Responses to Root-zone Water Content of Shrub Congeners from Eastern North America and Mediterranean California

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Abstract. Numerous genera of plants are distributed in both eastern North America and in portions of California with the dry summers of Mediterranean climates. We compared effects of flooding and drought on relative growth rate (RGR), photosynthesis, and biomass of seedlings of two genera, *Sambucus* L. and *Ptelea* L., with congeners in both regions. *Ptelea crenulata* Greene and *Sambucus nigra* ssp. *cerulea* (Raf.) R. Bolli from the San Francisco Bay area and *Ptelea trifoliata* L. and *Sambucus nigra* ssp. *canadensis* (L.) R. Bolli from mesic, deciduous forests in eastern North America were studied. Potted seedlings were subjected to six treatments, three extents of root-zone inundation and three severities of drought (irrigation when soil moisture by volume decreased to 5%, 10%, and 20%). After 5 weeks, deleterious effects of inundation were more pronounced among plants from the West than among their eastern congeners. For example, RGR of western and eastern *Sambucus* with completely inundated root zones was reduced 116% and 25%, respectively. All western and eastern *Ptelea* died when root zones were completely inundated, but inundating the lower half of the root zone killed all western plants but only reduced RGR among eastern plants. Photosynthesis of *Sambucus* from the West was lowest with complete inundation and was similar across the remaining treatments. In contrast, photosynthesis of eastern *Sambucus* was lowest during severe drought but otherwise similar. Photosynthesis of *Ptelea* was sensitive to both drought and flooding, and moderate root-zone water content led to the highest rates for both western and eastern plants. For both genera, maximal photosynthesis per unit leaf area was greater among western than eastern plants, but eastern plants had greater total leaf area and biomass. Root-to-shoot ratios of western *Sambucus* were greater than ratios of plants from the East after all treatments, whereas western *Ptelea* had greater root-to-shoot ratios than eastern *Ptelea* only under severe drought. Although comparative sensitivity to drought of plants from California and eastern North America varied in these genera, Mediterranean *Sambucus* and *Ptelea* both showed greater sensitivity to root-zone inundation than did their eastern congeners.

Numerous woody genera are distributed in both eastern North America and in portions of California with the dry summers of Mediterranean climates. Such genera may harbor substantial variation among congeners in response to soil water content. During drought, taxa from seasonally xeric habitats may maintain greater photosynthetic rates, allocate proportionally more photosynthates to root foraging, and survive at greater frequencies than their mesic counterparts (Abrams, 1990; Abrams et al., 1990; Baraloto et al., 2007; Chunyang et al., 2000; Kubiske and Abrams, 1992). Conversely, taxa restricted in

nature to mesic or seasonally flooded habitats may perform better after being planted at sites prone to flooding because of their capacities to maintain greater photosynthetic rates and to resist physiological stress in hypoxic soils (Baraloto et al., 2007; Keeley, 1979). Knowledge of variation in photosynthetic capacity, growth rate, and biomass accrual between congeners in Mediterranean California and the comparatively mesic eastern United States could enhance our ability to select the most suitable taxa for specific soil-moisture conditions in managed landscapes.

Shrubs and trees in the genera *Sambucus* and *Ptelea* are valued in horticultural landscapes. Members of the genus *Sambucus* produce showy clusters of white flowers followed by attractive fruits that attract wildlife and can be used for jellies and wines, whereas trees of *Ptelea* are shade-tolerant and display unusual fruits (Dirr, 1998). Congeners of *Sambucus* and *Ptelea* exist in eastern North America and in portions of California characterized by the dry summers

of Mediterranean climates. Because of morphological diversity across their distributions, taxonomic confusion persists within both genera, and various species and subspecies have been designated (Bailey, 1962; Bolli, 1994; Eriksson and Donoghue, 1997; Greene, 1906). *Sambucus nigra* ssp. *canadensis* (syn: *S. canadensis* L.) grows in damp, rich soils in much of eastern North America (Dirr, 1998), whereas *Sambucus nigra* ssp. *cerulea* (syns: *S. cerulea* Raf., *S. mexicana* Presl.) in the San Francisco Bay area grows in habitats ranging from upper riparian terraces to seasonally dry elderberry savannahs and chaparrals (Ackerly et al., 2002; Koch-Munz and Holyoak, 2008). *Ptelea trifoliata* inhabits moist understories in eastern North America (Dirr, 1998), whereas *Ptelea crenulata* grows in dry chaparrals and woodlands in California, where it is endemic (Corelli, 2005). For simplicity, we will refer to these taxa as eastern and western congeners.

The Mediterranean mesoclimate near the San Francisco Bay is characterized by an average annual precipitation of 25 to 75 cm, whereas the region from which we obtained germplasm of the eastern congeners (southern Wisconsin and southern Illinois for *Ptelea* and *Sambucus*, respectively) averages 80 to 120 cm of precipitation annually [Changnon, 2003; National Climatic Data Center (NCDC), 2012]. Temporal distribution of precipitation differs also. Habitats supporting the western congeners receive ≈ 1 cm of precipitation from June through September, whereas 30 to 40 cm of rain is typical during those 4 months where we collected germplasm farther east (NCDC, 2012). Such seasonality of precipitation may correspond to drought-adaptive characteristics of closely related woody taxa (Chunyang et al., 2000). The presence of congeners in these divergent habitats could be viewed as evidence for physiological divergence between the species, but the natural distributions of taxa are not necessarily predictive of their capacities to withstand stressors (Parolin et al., 2010; Schrader et al., 2005; Stewart et al., 2007). Therefore, we questioned whether the differences in precipitation in the habitats of the western and eastern congeners of the species of *Sambucus* and *Ptelea* we studied are predictive of their responses to dry and inundated root zones. Several traits suggest that eastern and western congeners of these genera have evolved to possess different degrees of drought resistance. Although the eastern congener of both genera has glabrous or nearly glabrous leaves, the western congener of *Sambucus* is pubescent on both the abaxial and adaxial foliar surfaces, and the western congener of *Ptelea* has adaxial pubescence (Corelli, 2005; Dirr, 1998). The western congener of *Ptelea* also has smaller leaves than its eastern counterpart. We tested the hypothesis that deleterious effects of inundation and drought are more pronounced among plants from western and eastern North America, respectively, compared with their congeners by measuring RGR, photosynthesis, and

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biomass accrual in response to different irrigation treatments in a common environment.

Materials and Methods

Fruits were collected from eastern and western congeners of *Sambucus* and *Ptelea* in Sept. 2009. Fruits of the western congener of *Ptelea* were collected in Contra Costa County, CA, from plants on a hilltop and absent of green leaves, consistent with drought-induced dormancy. Fruits of the western congener of *Sambucus* were collected in Alameda County, CA, from plants with green leaves in a dry ravine within a landscape characterized by undulating topography. The eastern congeners of *Ptelea* and *Sambucus* were collected from mesic forests in Dodge County, WI, and Johnson County, IL, respectively. Seeds were warm- and cold-stratified and germinated in the spring of 2010. Seedlings were transplanted singly into plastic pots with heights of 14.6 cm and top diameters of 15.2 cm that were filled with a soilless, peatmoss-based medium (Fafard[®] 52; Fafard, Inc., Agawam, MA). Seedlings of *Sambucus* were randomly assigned to one of six treatments of root-zone moisture when they were ≈ 3 months old and lengths of longest shoots were between 15 and 20 cm. Seedlings of the slower-growing *Ptelea* spp. were cultured with moist root zones for the growing season of 2010, held over winter in a minimally heated greenhouse, and subjected to treatments after resumption of growth in 2011, when shoots were 10 to 15 cm long.

The same six treatments were imposed during both experiments. Plants in three treatments were irrigated to container capacity with tap water when root zones were 5%, 10%, or 20% moisture by volume. Plants in the other three treatments were continuously inundated, either throughout the entire root zone or only in the lowest 7.5 or 3.5 cm, by placing growing containers into saucers of water. Root-zone moistures were measured by inserting an HH1 Theta Meter (Delta-T Devices, Cambridge, U.K.) probe into the substrate from above to determine whether irrigation was necessary. A completely randomized design was used for both experiments, with five (*Sambucus*) or four (*Ptelea*) replicate plants of each congener per treatment. Decisions to irrigate based on root-zone moisture were made for individual replicates rather than on means of replicates within treatments. Following this approach, plants irrigated at predetermined thresholds of root-zone moisture were subjected to as many as nine dry-down cycles when irrigated at 20% root-zone moisture to as few as three or four dry-down cycles when irrigated at 5% root-zone moisture. Experiments were conducted in a glass-glazed greenhouse in Ames, IA, with natural daylengths beginning 11 June (*Sambucus*) and 8 July (*Ptelea*). *Sambucus* were subjected to a mean photosynthetically active radiation (PAR) at solar noon of $630 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (SE = 42), and mean, minimum, and maximum daily temperatures were

24, 16, and 36 °C, respectively. For *Ptelea*, PAR at solar noon averaged $508 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (SE = 22), and mean, minimum, and maximum temperatures were 27, 24, and 32 °C, respectively. An AccuPAR LP-80 Ceptometer (Decagon Devices, Inc., Pullman, WA) was used to record PAR on three dates during each experiment.

Thirty-five days (*Sambucus*) or 38 d (*Ptelea*) after initiation of treatments, photosynthesis was measured on the youngest fully expanded leaf of each plant by using a LI-6400 photosynthesis system (LI-COR, Inc., Lincoln, NE) equipped with a reference CO_2 of $400 \mu\text{L}\cdot\text{L}^{-1}$ and a red-blue lamp providing $1000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR. Leaf temperature during measurements ranged from 25 to 33 °C. To determine the relationship between root-zone moisture and photosynthesis, root-zone moisture was measured immediately before photosynthesis by using an HH1 Theta Meter.

After photosynthesis was recorded, plants were harvested and surface area of leaves was measured with a LI-COR 3100 leaf area meter (LI-COR, Inc.), and roots and shoots (stems + leaves) were dried in a 69 °C oven for more than 3 d and weighed. The formula of (whole-plant RGR) = $\ln(\text{final dry weight}) - \ln(\text{initial dry weight}) / (\text{number of days})$ was used. Initial weights for each taxon were determined by harvesting five (*Sambucus*) or four (*Ptelea*) additional, randomly chosen plants of each congener when treatments were initiated. All data were analyzed with the Statistical Analysis System 9.1.3 (SAS

Institute Inc., Cary, NC) and Fisher's least significant difference test.

Results

Sambucus. Inundation of root zones decreased whole-plant RGR and/or survival of plants of western and eastern congeners of each genus (Fig. 1). Compared with the most favorable treatments, complete inundation of root zones reduced the RGR of the western and eastern congener of *Sambucus* by 116% and 25%, respectively. The marked reduction in RGR among western *Sambucus* with completely inundated root zones was the result of the death of most roots and shoots within 5 d of treatment initiation followed by a slow recovery as stems formed adventitious roots near the surface of the medium. Drying of root zones to 5% moisture by volume reduced the RGR of the western and eastern *Sambucus* by 42% and 28%, respectively.

Photosynthesis of *Sambucus* differed markedly between congeners in response to drought and inundation, and the western congener had greater rates of photosynthesis under various treatment conditions (Fig. 2). Photosynthesis of the western congener of *Sambucus* was lowest with complete inundation ($4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) but was otherwise similar across remaining root-zone conditions ($11 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), whereas photosynthesis of the eastern congener was lowest under severe drought ($1 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) but otherwise was 4 to $6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Measures of biomass showed that both congeners of *Sambucus* were sensitive to

Fig. 1. Relative growth rate of seedlings of *Sambucus* and *Ptelea* grown for 35 and 38 d, respectively, under six conditions of root-zone moisture. Each circle represents the mean root-zone moisture at the time of irrigation and the mean response of five (*Sambucus*) or four plants (*Ptelea*). Within taxa, each symbol represents, from left to right, plants irrigated when root zones dried to 5% moisture by volume to plants with root zones completely inundated (*Sambucus*) or plants with root zones shallowly inundated (*P. crenulata*) or moderately inundated (*P. trifoliata*). Treatments in which all plants of a taxon died are not represented.

drought and inundation and that moderate root-zone moistures fostered maximal root and shoot dry weights and leaf areas (Fig. 3). Root-to-shoot ratios were greatest when root-zone moistures were moderate to dry. Across treatment groups, plants of the eastern congener of *Sambucus* often produced root and

shoot biomass and leaf area equal to or exceeding that of their western counterparts (Fig. 3), whereas root-to-shoot ratios of eastern congeners never exceeded those of western congeners.

Ptelea. All plants of *Ptelea* died when root zones were fully inundated, whereas

moderate inundation killed all plants of the western congener and reduced RGR of plants of the eastern congener by 85% (Fig. 1). Drying root zones did not decrease RGR of either congener (Fig. 1).

Photosynthesis of *Ptelea* was similar between congeners in response to drought and inundation; dry and saturated root zones diminished the rate of photosynthesis, and both western and eastern plants had the greatest rate of photosynthesis ($14 \mu\text{m}^{-2}\cdot\text{s}^{-1}$ and 4 to $8 \mu\text{m}^{-2}\cdot\text{s}^{-1}$, respectively) under moderate root-zone moistures (Fig. 2). Plants from the West maintained greater rates of photosynthesis per unit leaf area under severe drought than did plants of the eastern congener.

Measures of biomass showed that both congeners of *Ptelea* were sensitive to drought and inundation and that moderate root-zone moistures fostered maximal root and shoot dry weights and leaf areas (Fig. 4). Root-to-shoot ratios were greatest when root-zone moistures were moderate to dry. Across treatment groups, plants of the eastern congener of *Ptelea* consistently produced root and shoot biomass and leaf area equal to or exceeding that of their western counterparts (Fig. 4), whereas plants of the western congener had root-to-shoot ratios greater than those of their eastern counterparts when root zones were allowed to dry.

Discussion

Consistent with their presence in the Mediterranean climate of the San Francisco Bay area, plants of *Sambucus nigra* ssp. *caerulea* and *Ptelea crenulata* were less tolerant of flooding than their eastern counterparts, *Sambucus nigra* ssp. *canadensis* and *Ptelea trifoliata* (Figs. 1 to 4). Previous work with *Sambucus nigra* ssp. *caerulea* demonstrated

Fig. 2. Photosynthesis of seedlings of *Sambucus* and *Ptelea* grown for 35 and 38 d, respectively, under six conditions of root-zone moisture. Each circle represents the mean root-zone moisture at the time of measurement and the mean response of five plants (*Sambucus*) or four plants (*Ptelea*). Within taxa, each symbol represents, from left to right, plants irrigated when root zones dried to 5% moisture by volume to plants with root zones completely inundated. For *Ptelea*, photosynthesis rates of zero are displayed when all plants of a taxon died from an inundation treatment. In some cases, the average root-zone moisture of plants in a more severe drought treatment group was greater than that of plants in a less severe drought treatment group at the time of measurement.

Fig. 3. Root dry weight, shoot dry weight, root:shoot, and total leaf area of seedlings of *Sambucus* grown for 35 d in each of six root-zone moisture conditions. Each circle represents the mean root-zone moisture at the time of irrigation and the mean response of five plants to treatments ranging from irrigation at 5% root-zone moisture by volume (left terminal) to complete inundation (right terminal).

Fig. 4. Root dry weight, shoot dry weight, root:shoot, and total leaf area of seedlings of *Ptelea* grown for 38 d in each of six root-zone moisture conditions. Each circle represents the mean root-zone moisture at the time of irrigation and the mean response of four plants to treatments ranging from irrigation at 5% root-zone moisture by volume (left terminal) to complete inundation (right terminal). Values of zero are displayed for dry weights and leaf area when all plants of a taxon died from an inundation treatment. The right terminals for root:shoot represent plants subjected to shallow inundation (*P. crenulata*) and moderate inundation (*P. trifoliata*) because root:shoot of dead plants is undefined.

that, although the taxon is found in habitats ranging from riparian terraces to drier chaparral, mortality from waterlogging of root zones was high in both greenhouse and field experiments (Richards and Chirman, 1994). This was not true of *S. nigra* ssp. *canadensis*, which not only tolerated complete inundation of root zones, but thrived under such conditions. Although the two genera were studied in separate experiments, precluding direct statistical comparison, *Ptelea* as a genus seems more susceptible to flooding than plants of *Sambucus* spp., because all plants of *Ptelea* died under complete inundation, and the western congener also died under partial inundation. Only *Sambucus nigra* ssp. *canadensis* represents a good choice for planting on sites characterized by saturation of root zones (Figs. 1 to 4). Our findings are consistent with previous studies demonstrating a similar relationship between the moisture availability of indigenous habitats of closely related taxa and tolerances of those taxa to root-zone flooding (Baraloto et al., 2007; Keeley, 1979).

Although growth of *Sambucus* from both regions was sensitive to drought, we found evidence that plants of the western taxon of *Sambucus* were more drought-adaptive than plants of the eastern congener. Plants of the western congener maintained higher rates of photosynthesis with drying of root zones and had greater root-to-shoot ratios under drought conditions, although plants of the eastern congener grew larger under all treatment conditions (Figs. 1 to 3). A reasonable interpretation is that *Sambucus nigra* ssp. *cerulea* may pay a physiological cost for the capacity to persist in a seasonally dry Mediterranean climate. Such a cost explains the greater root-to-shoot ratios and a greater capacity for photosynthesis under water deficit coupled with the lower

RGR and less accrual of biomass in roots and shoots under mesic conditions (Figs. 1 to 3). Despite the difference in rate of photosynthesis between congeners, specific leaf weight ($\text{mg}\cdot\text{mm}^{-2}$) did not differ consistently between them (data not shown). The performance of this taxon across a range of root-zone moistures indicates that although *S. nigra* ssp. *cerulea* fixes carbon at a higher rate, even when subjected to repeated episodes of drought, it lacks the capacity of its eastern congener to alter its growth strategy to take advantage of abundant water. This interpretation is consistent with the results of previous research demonstrating a diminished plasticity of growth associated with drought resistance in woody taxa distributed along a soil-moisture gradient (Brenes-Arguedas et al., 2008).

Further evidence for drought adaptiveness in the western congener of *Sambucus* was the stable presence of pubescence on adaxial and abaxial leaf surfaces of plants in our common greenhouse environment regardless of root-zone moisture treatment. Although not quantified, we observed that the western congener of *Sambucus* had densely pubescent leaves, whereas leaves of the eastern congener were nearly glabrous. This pubescence, described by Corelli (2005) for *S. nigra* ssp. *cerulea*, may both increase the thickness of the leaf boundary layer and help prevent excess heat gain by reflecting solar radiation, thereby diminishing water loss through transpirational cooling and enabling photosynthesis for a greater period during the onset of drought (Sandquist and Ehleringer, 1998).

In contrast to our findings for *Sambucus*, there was no evidence that congeners of *Ptelea* differed fundamentally in responses to drying root zones (Figs. 1, 2, and 4). Just as

plants of both congeners showed poor resistance to flooding, plants of both congeners likewise showed a similarly moderate resistance to drought. Habitat characteristics of the two congeners were not associated with strong differences in response to moisture stress. Other studies have shown that the woody taxa *Alnus maritima* (Marsh.) Muhl. ex Nutt., *Pinckneya pubens* Michx., *Magnolia virginiana* L., and *Taxodium distichum* (L.) Rich., all indigenous to bottomlands or waterlogged soils, have resistance to drought stress exceeding that expected based on moisture availability in their indigenous habitats (Nash and Graves, 1993; Schrader et al., 2005; Stewart et al., 2007). *Ptelea trifoliata* from eastern North America may likewise possess drought resistance greater than its native range would indicate and similar to that of *P. crenulata* from the Mediterranean climate of California. Although we did not measure the size of individual leaves, we observed the eastern *Ptelea* was characterized by leaves several times larger than those of the western congener. This difference has been noted in nature (Corelli, 2005), was stable in a common environment, and is likely adaptive in environments characterized by low soil moisture (Scoffoni et al., 2011).

Our findings provide new information about relative differences in response to root-zone water content between congeners of *Sambucus* and *Ptelea*, but additional evaluations with plants not restricted to containers are needed. The methods we used allowed for strict control over root-zone moisture and other components of the environment, but they precluded evaluation of potential stress-avoidance strategies. For example, Ackerly et al. (2002) found that

S. nigra ssp. *cerulea* growing on a dry chaparral tended to have high predawn water potentials, which suggests these plants rely on a strategy of drought stress avoidance through deep rooting to endure such environments. Comparisons in landscape performance between the two congeners of each genus may help to elucidate the degree to which these eastern and western congeners differ in rooting depth. Although we did not find evidence for differences in response to drought between *P. crenulata* and *P. trifoliata*, we have observed that leaves of *P. crenulata* senesce during the dry season in their native habitat in California. This phenomenon, referred to as summer-deciduousness, is a strategy to minimize water loss that has been noted among other woody plants that, like *P. crenulata*, are not sclerophyllous (Ackerly et al., 2002; Nilsen and Muller, 1980). Because we did not observe leaf desiccation in response to our treatments, we may not have imposed the degree of moisture stress *P. crenulata* undergoes in its native habitats. Alternatively, our use of seedlings and additional environmental factors in nature such as temperature, vapor pressure deficit, and duration of root-zone moisture deficit might explain why leaves of mature *P. crenulata* in the wild desiccated during summer drought but leaves of young plants in the greenhouse did not. An experiment designed to investigate greater or extended drying of root zones as well as correlated environmental factors might reveal a superior drought-tolerance strategy for the western congener when soil moisture is extremely low.

We investigated responses of plants from two regions to drought and flooding, but we recognize there likely is substantial variation in physiological tolerances among many populations throughout the ranges of these genera. Both genera occur in several habitats in eastern North America, throughout the Southwest, and along the West Coast with populations in the Mediterranean climate of the San Francisco Bay area. Future work with these genera could focus on a comprehensive evaluation of provenance variation within and among species or subspecies with particular attention to sampling the variation that exists among habitats. For example, plants of

S. nigra ssp. *cerulea* in the San Francisco Bay area notably occupy habitats ranging from upper riparian terraces to seasonally dry chaparral, and it is not known to what extent sampling plants in these different habitats would reveal variation in physiological tolerances that could be of value to horticulturists.

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