THE ROLE OF XYLEM SAP ABSCISIC ACID IN LEAF ABSCISSION OF DROUGHTED SEEDLINGS OF ISOHYDRIC AND ANISOHYDRIC TEMPERATE DECIDUOUS ANGIOSPERMS

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ABSTRACT.—Post-recovery patterns of leaf abscission were studied in relation to peak-drought xylem sap ABA concentration [ABA] for seedlings of five woody species [drought-sensitive, isohydric black walnut, black willow and eastern cottonwood, and drought-tolerant, anisohydric white oak and black oak]. The potential role of xylem sap [ABA] as a signal of the need for leaf area adjustment to reduce water loss was the object of study. Potted seedlings were allowed to deplete soil moisture and then were rewatered. At peak drought and during recovery, predawn and midday leaf water potential, and leaf abscission were measured. Xylem sap [ABA] was measured in well-watered and droughted seedlings before rewatering of the latter. Water potentials and xylem sap [ABA] recovered rapidly after rewatering. Long-term (six week) leaf abscission increased with water stress and xylem sap [ABA] measured at peak drought in isohydric species. However, anisohydric, drought tolerant oak species lost leaves only under severe water stress, although xylem sap [ABA] was elevated at peak drought. Xylem sap [ABA] may serve as a signal for leaf area adjustment in isohydric, but not anisohydric, species.

Introduction

While the recovery phase of leaf-level response to water stress is physiologically and ecologically significant, it has received far less attention than the period of developing water stress. The degree and rate of return of processes to pre-stress levels varies among species and can have a substantial impact on plant fitness (Quick and others 1992, Roe and others 1995). An important response to water stress that is often manifested after relief from water deficits is leaf senescence and abscission. Drought deciduousness is often linked with extreme environments, viz. deserts and Mediterranean regions (e.g., Addicott 1991, Kozlowski and others 1991), but also is obvious in certain species in temperate forests. Studies of black walnut (*Juglans nigra* L.), white oak (*Quercus alba* L.), post oak (*Q. stellata* Wangenh.), sugar maple (*Acer saccharum* Marsh.) and poplar (*Populus* spp.) (Parker and Pallardy 1985, Pallardy and Rhoads 1993, 1997) showed that post-drought leaf abscission is related to the peak level of plant water stress experienced. Additionally, field observations anecdotally suggest that drought-accelerated leaf abscission also occurs in other riparian species (e.g., willow (*Salix*), other poplars). While such abscission may be considered an effective avoidance mechanism (protecting critical meristem tissues in buds and cambium), it represents an obvious disadvantage for carbon gain and growth. These same taxa are characterized as light-demanding species and loss of leaf surface area would place them at a distinct competitive disadvantage in height growth capacity.

The concentration of xylem sap abscisic acid ([ABA]) in water-stressed woody plants often increases to very high levels (e.g., Loewenstein and Pallardy 1998a, b), suggesting that ABA from the roots might play a role in drought-induced senescence and abscission (when severe drought develops and very high ABA levels accumulate in xylem sap). While control of senescence and abscission is complex, involving actions and interactions of at least three plant hormones (ABA, ethylene and IAA) as well as plant developmental stage, there is a substantial body of literature showing that ABA plays an important role in these responses (reviewed by Nooden and Leopold 1988). Abscisic acid levels in leaves increase during senescence (Plummer and others 1991), and exogenous ABA promotes leaf senescence and

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Table 1.—Morphological characteristics (mean ± SE) of seedlings prior to initiating the experiments.

	height (cm)	diameter (mm)	number of leaves/leaflets
black willow	65.44 ± 2.16	3.31 ± 0.09	73.62 ± 4.65
cottonwood	40.47 ± 5.67	5.67 ± 0.13	28.62 ± 0.77
black walnut	22.75 ± 4.81	4.81 ± 0.10	41.07 ± 1.09
white oak	10.21 ± 0.64	2.75 ± 0.11	6.65 ± 0.56
black oak	37.27 ± 2.03	6.70 ± 0.18	22.34 ± 1.25

abscission (Plummer and others 1991, Suttle and Abrams 1993, Lin and others 1999). Although there have been a few reports of leaf abscission in plants in which xylem sap [ABA] has been elevated by water stress or introduction of exogenous ABA into the xylem stream (e.g., Chen and others 1997), there has been no study of the relationship between drought-induced elevation in xylem sap [ABA] levels and subsequent senescence/abscission responses of woody plants. Here we report on species variation in xylem sap ABA levels under drought as they relate to subsequent plant senescence/abscission responses, including both isohydric and anisohydric species (*sensu* Tardieu 1996). Isohydric species must maintain relatively high plant water potential (ψ) to avoid injury during drought while anisohydric plants exhibit substantial depression of ψ during drought without lasting impairment.

Methods and Materials

Plant Materials

Black walnut, black oak and white oak seeds from open-grown trees were obtained from the Missouri State Tree Nursery (Licking, MO, U. S. A.). Hardwood cuttings were collected from black willow (*Salix nigra* Marsh.) and eastern cottonwood (*Populus deltoides* Bartr. ex Marsh) trees near Columbia, MO, U. S. A. (38° N lat., 92° W long). Black willow, eastern cottonwood and black walnut are typically found in riparian habitats, are drought-sensitive, and exhibit isohydric patterns of water relations; white and black oaks are abundant in more xeric habitats, are more drought tolerant, and are anisohydric (Bahari and others 1985, Burns and Honkala 1990, Loewenstein and Pallardy 1998a,b). Seeds and cuttings were planted in 2.5 L (10.5-cm diameter) plastic pots containing a 2:1:1 mixture of sand, peat moss, and silt-loam soil. A top-dressing of slow-release fertilizer (14-14-14 N, P, K, Osmocote, Sierra Chemical Co., San Milpitas, CA, U.S.A.) was applied soon after plants were established and modified half-strength Hoagland's solution was applied approximately every two weeks. Plants were grown in an evaporation-cooled greenhouse under 50% shade. Photoperiod was extended to 14 h with sodium vapor lamps during short-day periods of the year. Experiments were conducted separately for each species and were initiated when plants were three to six months old.

Experimental Procedure

Prior to beginning treatments the height, diameter and number of leaves of all plants was determined (Table 1). Eighty-one plants per species were randomly assigned to either a drought treatment (D, n=24), a drought with recovery treatment (R, n=42) or a well-watered control (W, n=15) and then plants were randomly arranged on a greenhouse bench. Drought was imposed on plants in treatments D and R by withholding water. Plants were randomly selected from all three treatments throughout the dry-down period for assessment of predawn and midday leaf water potentials (ψ_{pd} and ψ_{md}, respectively) and midday stomatal conductance (g_s). Water potential of one leaf per plant was estimated before dawn and at midday with a pressure chamber (Pallardy and others 1991) and g_s was measured with a steady-state porometer (LI-1600, LI-COR, Inc., Lincoln, NE, U.S.A.) Upon completion of these measurements, plants selected for that sample day from treatment R were reirrigated and leaf abscission was monitored for six weeks. Xylem sap was collected for determination of xylem sap [ABA] from the D and W plants. (As collection of xylem sap involves excising the shoot, [ABA] data could not be gathered for the plants which were monitored for leaf abscission.) A total of 42 plants per species were monitored for leaf abscission over the six-week recovery period. Total length of soil drying ranged from 5 days (eastern cottonwood), 1 week (black willow), 2 weeks (black oak), 4 weeks (black walnut) to 6 weeks (white oak). The experiment was conducted over a two year period (1997-1998) at times of the year that varied from March to August. Leaf area was measured with a LI-3000 Leaf Area Meter fitted with a belt conveyor (LI-COR, Inc. Lincoln, NE, U. S. A.). A spot of water-based paint was placed on each leaf (with different colors for neighboring plants) to facilitate monitoring of leaf abscission. The paint had no obvious adverse effect on the leaves.

Analysis of ABA

Concentration of ABA in the xylem sap was determined by enzyme-linked immunoassay (ELISA) (Sigma, St. Louis, U.S.A.) (Loewenstein and Pallardy 1998a). Dilution/spike recovery tests (Jones 1987) indicated the presence of nonspecific interference in the sap of all five species. Lyophilization sufficiently reduced this interference that quantification of ABA in samples was possible (Loewenstein and Pallardy 1998a). Lyophilized samples were reconstituted with 25 mM Tris buffered saline adjusted to pH 7.5 with reagent-grade HCl. All samples were run in duplicate and ABA standards were included, in triplicate, in each assay for the construction of a standard curve.

Statistical Analysis

Species variation in daily water potential and g_s data obtained during recovery from water stress were subjected to analysis of variance. Relationships between leaf abscission and peak drought ψ_{pd} and xylem sap [ABA] were subjected to analysis using Pearson correlation coefficients calculated separately for each species.

Results

Water Potentials and Stomatal Conductance

In general, ψ_{pd} and ψ_{md} recovered rapidly after water-stressed plants were provided moist soil (data not shown, see Loewenstein and Pallardy 2002). Predawn ψ_l of water-stressed plants recovered to at least control levels within one day of rewatering for all five species. Further, significant over-recovery of ψ_{pd} was observed for rewatered black willow and eastern cottonwood plants on Day 1. Mean ψ_{pd} of rewatered black oak plants on Day 1 was somewhat lower than that of control plants (-0.32 MPa vs. -0.18 MPa, respectively), but the difference was not statistically significant in this species. For all species, recovery of g_s was somewhat more delayed after rewatering than was that of ψ, but there were no significant differences in g_s between previously droughted and well-watered plants by the second day after rewatering had begun.

Leaf Responses to Water Stress and Its Relief

While water stress generally induced some leaf abscission in all species, in black willow and eastern cottonwood severe water stress also resulted in retention of necrotic leaves. Water stress, if severe enough, may overtake and prohibit the carefully coordinated program of senescence leading to abscission (Dangl and others 2000). As these leaves are not functional, they are collectively referred to hereafter as "abscised." True abscission occurred only after plants had been rewatered. In the isohydric riparian species leaf abscission measured after 6 weeks at high soil moisture generally increased monotonically as the minimum ψ_{pd} to which the plant had been exposed declined (Figs. 1-3). Abscission commenced at relatively high ψ_{pd} values (> -0.5 MPa), especially in eastern cottonwood and black willow. Isohydric black walnut plants reached minimum ψ_{pd} values that were somewhat higher and lost proportionally less leaf area after 6 weeks compared to other species (cf Fig. 3 with Figs. 1 and 2). However, the relationship between leaf area loss and ψ_{pd} was still statistically significant ($r=0.62$, $p < 0.01$) in black walnut. In contrast with isohydric species, leaf abscission of black oak seedlings occurred only after ψ_{pd} had declined to -5 MPa or less (Fig. 4). There was no detectable pattern of leaf abscission in response to ψ_{pd} in white oak seedlings over the range of water stress induced in the experiment (minimum ψ_{pd} -3.6 MPa), and some seedlings exhibited abscission that appeared unrelated to water stress (Fig. 5). For example, a plant which exhibited ψ_{pd} of -0.65 MPa lost 75 percent of its leaves while one subjected to ψ_{pd} less than -3.4 MPa lost only one of 16 leaves (data not shown). Shoot die-back occurred in severely stressed black willow and, to a lesser degree, in eastern cottonwood plants.

The relationship between ψ_{pd} and leaf loss in black willow and eastern cottonwood depended on the time at which observations were made after rewatering. In these species, at ψ_{pd} values indicative of mild- to moderate water stress (>-1 MPa), leaf loss measured two weeks after rewatering was

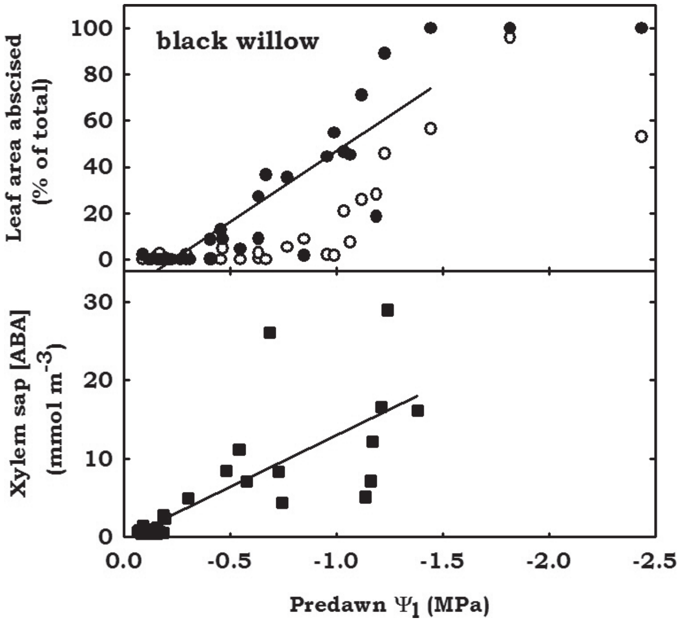

Figure 1.—Relationship between percent leaf abscission (top panel) and xylem sap ABA concentration (bottom panel) and minimum predawn leaf water potential developed during drought in black willow seedlings. Abscission and xylem [ABA] relationships were constructed from different sets of seedlings. (∘)—Leaf abscission after two weeks at high soil moisture; (•)—Leaf abscission after six weeks at high soil moisture. Linear regression line relationships between 6-week abscission and xylem sap [ABA] and ψ_{pd} are statistically significant ($p<0.05$). Mean total leaf area (abscised and retained leaves) after six weeks at high soil moisture was 545.7±22.1(SE) cm^2.

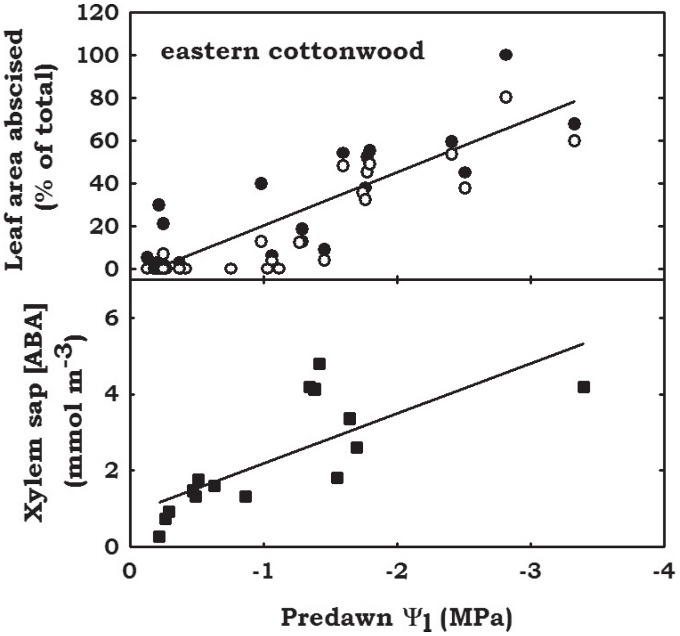

Figure 2.—Relationship between percent leaf abscission (top panel) and xylem sap ABA concentration (bottom panel) and minimum predawn leaf water potential developed during drought in eastern cottonwood seedlings. Abscission and xylem [ABA] relationships were constructed from different sets of seedlings. (∘)—Leaf abscission after two weeks at high soil moisture; (•)—Leaf abscission after six weeks at high soil moisture. Linear regression line relationships between 6-week abscission and xylem sap [ABA] and ψ_{pd} are statistically significant ($p<0.05$). Mean total leaf area (abscised and retained leaves) after six weeks at high soil moisture was 1106.2±29.4(SE) cm^2. Inset illustrates leaf abscission at high ψ_{pd}.

substantially less than that after six weeks (Figs. 1 and 2). Under more severe water stress (ψ_{pd} <-1 MPa), leaf loss in both species (including dead leaves that remained attached) was more rapid.

Xylem Sap ABA and Leaf Abscission

Because sampling for xylem sap [ABA] required sacrifice of the shoot, the response to water stress of this variable and leaf abscission was measured in different groups of plants. The relationships between xylem sap [ABA] and leaf abscission were thus examined by plotting both of them against measured ψ_{pd} (Figs. 1-5).

In the isohydric riparian species, which were more prone to drought-induced leaf abscission, xylem sap [ABA] and leaf loss after six weeks at high soil moisture both increased with decreasing ψ_{pd}. In black willow, black walnut and eastern cottonwood, leaf loss measured at six weeks and [ABA] were significantly correlated with predawn ψ ($r=0.60-0.84$; $p<0.01$). However, short-term (2-week) observations indicated that early leaf abscission in these species was not as well correlated with ψ_{pd} (or xylem sap [ABA]) (Figs. 1-3). The situation in the oaks was quite different. In both oak species, xylem sap [ABA] increased progressively with decreasing ψ_{pd}, but there was no leaf abscission even as xylem sap [ABA] increased to very high levels (Fig. 4, 5). The inability to express sufficient sap for analysis at the very low levels of ψ associated with abscission in black oak precluded inspection of xylem sap [ABA]-leaf abscission relationships in this region.

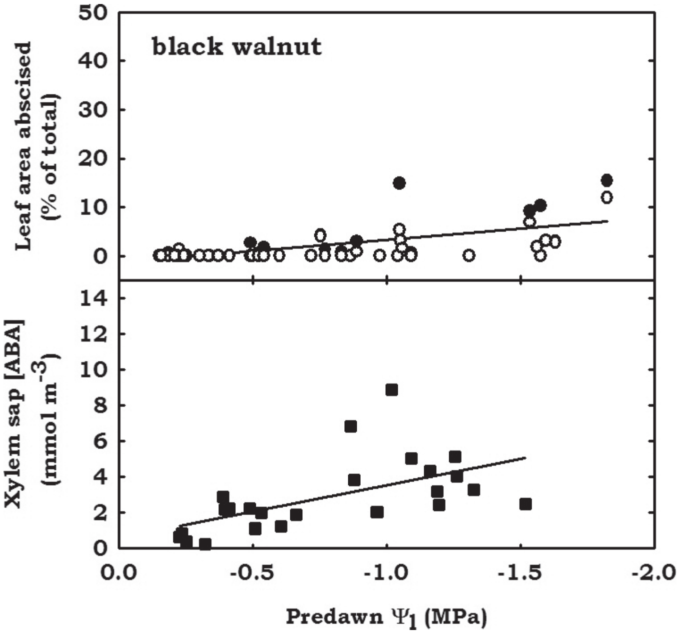

Figure 3.—Relationship between percent leaf abscission (top panel) and xylem sap ABA concentration (bottom panel) and minimum predawn leaf water potential developed during drought in black walnut seedlings. Abscission and xylem [ABA] relationships were constructed from different sets of seedlings. (◦)—Leaf abscission after two weeks at high soil moisture; (•)—Leaf abscission after six weeks at high soil moisture. Linear regression line relationships between 6-week abscission and xylem sap [ABA] and ψ_{pd} are statistically significant ($p<0.05$). Mean total leaf area (abscised and retained leaves) after six weeks at high soil moisture was 1069.0±37.1(SE) cm^2.

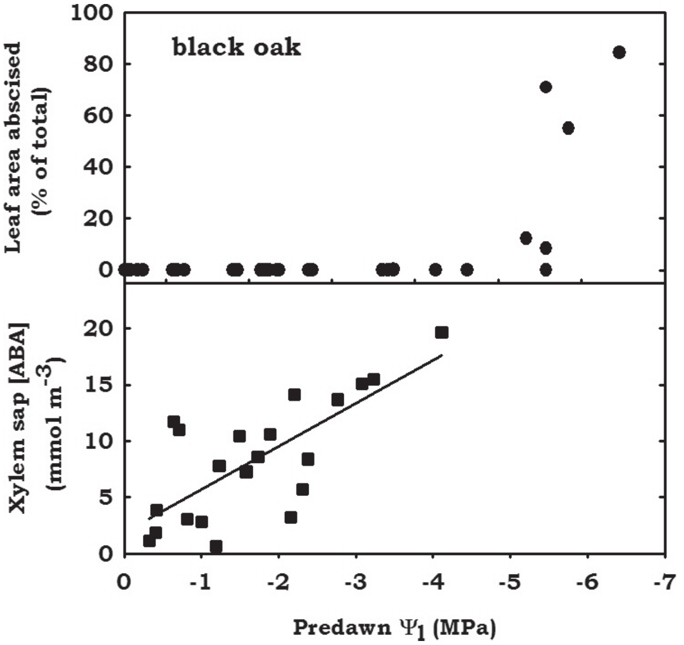

Figure4.—Relationship between percent leaf abscission (top panel) and xylem sap ABA concentration (bottom panel) and minimum predawn leaf water potential developed during drought in black oak seedlings. Abscission and xylem [ABA] relationships were constructed from different sets of seedlings. Linear regression line relationship between xylem sap [ABA] and ψ_{pd} is statistically significant ($p<0.05$). Mean total leaf area (abscised and retained leaves) after six weeks at high soil moisture was 1704.2±69.8(SE) cm^2.

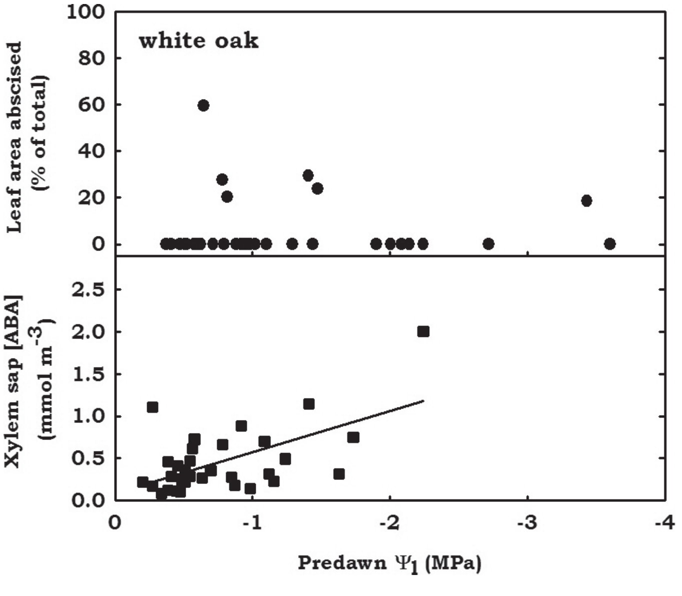

Figure 5.—Relationship between percent leaf abscission (top panel) and xylem sap ABA concentration (bottom panel) and minimum predawn leaf water potential developed during drought in white oak seedlings. Abscission and xylem [ABA] relationships were constructed from different sets of seedlings. Linear regression line relationship between xylem sap [ABA] and ψ_{pd} is statistically significant ($p<0.05$). Mean total leaf area (abscised and retained leaves) after six weeks at high soil moisture was 177.7±9.0(SE) cm^2.

Discussion

Two consistent, contrasting patterns of leaf abscission response to water stress were exhibited. In isohydric riparian species, a progressive increase in abscission was observed as water deficits exceeded mild levels (ψ_{pd}<-0.5 MPa). In contrast, there was very little leaf abscission in anisohydric oak seedlings unless water deficits were quite severe. The current and future carbon costs of leaf loss in the isohydric, riparian species may be one reason why they are restricted to habitats where abscission-inducing levels of water deficits are less frequent. On the other hand, the likelihood that most terrestrial habitats, even riparian ones, will experience severe soil water deficits at some point during the relatively long life of a forest tree suggests that the leaf abscission (and its consequent preservation of meristem hydration) protects tissues that are vital to long-term survival. Meteorological droughts are both frequently punctuated by sporadic rainfall and self-reinforcing (Dirmeyer 1994, Dole 2000); hence, abscission responses of temporarily rehydrated plants to a developing drought prepare the plant for the higher likelihood of prolonged soil moisture deficits.

The relationship between abscission and xylem sap [ABA] depended on species and time after rewatering had been resumed. In riparian species, the patterns of increase in abscission and xylem [ABA] with decreasing ψ_{pd} were similar if long-term (six week) leaf loss was considered. However, when abscission was assessed two weeks after rewatering, it was poorly correlated with both ψ_{pd} and xylem [ABA] unless water stress was severe. The delay in abscission in moderately-stressed plants is not altogether surprising because, once initiated, the orderly cellular disassembly of senescence which terminates in leaf abscission can be an extended process (Becker and Apel 1993). Under severe stress, leaves were prone to die before completion of senescence (Dangl and others 2000) but were here classified as functionally "abscised" even though they were still attached to the plant. In anisohydric oak species leaf abscission was lacking at all but the most severe levels of water stress, although xylem [ABA] increased linearly with declining ψ_{pd}.

The responses shown in the present study suggest that in isohydric species xylem sap [ABA] could serve as a signal of water stress severity and the degree of leaf area adjustment required. Xylem feeding or spray applications of ABA accelerate leaf and fruit abscission in numerous species, although the exact mechanism has not been determined. Abscisic acid induces senescence-related genes in daylily (*Hemerocallis* hybrid cv. 'Stella D'Oro') petals and detached leaves of *Arabidopsis thaliana* (Park and others 1998) and has a weak, but detectable, influence on a protease regulatory subunit that is upregulated during leaf senescence in *Arabidopsis* (Nakashima and others 1997, Kitsaki and others 1999). Exogenous ABA also reduced levels of free-radical scavenging enzymes in detached, senescing rice leaves (Lin and others 1999). In anisohydric species such as upland oaks, leaf abscission is apparently unresponsive to xylem [ABA] except, perhaps, at a threshold value indicative of severe water stress.

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