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Leaf gas exchange and growth of flood-tolerant and flood-sensitive tree species under low soil redox conditions

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Summary Seedlings of *Taxodium distichum* L., *Quercus lyrata* Walt. and *Q. falcata* var. *pagodaefolia* Ell. were grown for 22 days in a rhizotron system providing two soil redox potential regimes, +170 mV (low Eh) and +560 mV (high Eh). Leaf chlorophyll concentration and gas exchange, root alcohol dehydrogenase (ADH) activity, root and leaf ethylene production, and growth and biomass partitioning were measured.

In response to the low Eh soil treatment, stomatal conductance was reduced in *Q. falcata* and *Q. lyrata* but not in *T. distichum*, whereas net photosynthesis was reduced significantly in all species; however, net photosynthesis in *T. distichum* began to recover within 2 weeks of treatment initiation. Within each treatment, mean stomatal conductance and net photosynthesis were significantly greater in *T. distichum* than in the oak species. Leaf chlorophyll concentration was not affected by the soil treatments. All species showed significant reductions in root and leaf dry weights in response to the low Eh soil condition. The low Eh soil treatment resulted in increased root ADH activity and ethylene production in *T. distichum*, but had no effect on root ADH activity and ethylene production in the oak species.

Keywords: flooding, hypoxia, redox potential, Quercus falcata, Quercus lyrata, Taxodium distichum.

Introduction

Plants capable of withstanding soil oxygen deficiency caused by flooding often develop aerenchymatous tissues (Yamasaki 1952, Drew et al. 1979, Gleason and Zieman 1981, Schat 1984, Jackson et al. 1985*a*, Topa and McLeod 1986, Pezeshki 1991). In some species, there is a close relationship between ethylene production and aerenchyma formation (Drew et al. 1979, Jackson et al. 1985*a*, Atwell et al. 1988, Justin and Armstrong 1991, Armstrong et al. 1991, Brailsford et al. 1993). Morrell and Greenway (1989) demonstrated that ethylene promotes aerenchyma formation and influences root extension. Under hypoxic conditions, the precursor of ethylene (1-aminocyclopropane-1-carboxylic acid, ACC) is transported from hypoxic root tips to more mature aerated tissues where it is converted to ethylene (Bradford and Yang 1980). High concentrations of ethylene may reach leaves via intercellular spaces, affecting leaf physiology (Bradford 1983*a*, 1983*b*, Taylor and Gunderson 1988) and causing leaf chlorosis (Jackson et al. 1987).

The redox potential of flooded soil can be quantified by measuring the decrease in oxidation–reduction potential, Eh (Patrick and DeLaune 1977). Aerated well-drained soils have an Eh range of +400 to +700 mV, whereas the Eh range in flooded soils extends from +400 to −300 mV (DeLaune et al. 1990). Generally, oxygen is not present in soils having Eh values below +350 mV (Patrick and DeLaune 1977). Although root responses to O_2-deficient soils are caused by the absence of oxygen within the root tissue (Gleason and Zieman 1981, Yamasaki 1987), soil Eh measurements provide an indication of oxygen availability and the status of reduced substances in the soil environment (Yamasaki 1952).

We have examined the influence of soil Eh on root and shoot responses of three forest species that exhibit differing flood tolerance. *Taxodium distichum* L. is a highly flood-tolerant species that occupies sites with a wide range of flooding regimes, including continuous deep flooding. *Quercus lyrata* Walt. is a flood-tolerant species that can withstand periods of flooding up to 40% of the growing season (Hook 1984) and *Q. falcata* var. *pagodaefolia* Ell. is a flood-sensitive species that suffers high mortality, even among mature trees, if exposed to partial inundation (Hook 1984). The differences in extent of flood-tolerance suggest potential differences in physiological responses under flooded or reduced (oxygen-deficient) soil conditions. We hypothesized that low-Eh soil results in elevated foliar ethylene concentrations, and the magnitude of the increase is closely related to a species' flood-tolerance ranking.

Materials and methods

Plant material

Seeds were collected from trees growing in the vicinity of Louisiana State University Campus, Baton Rouge, LA, where certain portions of the area are subject to occasional flooding. Germinated seeds were grown in pots (25 cm diameter, 30 cm deep) containing commercial potting soil watered to excess and fertilized with a commercial water-soluble plant food (N,P,K = 23/19/17) once per week.

Experimental procedure

A rhizotron system described in detail by Pezeshki and DeLaune (1990) was used. Briefly, each rhizotron had inside dimensions of 50 × 30 × 1.7 cm and was supplied with gas mixtures through a 3-mm diameter Plexiglas tube. Two redox potential (Eh) electrodes similar to those described in detail by Patrick and DeLaune (1977) were installed at soil depths of 10 and 40 cm.

For each species, 24 seedlings of uniform size, averaging 9.8, 13.2 and 7.8 cm in height (*T. distichum*, *Q. lyrata* and *Q. flacata*, respectively), and having five to seven roots that were 2.9 to 8.7 cm in length were selected and randomly assigned to 12 rhizotrons. Each rhizotron was filled with soil from the Ap horizon of Mississippi River alluvial sediment and placed at an angle of 30° to promote root growth at the front window. Plants were sealed in the rhizotrons with nontoxic RTV rubber sealant (General Electric, Waterford, NY). By regulating the proportions of air and N_2 (Liquid Carbonics Inc., Gonzales, LA) entering each rhizotron at a flow rate of 15–25 ml min^{-1}, soil Eh was controlled to provide oxygen-deficient (+170 ± 28 mV, low Eh) soil conditions in six rhizotrons and well-aerated (+560 ± 35 mV, high Eh) soil conditions in the other six rhizotrons. Before initiation of the soil treatments, the plants were maintained in the rhizotrons for 7 days under well-aerated soil conditions. After the initial 7-day period, half of the rhizotrons were randomly assigned to the low Eh soil treatment; the soil in the other rhizotrons was kept well aerated (high Eh treatment). The treatments were applied over a 22-day period. Environmental conditions were day/night temperature of 25 ± 1.5/22 ± 1.5 °C, a 14-h photoperiod, and photosynthetic photon flux density (PPFD) between 700 and 900 μmol m^{-2} s^{-1} at canopy level. Root growth was measured on branched and nonbranched basal and lateral roots of all seedlings in each rhizotron.

Stomatal conductance, net photosynthesis and leaf chlorophyll

Between 4 and 6 h after the start of the photoperiod on Days 2, 4, 6, 7, 10, 14, 18 and 22, leaf conductance (g_w) and net carbon assimilation (A) were measured on eight intact, attached leaves per treatment with an open gas exchange system equipped with a temperature- and humidity-controlled multicuvette system (Pezeshki 1987). An infrared gas analyzer (Model LCA-2, Analytical Development Corp., Hitchin, U.K.) was used for differential CO_2 measurements. The PPFD was measured with quantum sensors (Li-Cor Inc., Lincoln, NE), and leaf and air temperatures were measured with fine-wire copper-constantan thermocouples. A multichannel recorder was used to record these variables throughout the experiment.

Both g_w and A were calculated per unit leaf area (single surface) determined with a surface area meter (Model S1701, SKYE Instruments, Inc., Buckingham, PA). Leaf conductance was calculated from leaf transpiration rates determined from the vapor difference across the leaf chamber. Values of A were calculated from the flow rate of air and the difference in CO_2 partial pressures entering and leaving the cuvette. On Days 7, 14 and 22, leaf chlorophyll concentrations were determined as described by Hiscox and Israelstam (1979) on the same leaf samples used for gas exchange measurements

Alcohol dehydrogenase

On Days 7 and 22, ADH (EC. 1.1.1.1) activity was assayed in newly developed root tissues, primarily root tips, of three and nine samples per treatment per species, respectively (John and Greenway 1976). The extraction buffer described by Flynn (1986) was used to extract ADH from *T. distichum* root tissues, and the extraction buffer described by Good (1985) was used for the extraction of ADH from root tissues of *Q. falcata* and *Q. lyrata*. Oxidation of NADH was measured spectrophotometrically at 340 nm. Enzyme activity is expressed as μmol NADH oxidized g_{FW}^{-1} h^{-1}.

Ethylene

Ethylene in roots and leaves was assayed by the method described by Saltveit (1982) and Saltveit and Yang (1987). On Days 7 and 22, three and nine samples per treatment per species, respectively, were harvested and transferred to 25-ml vials on filter paper moistened with 1 ml of distilled water. The vials were flushed with a known mixture of air from air tanks, sealed tightly with rubber serum caps, and wrapped with aluminum foil. Ethylene accumulated over a 2-h period (including wound-induced ethylene production) was determined by withdrawing 1-ml gas samples with a hypodermic syringe and analyzing them with a Perkin-Elmer 900 gas chromatograph equipped with a stainless steel column (1.5 m long, 3 mm diameter; HayeSep D, Hayes Separations, Bandera, TX) and a flame ionization detector. Chromatographic conditions were: injector temperature = 150 °C at 24 °C min^{-1}, and carrier gas = N_2 at 30 ml min^{-1}. Ethylene concentrations were calculated by calibration with known ethylene standard mixtures using a Hewlett Packard 3396 Series II integrator. Identification of ethylene was confirmed by analysis of a certified standard containing several gaseous hydrocarbons including ethylene and ethane. Sensitivity of the measurement technique to ethylene was 0.4 μl l^{-1} (ppm) for the specified standard conditions.

Net biomass growth

At the beginning of the study, height and total fresh weight of 12 representative plants per species were measured. On Day 22, biomass partitioning was determined by separating each sample plant into leaf, stem and root components. Biomass components were dried at 70 °C, and root, leaf and total dry weight per plant were recorded. The net biomass growth was calculated based on the increment in dry weight of each component during the 22-day experimental period. For each species, initial dry weights for each component (leaf, stem and root) were based on models developed from the initial measurements of height and total fresh weight of the 12 representative plants.

Data were analyzed by a split-plot design, where soil redox regime was the main plot and species were subplots, using a fixed model ANOVA and GLM procedure (SAS Institute, Cary, NC). Two error terms were considered in the analysis, rhizotron (treatment) and plant (rhizotron × treatment). A Stu-

dent's *t*-test was used to compare means for each species between treatments. The stomatal and photosynthetic data were analyzed by a repeated measures design (Moser et al. 1990).

Results and discussion

In response to low Eh soil, mean g_w of *Q. falcata* and *Q. lyrata* was significantly reduced ($P < 0.05$) throughout the 22-day treatment period, whereas mean g_w of *T. distichum* recovered rapidly after the onset of the treatment (Figure 1, Table 1). Net photosynthesis was significantly reduced by the low Eh soil treatment in all species (Table 1); however, in *T. distichum*, *A* returned to 87% of the control value within 2 weeks after the start of the treatment (Figure 1). Within each treatment, mean g_w and *A* were significantly greater in *T. distichum* than in the oak species, but there were no significant differences in g_w and *A* between the oak species (Table 1). Despite the reductions in carbon assimilation, the low Eh soil treatment had no effect on leaf chlorophyll concentration of any of the species ($P < 0.05$, Table 2), although chlorophyll concentrations were significantly greater in *T. distichum* and *Q. lyrata* than in *Q. falcata*. Thus, our data do not support the hypothesis that the reduction in photosynthesis in the low Eh soil treatment was caused by leaf chlorophyll degeneration (cf. Tables 1 and 2). However, the decrease in g_w in oaks indicates increased stomatal limitations on photosynthesis in the low Eh soil treatment (Kozlowski 1984). Photosynthetic processes may also be adversely affected by the metabolic consequences of hypoxia (Bradford 1983*a*, 1983*b*). For example, a low Eh soil treatment could cause a reduction in net photosynthesis as a result of decreased leaf water potential, reduced Rubisco activity (Vu and Yelenosky 1992, Pezeshki 1994), disruption in photosynthate transport, alteration in source–sink relationships, or reduced sink demand (Wample and Thornton 1984, Drew 1990).

In response to the low Eh soil treatment, root ADH activity increased in *T. distichum* seedlings but not in *Q. lyrata* and

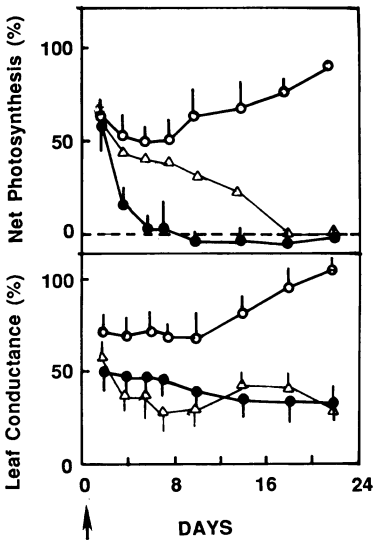

Figure 1. Time-course of responses of stomatal conductance (g_w) and net carbon assimilation (*A*) to low soil redox potential conditions in *Quercus falcata* (●), *Q. lyrata* (△) and *Taxodium distichum* (○). Arrow indicates beginning of low redox treatment. Values are means (± SE) for eight measurements and are presented as percentage of control plants of the respective species.

Table 1. Stomatal conductance and net carbon assimilation in *Taxodium distichum*, *Quercus falcata* and *Q. lyrata* under control (aerated) and low soil redox potential conditions. Values represent the mean for measurements recorded over the 22-day experimental period. An asterisk denotes significant differences ($P < 0.05$) for a given species between treatments. Significant differences ($P < 0.05$) among species within each treatment are denoted by different letters.

Treatment	Stomatal conductance ($mmol\ m^{-2}\ s^{-1}$)	Net carbon assimilation ($\mu mol\ m^{-2}\ s^{-1}$)
Taxodium distichum		
Aerated	143 a	15.8 a*
Low Eh soil	131 a	13.2 a
Quercus falcata		
Aerated	65 b*	3.1 b*
Low Eh soil	21 b	−0.5 b
Quercus lyrata		
Aerated	50 b*	3.82 b*
Low Eh soil	20 b	0.41 b

Table 2. Ethylene production, root ADH activity and leaf chlorophyll concentration in *Taxodium distichum*, *Quercus falcata* and *Q. lyrata* under control (aerated) and low soil redox potential conditions. Values represent the mean for measurements recorded over the 22-day experimental period. An asterisk denotes significant differences ($P < 0.05$) for a given species between treatments. Significant differences among species within each treatment are denoted by different letters.

Species	Treatment	Ethylene production ($\mu l\ kg_{FW}^{-1}\ h^{-1}$)		Root ADH activity ($\mu mol\ g_{FW}^{-1}\ h^{-1}$)	Leaf chlorophyll ($mg\ g_{FW}^{-1}$)
		Foliage	Roots		
Taxodium distichum	Aerated	8.4 b*	8.1 b*	247 a*	0.73 a
	Low Eh soil	16.5 a	17.1 b	583 a	0.71 a
Quercus falcata	Aerated	20.8 a	35.9 a	194 b	0.33 b
	Low Eh soil	14.2 a	30.6 a	180 b	0.27 b
Quercus lyrata	Aerated	20.2 a	38.7 a	163 c	0.89 a
	Low Eh soil	15.7 a	34.9 a	148 c	0.74 a

Q. falcata seedlings (Table 2). Increased ADH activity in response to flooding has been reported for flood-tolerant crop species (John and Greenway 1976) and woody species (Keeley 1979). It has been suggested that the increase in ADH activity in flooded roots of *Betula nigra* L. (Tripepi and Mitchell 1984), *Nyssa sylvatica* var. *biflora* Marsh. (Keeley 1979) and *Fraxinus pennsylvanica* Marsh. (Good 1985) is evidence that flood-tolerant species are capable of increasing anaerobic respiration to compensate for oxygen depletion. In *T. distichum* seedlings, the low Eh soil treatment resulted in an initial increase in ADH activity followed by a decrease in ADH activity by Day 22. This response pattern has been attributed to the development of aerenchyma tissue, which facilitates oxygen transfer to the roots thereby reducing the oxygen stress that triggered the initial rise in ADH activity (Flynn 1986).

In some species, increased ADH activity in response to oxygen deficiency is accompanied by an increase in ethylene concentration which enhances aerenchyma formation (Drew et al. 1979, Jackson et al. 1985*b*, Morrell and Greenway 1989). In response to the low Eh soil treatment, leaf and root ethylene production increased in *T. distichum* seedlings but not in *Q. lyrata* and *Q. falcata* seedlings (Table 2). Generally, ethylene production was greater in roots than in shoots of the oak species, whereas ethylene production was similar in roots and shoots of *T. distichum*. In the high Eh soil treatment, leaf and root ethylene production was significantly higher in the oak species than in *T. distichum*, whereas in the low Eh soil treatment, ethylene production was significantly higher in oak roots than in *T. distichum* roots (Table 2). In many woody species, ethylene concentrations in both root and shoots increase in response to soil flooding (Tang and Kozlowski 1984, Topa and McLeod 1988,Vossenek et al. 1993). Ethylene has been implicated in several responses of woody species to flooding including growth reduction (Kozlowski 1984), leaf senescence (Sena Gomes and Kozlowski 1986), hypertrophy of lenticels (Angeles et al. 1986, Topa and McLeod 1988), formation of aerenchyma tissues (Hook 1984, Topa and McLeod 1988) and adventitious root formation on submerged stems (Tsukahara and Kozlowski 1985). The apparent lack of change in ethylene production in the oak plants in the low Eh soil treatment may account for the absence of aerenchyma tissue development in these species (Brailsford et al. 1993).

In the high Eh soil treatment, root elongation was greater in the oak seedlings than in the *T. distichum* seedlings (Figure 2). The low Eh soil treatment significantly reduced ($P < 0.05$) root elongation by 67, 94 and 78% for *T. distichum*, *Q. falcata* and *Q. lyrata*, respectively (Figure 2), indicating that root growth was inhibited in all three species when soil Eh fell below +350 mV, the Eh value signifying the onset of oxygen disappearance from the soil system (DeLaune et al. 1990). Inhibition of root growth in response to soil flooding has been reported for many species under different experimental conditions (Yamasaki 1952, Cobb and Kennedy 1987, Pezeshki and DeLaune 1990, Liu and Dickmann 1992, Topa and Cheeseman 1992).

The low Eh soil treatment caused reductions in all oak plant biomass components (Figures 3A–C), whereas in *T. distichum*, the treatment resulted in decreased leaf (Figure 3A) and root

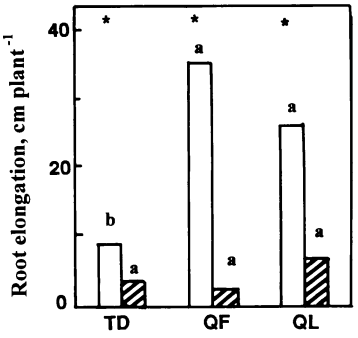

Figure 2. Root elongation in *Taxodium distichum* (TD), *Quercus falcata* (QF) and *Q. lyrata* (QL) under aerated (open bars) and low soil redox potential (dashed bars) conditions. Values are means for the 22-day experimental period. An asterisk denotes significant differences ($P < 0.05$) for a given species between treatments. Significant differences among species within each treatment are denoted by different letters.

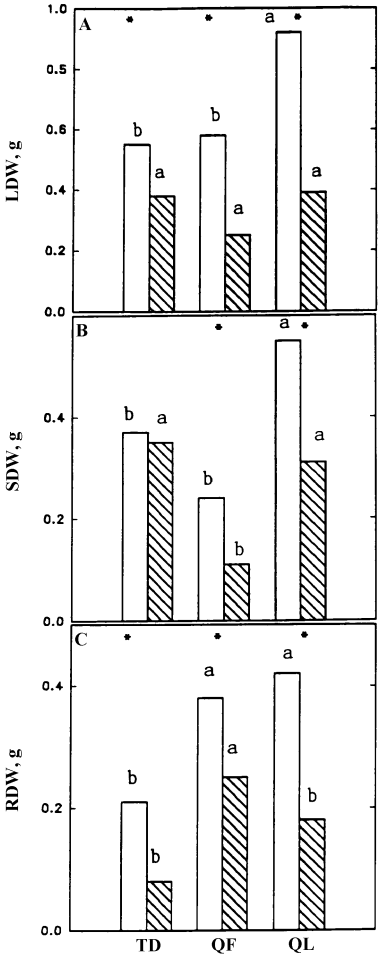

Figure 3. (A) Net leaf dry weight (LDW), (B) net stem dry weight (SDW) and (C) net root dry weight (RDW) accumulation during the 22-day experimental period in *Taxodium distichum* (TD), *Quercus falcata* (QF), and *Q. lycrata* (QL) under aerated (open bars) and low soil redox potential (dashed bars) conditions. An asterisk denotes significant differences ($P < 0.05$) for a given species between treatments. Significant differences among species within each treatment are denoted by different letters.

dry weights (Figure 3C) but had no effect on stem dry weight (Figure 3B). In the high Eh soil treatment, both oak species had greater root dry weights than *T. distichum*. In the low Eh soil treatment, there were no significant differences in leaf dry weight among species, but stem dry weight was greater in *Q. lyrata* and *T. distichum* than in *Q. falcata*. Although root dry weight was higher in *Q. falcata* than in the other species, the root dry weights for *Q. falcata* may be in error because the model developed to estimate initial root dry weight for *Q. falcata* had relatively low predictability compared with the models developed for the other species.

We conclude that enhanced ADH activity and ethylene production in *T. distichum* plants under low Eh soil conditions may have adaptive significance enabling the species to survive in oxygen-deficient environments.

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