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Photosynthesis and Shoot Health of Five Birch and Four Alder Taxa After Drought and Flooding[1]

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Abstract

Selection of under-used taxa of birches (*Betula* L.) and alders (*Alnus* Miller) for use in managed landscapes can be guided by information on their responses to moisture extremes in the root zone. Our objective was to compare the photosynthesis, leaf surface area, and subjective health ratings of eight relatively obscure birches and alders when treated with drought and flooding in a greenhouse. We also treated 'Whitespire Sr.' birch (*Betula populifolia*) to demonstrate responses of a cultivar common in the nursery trade. Plants used as controls were irrigated daily, whereas pots of flooded plants were immersed. All water was withheld from the drought-treated taxon that showed the least evapotranspiration each day, while amounts of water less than that lost to evapotranspiration each day were added to plants of the other taxa subjected to drought. After three cycles of drought that induced wilting and a reduction in photosynthetic rate, leaf surface area of *A. hirsuta* had decreased the least, 12%, among the alders. While drought reduced the photosynthesis of all birches during the study, mean photosynthetic rate of drought-treated *B. uber* was higher than that of *B. albosinensis* and *B. davurica* subjected to drought. Flooding for 7 days did not influence photosynthetic rate of any alder but reduced photosynthesis of all the birches except *B. davurica*. After 21 days of flooding, only plants of *B. albosinensis* and *B. costata* were killed, and *A. maritima* was the only alder that fully sustained photosynthesis. While our data support the idea that most alders and birches are adapted to wet and well-drained sites, respectively, responses to drought varied among the four alders, and the four uncommon birches we grew responded differently to flooding. Specifically, additional evaluations under field conditions should be done to confirm the resilience of *A. hirsuta* and *A. maritima* to recurrent drought and to verify whether the comparatively promising (*B. davurica* and *B. uber*) and poor (*B. albosinensis* and *B. costata*) flood resistance we observed among the birches is meaningful in the landscape.

Index words: tree physiology, germplasm evaluation, stress.

Species used in this study: *Alnus hirsuta* (Spach.) Turcz. ex Rupr. (Manchurian alder), *Alnus incana* (L.) Moench subsp. *tenuifolia* (Nutt.) Breitung (white alder), *Alnus japonica* (Thunb.) Steud. (Japanese alder), *Alnus maritima* (Marshall) Muhl. ex Nutt. (seaside alder), *Betula albosinensis* Burkill (Chinese red birch), *Betula costata* Trautv. (Amur birch), *Betula davurica* Pall. (Asian black birch), *Betula uber* (Ashe) Fernald (Virginia round-leaf birch), *Betula populifolia* Marshall (gray birch) 'Whitespire Sr.'

Significance to the Nursery Industry

Trees that thrive after installation in managed landscapes commonly tolerate or avoid stresses caused by extremely dry or wet soil. Primarily because of moisture extremes in the root zone, only a small number of taxa are recommended for the harshest sites, such as those along city streets. Frequent use of a few taxa raises concerns about overuse and the consequences of limited diversity. The nursery industry and the consumers it serves will benefit from an improved understanding of drought and flood resistance of less common species with horticultural merit. We focused on eight such species in the family Betulaceae and have demonstrated differences among their responses to root-zone inundation and moisture deficit under conditions in a greenhouse. These initial data provide a basis for further research on responses of these taxa to stressors in the field and for identifying promising germplasm for breeding and selection.

Introduction

About 60 species of alders (*Alnus* Miller) and birches (*Betula* L.) are native to temperate, boreal, and arctic regions of the Northern Hemisphere, with a few species also found in high elevations in Central and South America and subtropical Asia (5). Although these diverse trees and shrubs of the Betulaceae inhabit a wide range of habitats and have many attractive characteristics, relatively few are commonly cultivated in North American nurseries and landscapes (2, 4).

Alders form symbioses with *Frankia* Brunchorst, an actinomycete that fixes atmospheric nitrogen (5). This rare trait, combined with the capacity of many alders to tolerate poorly aerated or flooded soils, indicates that this genus should be investigated as a source of trees tolerant to the infertile soils and inadequate drainage of urban landscapes. Their moderate size, rapid rate of development, fine texture, and the winter interest of their strobili are also horticultural attributes. A few birch species, such as river birch (*Betula nigra* L.), paper birch (*Betula papyrifera* Marshall), and European white birch (*Betula pendula* Roth), are widely cultivated for their striking bark characteristics. Other birches also have very attractive bark in a wide range of colors and textures or display attractive leaf color during autumn (2). The natural habitats of birches range from rocky or sandy, well-drained sites to peat bogs and marshes (5), indicating a wide range of tolerances to inundation and drought. Given the ornamental potential of this genus, surprisingly few birches are widely

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used, in part because of the potential for plants of many species to be attacked by bronze birch borer (*Agrilus anxius* Gory) (6).

Birch species commonly cultivated in North America vary widely in their responses to flooded soils (7). Alders generally are recommended for use on wet soils (4), but their responses to long-term root-zone inundation is unclear. Although many birches thrive on well-drained soils, their responses to drought have received little formal attention; likewise, the drought tolerance of most alders is poorly understood. Therefore, our objective was to screen eight relatively uncommon alder and birch species for their responses to drought and flooding by comparing the photosynthetic rates of young plants held in containers subjected to three moisture regimens. We also measured leaf surface areas and subjectively rated the overall health of plants at the end of the moisture treatments. A widely grown birch (*Betula populifolia* Marshall 'Whitespire Sr.') (9) was included in the study to demonstrate responses of a cultivar common in the nursery trade.

Materials and Methods

Plants of 11 accessions representing the nine taxa were propagated from seed, stem cuttings, or tissue culture (Table 1). Taxa produced from seed and stem cuttings were propagated in 1999, potted, held in a greenhouse, overwintered in coolers, and treated in 2000. Propagules of *B. populifolia* 'Whitespire Sr.' were obtained in 2000. All plants were grown singly in 700 cm^3 (43 in^3) of field soil:sphagnum peat moss:perlite (1:3:1 by vol) in plastic containers with a top diameter of 15 cm (6 in). For seven taxa, we began with 24 plants from one accession per taxon. For *A. japonica* and *A. maritima*, two accessions were combined to create a population of 24 plants per taxon (Table 1). Three plants of each taxon chosen randomly were harvested destructively on the day treatments began to assess differences in initial size among the taxa. Mean shoot dry weight when irrigation treatments began on June 21, 2000, ranged from 2.6 g for *Betula uber* to 18.0 g for *Alnus hirsuta* (Table 2). Seven additional plants of each taxon were selected and assigned randomly to each of three moisture treatments: drought, flooding, and control. Plants were arranged in a completely randomized design in a glass-glazed greenhouse where a data logger recorded air temperature and photosynthetically active radiation (*PAR*) every 15 min. Mean daily minimum and maximum air temperatures during the treatment period were 22 and 30C (72 and 86F), respectively. Supplemental irradiance was not used, and mean *PAR* during the middle of the photoperiod was 619 mmol·s^{-1}·m^{-2} (range = 460–843 mmol·s^{-1}·m^{-2}).

Tap water was applied once daily to saturate the root zones of plants in the control treatment. Root zones of flooded plants were immersed continuously in tap water by preventing drainage from their pots. Drought was imposed by withholding irrigation through three drought cycles. The cycles were separated by irrigation of all plants, including those in the control and flood treatments, to container capacity with water to which N at 10.8 mol·m^{-3} (150 ppm) was added from Peters Excel All-Purpose 21N–5P_2O_5–20K_2O and Peters Excel Cal-Mag Special 15N–5P_2O_5–15K_2O (Scotts, Marietta, GA). All subsequent fertilizations were done with these materials, in which about 63% of the N was from the Cal-Mag Special

Table 1. Accession, origin, and mode of propagation of four *Alnus* and five *Betula* taxa evaluated for responses to root-zone inundation and deficit irrigation. Plants of two accessions each of *Alnus japonica* and *Alnus maritima* were combined to equal the number of plants used for the other taxa. In these cases, plants of the two accessions were randomly assigned in the same proportion among the three irrigation treatments.

Taxon	Accession[z]	Origin	Mode of propagation
Alnus			
hirsuta (Spach.) Turcz. ex Rupr.	PI 479294	Japan, Tokyo Univ. Furano Forest Arboretum,Yamabe, Furano-shi, Hokkaido	stem cuttings
incana (L.) Moench subsp. *tenuifolia* (Nutt.) Breitung	PI 495875	United States, Kremmling, Grand Co., CO	stem cuttings
japonica (Thunb.) Steud.	PI 479297 Ames 25022	Japan, 7 km east of Kushiro, Kushiro-shi, Hokkaido Russian Federation, Primorye	stem cuttings stem cuttings
maritima (Marshall) Muhl. ex Nutt.	DE 216 OK 13	Marshyhope Creek, Dorchester Co., MD Pennington Creek, Johnston Co., OK	seed seed
Betula			
albosinensis Burkill	Ames 23593	China, Ningxi Forest Bureau, Pu He Forest Station, near Lan Ni Hu, Ning Shan District, Shaanxi Province	seed
costata Trautv.	Ames 24086	China, along Yalu River, Changbai County, Jilin Province	seed
davurica Pall.	Ames 10079	China, Forest Botanical Garden, Renjiaqiao, Harbin, Heilongjiang Province	stem cuttings
uber (Ashe) Fernald	Ames 12981	United States, Virginia	stem cuttings
populifolia Marshall	'Whitespire Sr.'	United States, Univ. of Wisconsin Arboretum, Madison	microshoots

[z] Accession numbers prefixed by PI and Ames were supplied by the North Central Regional Plant Introduction Station, Ames, IA, and are conserved there as part of the U.S. National Plant Germplasm System. Accessions DE 216 and OK 13 were collected from the wild by J.A. Schrader of Iowa State Univ. 'Whitespire Sr.' was supplied by Knight Hollow Nursery, Inc., Middleton, WI.

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Table 2. Shoot weight when treatments began, total volume of water applied to the seven plants of each taxon subjected to drought, and leaf surface area and visual health score of plants as irrigation treatments ended. Values for initial shoot dry weight are means and (SE) of three replicates. Values for leaf area and health score are means of seven replicates. Means for leaf area followed by the same letter within rows are not different according to Fisher's least significant difference test at the 5% level. Means for health score followed by the same letter within rows are not different according to the Kruskal-Wallis test at the 5% level.

Taxon	Initial shoot dry weight (g)	Water applied during cycle (ml)			Leaf area by treatment (dm^2)			Health score by treatment[z]		
		one	two	three	drought	control	flood	drought	control	flood
Alnus										
hirsuta	18.0 (1.7)	9031	9226	7582	29.8a	34.0a	27.2a	4.3a	4.4a	3.7a
incana subsp. *tenuifolia*	14.2 (3.4)	4977	5273	4446	22.6b	35.0a	14.8b	3.6a	3.9a	2.8b
japonica	3.6 (0.7)	1034	1051	1306	9.8a	18.0a	13.6a	2.9a	3.4a	3.4a
maritima	3.3 (0.2)	1276	1898	2573	12.4b	18.0a	12.0b	3.7a	4.2a	3.6a
Betula										
albosinensis	13.2 (2.9)	4264	2434	2405	15.3a	23.8a	0.0b	3.1a	3.6a	1.4b
costata	4.7 (0.6)	32	0	0	3.2a	4.9a	0.0b	2.5a	2.5a	1.0b
davurica	6.0 (1.1)	963	614	1059	5.8a	10.6a	7.1a	2.9a	3.2a	2.2a
uber	2.6 (0.3)	347	788	843	6.0a	5.0a	1.4b	3.3a	2.9a	2.3a
populifolia 'Whitespire Sr.'	7.2 (1.8)	944	1625	1521	10.0a	16.3a	8.1a	3.6a	3.7a	3.1a

[z] Health of plants was subjectively rated by two evaluators whose ratings were averaged before analysis. A rating of 1 was ascribed to dead plants, and 5 was ascribed to plants that appeared in excellent health. Ratings of 4, 3, and 2 were ascribed to plants based on progressively poorer appearance of foliage due primarily to necrosis and chlorosis.

fertilizer. We wished to have drought-treated plants of all taxa exposed to similar, low percentages of root-zone water, and we sought to have these percentages achieved at similar rates for all taxa. Achieving these goals was complicated by differences in water use among taxa, which were due, in part, to the differences in the size of shoots (Table 2). We attempted to minimize differences in daily evapotranspiration rates among taxa, thereby treating plants of disparate size with similar percentages of moisture in the root zone. Water use was estimated by tracking the total weight of the seven replicates of each taxon in the drought treatment within all drought cycles. Decreases in weight were assumed to be due to evapotranspiration.

Evapotranspiration values for each taxon were determined once daily during drought cycles. The taxon that showed the lowest evapotranspiration served as a baseline for that day. Nothing further was done to the plants of that taxon. Tap water was added to the root zones of the other taxa in the drought treatment to replace the amount lost to evapotranspiration in excess of the baseline value. Additions of water were done by placing the seven drought-treated plants of a taxon in a tray that contained the specified amount of water. Plants were kept in the trays until all water was absorbed in the root zones via drainage holes in the pots. Absorption required 1 to 3 hours. Total volumes of water added during all drought cycles ranged from 32 to 25,839 ml (1.1 to 874 oz) (Table 2). Drought cycles were ended the first day when leaves of at least five of the nine taxa were wilted before a daily irrigation. Drought cycles 1, 2, and 3 each lasted 7 days. All plants were irrigated once daily to container capacity with tap water that contained fertilizer during a 7-day recovery period between cycles 1 and 2, but cycle 3 began the day after cycle 2 ended. Roots of flooded plants were inundated with water during the same cycles that irrigation was withheld from plants in the drought treatment. Flooded containers were drained during recovery periods between drought cycles, and all plants were irrigated during these periods with tap water that contained fertilizer.

Photosynthetic rate of the youngest fully expanded leaf on each plant was measured on the days cycles 1 and 3 ended by using a LI-COR 6400 Photosynthesis System (LI-COR, Lincoln, NE). Measurements were made before plants were irrigated for the day, and moisture content of the upper 6 cm of the root medium of each plant was measured with a model HH1 Theta Probe equipped with a model ML1 sensor (Delta-T Services, Cambridge, England). Health of shoot systems was subjectively rated on the day cycle 3 ended by two evaluators whose ratings were averaged before analysis. A rating of 1 was ascribed to dead plants, and 5 was ascribed to plants that appeared in excellent health. Ratings of 4, 3, and 2 were ascribed to plants based on progressively poorer appearance of foliage due primarily to necrosis and chlorosis. Health-rating data were analyzed and means were separated by the Kruskal-Wallis test at the 5% level of probability (1). All leaves of plants then were removed to determine the total leaf surface area of each plant by using a model 3100 area meter (LI-COR). Data on photosynthesis and leaf surface area were analyzed by analysis of variance for a completely randomized design. Each plant was considered an experimental unit. When F tests showed significant treatment effects, means were separated by using Fisher's least significant difference test at the 5% level.

Results and Discussion

Relative to the plants of the various taxa in the control treatments, drought reduced photosynthetic rates of *A. hirsuta*, *A. japonica*, *B. costata*, *B. populifolia* 'Whitespire Sr.', and *B. albosinensis* at the end of the first drought cycle (Fig. 1). Flooding did not influence photosynthesis of any alder after the first treatment cycle, but flooding did reduce mean photosynthetic rate of all the birches except *B. davurica*, relative to their respective control plants (Fig. 1). After the third drought cycle, *A. hirsuta* was the only alder that showed a drought-induced decrease in photosynthesis, and *A. maritima* was the only alder for which photosynthesis was unaffected by flooding (Fig. 1). Photosynthesis of all birches except *B. albosinensis* was reduced by drought, and photosynthesis of all birches decreased in response to flooding, relative to their respective control plants (Fig. 1). Leaf senescence of flooded

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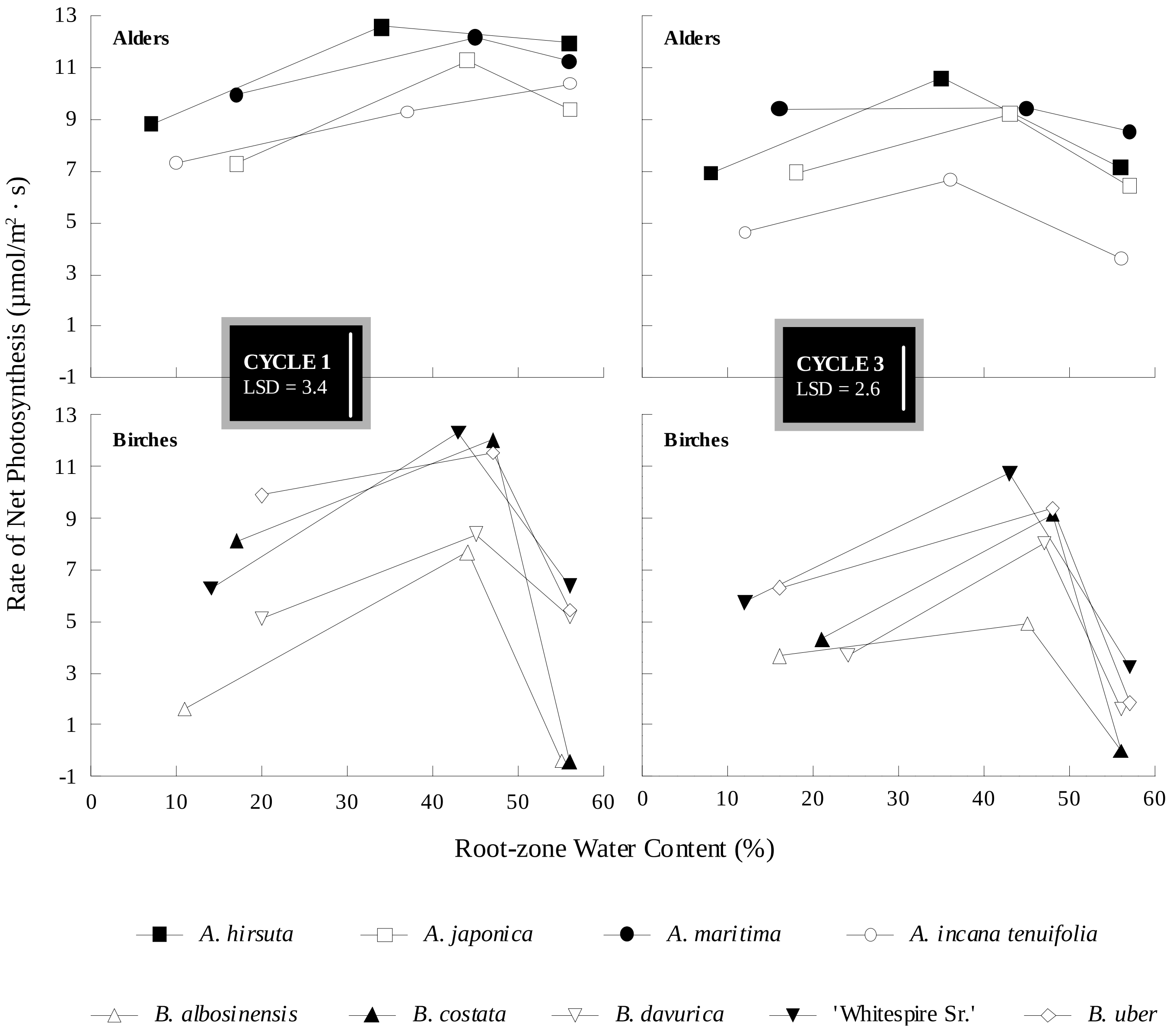

Fig. 1. **Rate of net photosynthesis of four species of *Alnus* and five taxa of *Betula* treated with drought and flooding. Additional plants were irrigated once daily as controls. Drought was imposed by withholding irrigation from potted plants until the end of a drought cycle, which was defined as the first day when at least five of the nine taxa showed wilted leaves. Three drought cycles were imposed; photosynthesis and the root-zone moisture content of each plant were measured at the end of the first and third cycles. Root zones of flooded plants were continuously immersed in water during the drought cycles. Each point is a mean of seven replicates. Within each line, the data point on the left, in the center, and on the right represent the mean for plants in the drought, control, and flood treatments, respectively. Vertical bars represent Fisher's least significant difference values (5% level) for comparing any two means within cycles.**

B. albosinensis and *B. costata* was evident after 3 d, and all flooded plants of these species died during treatment. All flooded plants of the other taxa survived, but leaf area of *A. incana* subsp. *tenuifolia*, *A. maritima*, and *B. uber*, and subjective visual health score of *A. incana* subsp. *tenuifolia*, were reduced from those of the respective control plants (Table 2). Leaf area was reduced by drought for plants of *A. incana* subsp. *tenuifolia* and *A. maritima* only, yet the health scores of all taxa were similar for control and drought-treated plants (Table 2).

The data on photosynthesis should be considered with regard to the differences among control plants of the various taxa that existed after both cycles 1 and 3. These differences affect how the data on drought and flooding effects should be interpreted. For example, while *B. albosinensis* was the only birch that showed fully sustained photosynthesis after three cycles of drought, mean photosynthetic rate of control plants of this taxon was low at that stage of treatments (Fig. 1). Low rates among controls make the relevance of a lack of a drought-induced decrease in photosynthesis of this taxon unclear. Consideration also should be given to the differences among taxa in the root-zone water content at the time photosynthetic data were collected. Root zones of flooded plants contained 55 to 57% water regardless of taxon (Fig. 1), so data on photosynthesis among taxa can be compared easily. In contrast, water in the root zones of plants in the drought treatment ranged from 7 to 20% (cycle 1) and 8 to 24% (cycle 3) among taxa (Fig. 1). The mean rates of photosynthesis of

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~9 (cycle 1) and ~7 (cycle 3) µmol/m^2·s of *A. hirsuta* subjected to drought were particularly noteworthy considering that these plants had the driest root zones among all drought-treated plants (Fig. 1).

These data revealed several differences among the taxa under greenhouse conditions that, if confirmed in the field, could be significant to those who design and manage horticultural landscapes. Among the alders, *A. incana* subsp. *tenuifolia* was most sensitive to flooding. Drought reduced photosynthesis of this taxon, along with *A. hirsuta* and *A. japonica*, relative to their controls after cycle 3, but flooding reduced the health score of only *A. incana* subsp. *tenuifolia* (Table 2). Despite its sensitivity to flooding relative to the other alders, *A. incana* subsp. *tenuifolia* was quite tolerant of flooding compared to the birches and can be a useful ornamental where soils are wet (2). Although *A. incana* subsp. *tenuifolia* is native along the banks of streams (3), our results indicated it is more sensitive than other alders to complete inundation of the root zone. We have observed indigenous populations of *A. incana* subsp. *tenuifolia* along rapidly flowing streams in mountainous areas. Water near the roots of trees at such sites may be highly oxygenated, which may help to explain the sensitivity of the species to immersing roots in water that was not stirred during this experiment.

Our data on *A. maritima* showed that flooding curtailed shoot development but failed to reduce photosynthesis or cause shoots to appear damaged. Photosynthesis was unaffected by flooding for one treatment cycle only among plants of *A. maritima* (Fig. 1), and the health score of flooded plants of *A. maritima* also was sustained (Table 1). Because leaves lacked necrosis and did not abscise, we attributed the reduction in leaf area of flooded *A. maritima* (Table 1) to reduced growth. The relative insensitivity of photosynthesis of *A. maritima* to flooding was consistent with the ecology of this species. In its native habitats, *A. maritima* is found exclusively on saturated soils, most often in standing water (10).

All the birches were sensitive to flooding, but data on photosynthesis (Fig. 1), leaf area, and health score (Table 2), indicated that further screening of *B. davurica* and *B. uber* for superior flood resistance is warranted. Among the flooded birches, those two species sustained photosynthesis and responded similarly to the commercially important *B. populifolia* 'Whitespire Sr.' after the first cycle, while net photosynthesis of *B. albosinensis* and *B. costata* was <0 (Fig. 1). The same trends were apparent after cycle 3, but effects of flooding were more pronounced on all birches after that duration of treatment (Fig. 1). Use of *B. davurica* in managed landscapes has been rare, but the species appears to have potential at sites where *Betula nigra* L. thrives (4). Native on wet soils that flood periodically (2), *B. nigra* is more tolerant of flooding than are many other birches (11). Our data were consistent with the premise that *B. davurica*, like *B. nigra*, may be unusually well-adapted among birches for landscapes prone to episodes of flooding. Similarly, more extensive trials under field conditions are warranted to examine the potential for flood resistance of *B. uber*, a rare species native to a flood plain (2). The protection status of *B. uber* was relaxed by the U.S. Fish and Wildlife Service from endangered to threatened in December 1994. Mature trees remain less than 15 m (50') in height and may display vibrant yellow leaves in the autumn (2).

The drought resistance of *A. hirsuta* merits further attention. Plants of this taxon had drier root zones than did other taxa in the drought treatment (Fig. 1), yet drought-treated plants of *A. hirsuta* sustained photosynthesis and had only a 12% reduction in leaf area. In contrast, leaf area of the other three alder taxa was reduced 31 to 46% by drought (Table 2). Although drought reduced the photosynthesis of all birches during one or both cycles when it was measured (Fig. 1), the leaf area and health-score data were unaffected by drought for all birches (Table 2). While these results are promising, effects of drought on root systems, and responses of these taxa to drought under field conditions are not known. Possible direct effects of extended drought in the landscape and indirect effects on such properties as the capacity to overwinter or to resist pests and diseases should be investigated. The performance of *B. davurica* in dry soils may be superior to that of *B. nigra* (2). If so, the relative sensitivity of photosynthesis of *B. davurica* to drought (Fig. 1) indicates the drought resistance of all five of the birches we treated may surpass that of *B. nigra*. Mean photosynthetic rate of *B. uber* after three cycles of drought was similar to that of *B. populifolia* 'Whitespire Sr.', which is comparatively resistant to drought due to maintenance of turgor at low water potentials (8), and was higher than that of *B. albosinensis* and *B. davurica* (Fig. 1). Thus, while *B. albosinensis* and *B. davurica* may be quite sensitive to drought in the landscape, further evaluation of the drought resistance of *B. uber* may prove particularly useful.

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