwick, 1975). The reduction in root and stem dry mass in katsura may have been due to both the decreased growth associated with a limited supply of water and decreased photosynthate due to leaf abscission.

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

During drought phases, net assimilation rate and relative growth rate of drought treatments were negative (Table 2). This was likely due to leaf abscission. During phases two and four, plants in all treatments had positive net assimilation rates that 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 control plants, indicating that during recovery, plants in the single-drought treatment were temporarily more efficient at assimilating carbon than were plants in the control treatment. 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 was not enhanced. 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). Similar to our observations of katsura trees recovering from drought, Madgwick (1975) found that the photosynthetic efficiency of leaves in tuliptree, expressed as unit leaf rate, increased with severity of defoliation, as did the rate of leaf production.

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. Drought reduced height growth in the drought treatments by ≈34% at the conclusion of the study; control, multiple-drought, and single-drought treatments had increased stem length by 43, 28 and 29 cm, respectively. After three weeks of severe drought, stem elongation of eastern cottonwood 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 stress interruption at the conclusion of the study led to a flush in height growth of ≈12 cm. In our study, 22 to 24 d of stress interruption resulted in an increase in height growth of only 1 cm. Differences among treatments in internode length and specific leaf mass were not observed.

Ludlow (1989) states that drought-induced leaf abscission reduces photosynthesis and leads to a slow recovery once stress is relieved. While it is true that leaf shedding likely reduced photosynthate, 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 katsura replaced 112% of its lost leaf dry mass 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 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 may be severe. In addition to the loss of photosynthate associated with leaf abscission, additional reductions in root dry mass, stem diameter and height may compromise the growth of trees. The elongation of short-shoot spurs into juvenile long shoots will likely temporarily decrease the sexual reproductive capacity of established trees, since flowers are only produced on the mature spur branches. The variability in growth habit (single- versus multistem) of katsura trees has been anecdotally associated with provenance and gender. 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 in mature trees is warranted. To date, there are no genotypes of katsura selected for resistance to drought or other forms of environmental stress. The identification and selection of drought-tolerant genotypes would strengthen the appeal of this ornamental landscape tree.

Literature Cited


Table 1. Soil moisture content, predawn leaf water potential, dry matter partitioning, leaf surface area (LSA), and LSA : root dry mass ratio of katsura trees (*Cercidiphyllum japonicum*) 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 treated with drought. Values are the means of 12 replicates.

<table>
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<th>Treatment</th>
<th>Irrigation phase</th>
<th>Soil moisture content (m³·m⁻³)</th>
<th>Predawn leaf water potential (-MPa)</th>
<th>Dry mass (g)</th>
<th>LSA</th>
<th>LSA : root dry mass ratio (cm²·g⁻¹)</th>
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<td>36.1 a</td>
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<td>42.4 a</td>
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<td>15.6 c</td>
<td>28.9 b</td>
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<td>35.5 b</td>
<td>81.2 b</td>
</tr>
</tbody>
</table>

*Means followed by the same letter are not significantly different (P < 0.05) within each harvest.*
Table 2. Net assimilation rate (NAR) and relative growth rate (RGR) of katsura trees (*Cercidiphyllum japonicum*) 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 treated with drought. Values are the means of six replicates.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Irrigation phase</th>
<th>NAR (μg·cm⁻²·day⁻¹)</th>
<th>RGR (mg·g⁻¹·day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Phase one</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>Hydrated</td>
<td>60 a²</td>
<td>5.6 a</td>
</tr>
<tr>
<td>Drought</td>
<td>Droughted</td>
<td>-97 b</td>
<td>-2.3 b</td>
</tr>
<tr>
<td><strong>Phase two</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>Hydrated</td>
<td>82 a</td>
<td>9.7 a</td>
</tr>
<tr>
<td>Drought</td>
<td>Hydrated</td>
<td>62 a</td>
<td>3.1 a</td>
</tr>
<tr>
<td><strong>Phase three</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>Hydrated</td>
<td>143 b</td>
<td>13.1 a</td>
</tr>
<tr>
<td>Multiple drought</td>
<td>Droughted</td>
<td>-144 c</td>
<td>-1.7 b</td>
</tr>
<tr>
<td>Single drought</td>
<td>Hydrated</td>
<td>257 a</td>
<td>18.7 a</td>
</tr>
<tr>
<td><strong>Phase four</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>Hydrated</td>
<td>198 a</td>
<td>13.7 a</td>
</tr>
<tr>
<td>Multiple drought</td>
<td>Hydrated</td>
<td>63 a</td>
<td>7.6 a</td>
</tr>
<tr>
<td>Single drought</td>
<td>Hydrated</td>
<td>115 a</td>
<td>10.1 a</td>
</tr>
</tbody>
</table>

*Means followed by the same letter are not significantly different (P < 0.05) within each phase.*
CHAPTER 3. STRATIFICATION AND LIGHT IMPROVE
GERMINATION OF KATSURA TREE SEED

A paper submitted to HortScience
Michael S. Dosmann, Jeffery K. Iles, and Mark P. Widrlechner

Additional index words. Cercidiphyllum japonicum, Cercidiphyllum magnificum, sexual
propagation, dormancy, woody landscape plants

Abstract. Recommendations for seed propagation of katsura tree (Cercidiphyllum spp.) vary,
and data that pertain to pretreatment and germination requirements of seed are lacking in the
literature. This study was designed to determine conditions for optimal seed germination of
Germinability of two half-sib seed sources of C. japonicum (accession numbers 1150-67 and
882 from the Arnold Arboretum of Harvard Univ.) and one seed source of C. magnificum was
determined after not stratifying or stratifying seeds at 3.5 ± 0.5 °C for 8 days and germinating
them at 25 °C in darkness or under a 15-hour photoperiod of 64 ± 8 μmol·m⁻²·s⁻¹
photosynthetically active radiation (PAR) for 21 days. Stratification was not required for
germination, but did increase germination percentage, peak value, and germination value for
both species. Stratification increased germination percentages of C. japonicum accessions
1150-67 and 882 from 41% to 90% and 43% to 60%, respectively, and germination percentage
of C. magnificum from 12% to 24%. PAR enhanced germination of unstratified seeds of
accession 882 of C. japonicum and of C. magnificum, increasing germination percentages
from 34% to 52% and 8% to 15%, respectively. Stratification improved germinability of both
species and obviated any preexisting PAR requirements the seeds may have had. We
recommend that katsura seeds be stratified for at least 8 days to improve germination.
Introduction

The genus *Cercidiphyllum* comprises two species, both known as katsura tree. Common katsura (*Cercidiphyllum japonicum*) is indigenous to China and Japan. The survival of the species is threatened in China, where it has been classified as rare (Chien, 1992). As a specimen tree, it is appreciated for its pyramidal to broadly spreading form, apricot-yellow autumn leaves, and slightly furrowed bark. Because of these and other attributes, it was selected as the 1997 Tree of the Year by the International Dendrology Society (Andrews, 1998). The second species, *Cercidiphyllum magnificum*, has a limited natural range and is native to isolated mountainous regions of Japan. Although this species is rarely produced in commercial nurseries, it has potential merit as a landscape tree (Lancaster, 1997).

*C. japonicum* can be propagated vegetatively by softwood cuttings (Dirr and Heuser, 1987), but commercial propagation is typically dependent on seed germination. Unfortunately, substantiated information about the pretreatment and germination requirements of katsura seed is scant; there is only a single report that the optimal air temperature range for seed germination of *C. japonicum* is from 21 to 25 °C (Rohde, 1977).

General recommendations for seed propagation vary. Dirr and Heuser (1987) stated that stratification is not required for germination. Yet, to achieve maximal germination, some nurseries sow seeds in spring after stratifying them for periods of up to 60 d (H. Kunkel, personal communication). Although not given a controlled stratification treatment, seed sown outdoors immediately after ripening in autumn germinates near capacity the following spring (D. Hinkley, personal communication). Other nurseries have found stratification unnecessary and sow seed outdoors directly in spring (M. Anderson, personal communication).

Effects of PAR on katsura seed germination are unknown. The seeds are small (=5 mm long in *C. japonicum* and =6 mm long in *C. magnificum*) with thin seed coats, characteristics associated with light sensitivity (Bewley and Black, 1982; Li et al., 1994). Because of these
morphological characters, we hypothesized that germination of katsura seed may be light sensitive.

Variations in seed pretreatment practiced by nurseries, in conjunction with the lack of data in the scientific literature, led us to study the requirements for optimal germination of seeds of these landscape trees. Our objectives were to determine the effects of stratification and PAR on germination of the two species of katsura, thereby providing information of potential value for commercial production.

**Materials and Methods**

*Cercidiphyllum japonicum*. On 26 Sept. 1996, we obtained ripened follicles from two open-pollinated *C. japonicum* trees located at the Arnold Arboretum of Harvard Univ. (Jamaica Plain, Mass.). These half-sib seed sources were identified by the accession numbers of the maternal parent trees, 1150-67 and 882. Upon receipt, we dried the follicles in shallow trays on a glasshouse bench for three weeks. After drying, seeds were shaken from the follicles, sealed in airtight plastic containers, and stored in darkness at 7 °C.

Treatments began on 2 Dec. 1996. We placed seeds (25 per dish) in 100 × 15 mm petri dishes (Fisherbrand, Pittsburgh) on one piece of germination paper (Anchor Paper, Hudson, Wis.) moistened with ~5.4 ml of deionized water. We stratified seeds in darkness at 3.5 ± 0.5 °C for 8 d in a ScienTemp programmable freezer (ScienTemp Corp., Adrian, Mich.). Temperature and duration of stratification were based upon preliminary research. After stratification, unstratified seeds were placed in dishes in the same manner as the stratified seeds.

Stratified and unstratified seeds were germinated within the same Sherer CEL-8 Growth Chamber (Conviron, Asheville, N.C.) at 25 °C (Rohde, 1977) with a photoperiod of 15 h or in complete darkness. Cool-white fluorescent lamps provided 64 ± 8 µmol·m⁻²·s⁻¹
PAR at dish level measured with a LI-COR quantum radiometer (LI-COR, Lincoln, Nebr.). We randomly arranged dishes on the same rack. To germinate seeds without PAR, we randomly placed dishes in light-tight containers. Throughout the study, we remoistened filter paper as needed with deionized water to prevent dehydration. Dishes in the dark treatment were opened only briefly to remoisten paper and count germinated seeds. We concluded the experiment after 21 d.

We computed germination percentage for each dish once daily. Germination was defined as the percentage of seeds that showed radical emergence, without correction for nonviable seeds. We computed peak value and germination value (Czabator, 1962). Peak value is an index of vigor and is obtained by dividing, for each day of measurement, the cumulative germination percentage by the number of days from the beginning of the germination test. The maximum daily value is defined as the peak value. Germination value is the product of peak value and the mean daily germination percentage, which is determined by dividing final germination percentage by the number of days for completion of germination. Germination value indicates both speed and totality of germination.

Our treatment design was a factorial arrangement of two accessions, two pregermination treatments, and two PAR treatments. Each treatment combination was replicated three times, and the entire experiment was done three times. Each dish was considered an experimental unit for statistical analysis. Data were analyzed with the Statistical Analysis System (SAS Institute, Cary, N.C.). Analyses of variance, performed with the General Linear Model (PROC GLM), were used to test the significance of accession, pregermination treatment, and PAR effects on germination percentage, peak value, and germination value. High-order interactions (replication over time × accession × pregermination treatment × photoperiod × within treatment replication) were included as a measure of
experimental error. Means were separated by using Fisher's least significant difference (LSD) test at $P \leq 0.05$.

*Cercidiphyllum magnificum.* On 16 Dec. 1996, we received *C. magnificum* seeds from the Forest Experimental Station of the Warsaw Agricultural Univ. Arboretum (Rogów, Poland). The seeds had been collected from four open-pollinated trees during the first half of Sept. 1996, dried, and kept in unsealed storage containers at temperatures that ranged from -3 to 10 °C. Upon receipt, we sealed the seeds in an airtight plastic container and stored them at 7 °C.

On 5 Mar. 1997, we began treatments on this species. Seed pretreatment and statistical analysis were the same as those for the first experiment, except that a fourth replication over time was added. Experimental error during analysis of variance included the interaction of replication over time × pregermination treatment × photoperiod × within treatment replication.

**Results**

*Cercidiphyllum japonicum.* Germination was complete 7 to 11 d after placing seeds in the growth chamber. Germination percentage, peak value, and germination value differed between accessions ($P > F = 0.0001$). Across all treatments for accessions 1150-67 and 882, germination was 65% and 51%, peak value was 13.1 and 10.4, and germination value was 168 and 92, respectively. An accession × pregermination treatment interaction existed for germination percentage, peak value, and germination value ($P > F = 0.0001$). For all three variables, stratification increased the response for accession 1150-67 to a greater degree than for accession 882 (Table 1). Germination percentage, peak value, and germination value for accession 1150-67 were unaffected by PAR. However, germination percentage and peak value were greater for unstratified seeds of accession 882 exposed to a 15-h photoperiod than for those germinated in darkness. The same interaction was not significant for germination value.
Germination percentage, peak value, and germination value for stratified seeds of accession 882 were unaffected by PAR (Table 1).

*Cercidiphyllum magnificum*. Seeds germinated in 8 to 11 d. Similar to *C. japonicum*, stratification affected germination percentage, peak value, and germination value ($P > F = 0.0001$). Germination percentages and peak values for stratified seeds were more than two and three times greater, respectively, than those for unstratified seeds germinated in darkness (Table 1). The germination value for stratified seeds was more than eight times that for unstratified seeds germinated in darkness. Germination percentage for unstratified seeds increased with irradiance, but peak value and germination value for the unstratified treatments were not different. Stratified seeds were unaffected by PAR (Table 1).

**Discussion**

Stratification was not required for germination of *Cercidiphyllum* spp., but prechilling seeds increased germination percentage, peak value, and germination value for both species. Likewise, PAR was not required for germination, yet germination percentage for unstratified seeds of *C. magnificum*, and germination percentage and peak value for unstratified seeds of accession 882 of *C. japonicum* increased when exposed to PAR.

The reduction or removal of PAR requirements by stratification has been observed in many taxa. It was demonstrated that neither stratification nor PAR were required for germination of seeds of *Paulownia tomentosa* (Thunb.) Steud., but that continuous irradiance improved germination of unstratified seeds when compared with seeds germinated in darkness (Carpenter and Smith, 1981). We observed similar responses in accession 882 of *C. japonicum* and in *C. magnificum*. By stratifying seeds for two weeks at 4 °C, percentage germination of *P. tomentosa* was improved to near capacity in both photoperiod treatments, indicating that PAR requirements of the seeds were removed by stratification (Carpenter and Smith, 1981). The speed of germination, expressed as peak value, was increased by
stratification for all seed sources and by PAR for unstratified seed of accession 882 of *C. japonicum*. Germination value was unaffected by PAR, yet was increased by approximately 530%, 156%, and 540% in *C. japonicum* accessions 1150-67 and 882, and *C. magnificum*, respectively, with stratification. This suggests that stratification is more important than irradiance in the germination of katsura seeds. Similar responses to stratification and irradiance have been observed in *Betula pubescens* Ehrh. (Black and Wareing, 1955), *Tsuga canadensis* (L.) Carr. (Stearns and Olsen, 1958), and *Pinus palustris* Mill. (McLemore and Hansbrough, 1970).

Although the seeds of *C. magnificum* were exposed to fluctuating temperatures before we received them, we speculate that this had little to no impact because the seeds had been dried. Had the seeds imbibed water during this period, dormancy may have been altered or removed (Bewley and Black, 1982).

We cannot fully explain the differences observed between the two accessions of *C. japonicum*. These differences may be due to unique circumstances of the two parent trees at the Arnold Arboretum, including provenance or microclimate (Bewley and Black, 1982). Variability in seed maturity and physiological status of the two accessions also may account for our observations. Our quantification of the differences may help to explain the variable methods used by industry to produce katsura from seed. Because individual trees may show variation in specific dormancy requirements, growers that propagate katsura from seed should monitor their seed sources carefully to maximize germination. We believe that additional study of the germinability of *C. magnificum* is warranted because our study produced maximum germination percentages that were less than 25%. Future investigations with a larger number of sources of known provenance also would be worthwhile and may help characterize the variability associated with geographic origin. It is unknown how germinability may be affected by stratification periods other than 8 d.
Propagators that germinate katsura seeds may find it beneficial to stratify seeds for a short period of time to improve germination. While our study did not test the effect of overwintering, seeds sown in the field during fall may have their dormancy requirements removed. Exposing the seeds to PAR is not necessary for germination, and does not improve germinability of stratified seeds.

Literature Cited


Table 1. Mean germination percentage, peak value, and germination value of *Cercidiphyllum japonicum* and *Cercidiphyllum magnificum* seeds unstratified or stratified at 3.5 ± 0.5 °C for 8 d and placed under complete darkness or a photoperiod of 15 h during germination. Values for *C. japonicum* and *C. magnificum* are the means of nine or 12 replicates, respectively.

<table>
<thead>
<tr>
<th>Seed source</th>
<th>C. japonicum (accession no.)</th>
<th>C. magnificum</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1150-67 882</td>
<td>1150-67 882</td>
</tr>
<tr>
<td>Pregeneration Photoperiod</td>
<td>Germination percentage¹</td>
<td>Peak value²</td>
</tr>
<tr>
<td>treatment</td>
<td>(h)</td>
<td></td>
</tr>
<tr>
<td>Unstratified</td>
<td>0</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>42</td>
</tr>
<tr>
<td>Stratified</td>
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<td>90</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>89</td>
</tr>
<tr>
<td>LSDw</td>
<td>10</td>
<td>2.3</td>
</tr>
</tbody>
</table>

¹Percentage of seeds showing radical emergence without correction for nonviable seeds.

²Unitless index of vigor; maximum daily value obtained by dividing cumulative germination percent by cumulative number of days of germination.

³Unitless indication of speed and totality of germination; product of peak value and mean daily germination percentage.

wFisher's least significant difference (LSD) within each dependent variable is at $P < 0.05$. 
CHAPTER 4. GENERAL CONCLUSIONS

My objectives for conducting this research project were twofold. One goal was to generate useful information by way of scientific experimentation. I wanted to fill some of the gaps in the literature on drought resistance and seed germinability of katsura. My intentions did not stop there, however. My second goal was to learn as much as possible about other aspects of this most interesting of trees including the katsura’s general history, landscape usage, taxonomy, and physiology.

I believe that the results obtained from the drought study establish that the common katsura avoids drought by shedding its leaves. This response was impressive to say the least. Each drought exposure resulted in a loss of approximately 30% of the leaf dry mass. While drought-induced leaf abscission abruptly decreased the transpirational water loss, it also likely decreased the amount of photosynthate. However, drought did not appear to have a lasting negative effect on net assimilation rate and relative growth rate, within the limited duration of our examination. After removal from drought, both rates were maintained at least at the rates associated with plants in the control treatment. The temporarily higher net assimilation rate may have lent itself to an enhanced capacity for refoliation. Within 24 days after being removed from drought, plants in the single-drought treatment had replaced 112% of the lost leaf dry mass.

Although trees refoliated after abscising leaves, drought still seriously reduced the growth of katsura trees. A single drought phase in our study reduced height growth and diameter by approximately 34% and 16%, respectively. If these responses occur similarly in the production of nursery stock, the effect could be noteworthy. Likewise, the increased production of juvenile shoots (due to refoliation) on young nursery-grown trees may result in stock with an abundance of lower stems and branches. While our research did not examine this effect specifically, the variability in habit and form of katsura trees may not necessarily be a
reflection of gender or provenance, as has been previously hypothesized, but of the interplay of
dimorphism and drought (or other circumstances resulting in the removal of apical dominance).
The selection of genetic material that responds less harshly to drought would help alleviate
these problems and likely increase the marketability of this tree. Until that time comes, I must
echo and reiterate the recommendations of so many and stress the importance of proper site
selection and/or management.

The investigation of katsura seed germinability also yielded useful information. Until
this study, there were not any published reports stating that germination of katsura seed was
affected by stratification and photosynthetically active radiation (PAR). Our results show that a
short period of stratification (8 days) improved germination of katsura seed, especially C.
japonicum. Furthermore, PAR improved germination of some unstratified seeds,
demonstrating the presence of light sensitivity. I believe that this information can be
incorporated into commercial seed-propagation practices without much difficulty and will
hopefully result in improved production of katsura.

In addition to the two research projects summarized above, I believe that my work has
contributed in some way to the promotion and improved recognition of Cercidiphyllum.
Furthermore, I believe that my association and communication with botanists, horticulturists,
plant enthusiasts and members of the nursery and landscape industries from around the globe
has led to a re-evaluation of katsura. Hopefully, in the future this tree can be the subject of
further scientific investigation, conservation, and broadened horticultural usage.
ACKNOWLEDGEMENTS

While the title page of this piece of work has but my name upon it, the whole product is the result of many. I can acknowledge only a few of the many below.

First and foremost, I heartily thank Dr. Jeff Iles, my major professor. For his guidance, his expertise, his candor, his friendship, I will always be grateful. I could not have asked for, nor received, any better. I also thank the other members of my graduate committee: Drs. Bill Graves, Mark Widrlechner and Don Farrar. Their advice and time dedicated to my program are sincerely appreciated.

Many faculty, staff, and graduate students helped make obtaining this degree possible (or at least more enjoyable). In particular, I acknowledge Dr. Kathleen Delate for the office accommodations, Lois Benning for the secretarial assistance, and Tony Aiello for miscellaneous help as I planned and executed these studies. For the late-night thesis sessions and the fishing, I thank Dr. Michael Kolomiets (Ukraine and molecular biology could not have a better ambassador). For the Scotch, the philosophy, and the friendship, I tip my hat to organic chemist Andrew Chubb. Dr. Dave Cox provided statistical advice and more, teaching me that, yes, 'speech is the short change of silence.' Drs. Mike Evans, Clint Hodges, Dick Gladon, and Brian Whipker are also to be acknowledged for their various inputs (most of them humorous). I also acknowledge Dr. Harrison Flint, who helped start me down this path at Purdue University and instilled in me the desire to become a plantsman.

Last, but not least, I owe a tremendous amount of gratitude to my family. Their support throughout my life has made the difference and I would not be here today if it were not for them. This work, in part, is theirs.