Relationships among rhizosphere oxygen deficiency, root restriction, photosynthesis, and growth in baldcypress (*Taxodium distichum* L.) seedlings

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Abstract

Seedlings of baldcypress (*Taxodium distichum* L.) grown in sealed containers containing nutrient solution were subjected to root-zone oxygen deficiency, physical restriction, and the combined stresses in a greenhouse. After six weeks of treatments (Phase I), half of the plants were harvested. The remaining half were allowed to continue (Phase II) under various treatments except plants that had restricted roots were freed thus allowing free expansion of roots into the nutrient solution. Oxygen deficiency and root physical restriction inhibited plant gas exchange parameters. Net photosynthetic rate (P_N) was significantly higher in aerated unrestricted root (AUR) plants than in aerated root restricted (AR) plants and in anaerobic root unrestricted (FUR) plants than in anaerobic root restricted (FR) plants. After Phase I, FUR plants' shoot and root biomasses were 57.0 and 30.6 % lower than those of AUR plants, and AUR plants showed 3.3 and 3.8 times greater shoot and root biomasses than the AR plants, respectively. During Phase II, P_N recovered rapidly in plants under aerated conditions, but not in plants under anaerobic conditions. The removal of physical root restriction under both aerated and anaerobic conditions resulted in rapid shoot and root growth in seedlings. Hence, root restriction or root-zone anaerobiosis, reductions in plant gas exchange, and biomass production in baldcypress were closely interrelated. In addition, root release from restriction was related to the regain of photosynthetic activity and biomass growth. The results support the previously

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Abbreviations: APR, aerated previously root restricted; AR, aerated root restricted; AUR, aerated root unrestricted; FPR, anaerobic previously root restricted; FR, anaerobic root restricted; FUR, anaerobic root unrestricted; g_S, stomatal conductance to water vapor transfer; P_N, net photosynthetic rate; RGR, relative growth rate.

proposed source-sink feed-back inhibition of photosynthesis in plants subjected to root-zone oxygen deficiency or physical restriction.

Additional key words: anaerobiosis; biomass; relative growth rate; root:shoot ratio; shoot.

Introduction

Soil flooding or oxygen deficiency in rhizosphere impede root growth substantially even in species considered to be highly tolerant of such conditions (Pezeshki 1991). The dramatic adverse impact on root growth is similar to other environmental factors that restrict root growth. For instance, physical restriction on roots due to soil compaction reduces root growth by limiting root expansion. Severe inhibition of root elongation in response to physical root restriction (Carmi and Heuer 1981, Carmi *et al.* 1983, Bengough and Mullins 1990) or low soil oxygen conditions (Pezeshki 1991) has been reported for numerous plant species under various experimental conditions. Such response has been attributed to effects of both stressors on growth regulator balances, translocation of photosynthates to the root (Carmi *et al.* 1983), and ability of roots to utilize the available photosynthates (Barta 1987, 1988a,b). The mechanism(s) involved in inhibition of translocation of saccharides or root saccharide utilization under root restriction is not well understood. In plants subjected to rhizosphere oxygen deficiency, there is some evidence of potential involvement of toxic products of anaerobic respiration whereas plants under physical restriction may invoke root to shoot signals *via* chemical means (Carmi and Heuer 1981, Carmi *et al.* 1983, Cook *et al.* 1996).

The interrelationships among environmental stressors, photosynthetic responses, and biomass production and partitioning have received considerable attention (Neales and Incoll 1968, Carmi *et al.* 1983, NeSmith 1993, Pezeshki 1994, Cook *et al.* 1996). Plants of certain species subjected to root restriction had low P_N whereas in other species P_N was improved (Carmi and Heuer 1981, Carmi *et al.* 1983). Anaerobic conditions in the root zone also may lead to significant reductions in P_N even in plants with a wide range of flood-tolerance capabilities (Pezeshki 1994 and the references cited therein). Reduced plant growth under both stresses may be attributed to a diminished ability of the plants to continue accumulation of photosynthates in the sink organs including roots. Thus one explanation for the observed reduction in P_N is that the reduction occurs presumably through a feedback inhibition mechanism responding to the accumulation of photosynthates in the sink organs, thus through the exhaustion of sink capacity (Neales and Incoll 1968). Roots are major sink for saccharides produced in photosynthesis (Kramer 1983, Kozlowski 1984). Photosynthate accumulation in photosynthetic tissues may also occur due to the reduction in translocation rate to the available sinks (Neales and Incoll 1968). In addition to inhibition of root growth, root physical restriction or oxygen deficiency also affect shoot growth (Carmi and Heuer 1981, Krizek *et al.* 1985, Pezeshki 1991, 1994) but such effects may be species-specific (Cook *et al.* 1996).

In the present paper, we have examined the changes in P_N in seedlings of a highly flood-tolerant species, baldcypress, in response to root restriction and root-zone anaerobiosis and the interrelationships with root and shoot growth. The specific

objectives were to evaluate: (*1*) photosynthetic responses to root restriction, root-zone oxygen deficiency, and the combined stresses, and (*2*) the interrelationships among changes in photosynthetic rates, and root and shoot growth. In addition, we re-examined the feed-back inhibition model using this species under both physical root restriction and root oxygen deficiency.

Materials and methods

Plants: Baldcypress (*Taxodium distichum* L.) cones collected from trees growing in City Park, Baton Rouge, Louisiana, USA were bench-dried for two months. The seeds were then separated from the cones manually, soaked in tap water for seven days, washed with ethanol, and stored in a refrigerator for three months at a temperature of 4 °C. After the final stratification, seeds were sown on germination trays containing moist vermiculite. Seedlings approximately 10 cm tall (two months old) were transplanted into plugs (2.5 cm diameter, 15 cm deep). The experiment was done in a ventilated greenhouse (irradiance maintained at >400 μmol m^{-2} s^{-1} at canopy level using a combination of sunlight and supplemental irradiation; average maximum/minimum temperatures 30/20 °C). Initial fresh and dry masses of shoot and root biomass were measured on 12 additional plants selected randomly for the initial destructive sampling at the time the transplanting into the containers was initiated. These values were later utilized to calculate relative growth rates (RGR) for each biomass component.

Sixteen plastic containers, 24.2 cm in height and 23.8 cm in diameter (*Dyson Oil*, Ark, USA), were filled with 7 000 cm^3 of 1/4 strength Hoagland solution. The plugs containing plants were introduced into the Hoagland Solution through holes in the lids. The plugs were sealed onto the lid of each container and the lid was then sealed to the containers using silicone rubber. Eight randomly selected containers received continuous air treatment using air pumps thus creating aerobic conditions (A), and eigth containers received N_2 treatment using compressed gas source thus subjecting the plants to oxygen-deficient conditions (F). Each container had four plants, two assigned to root restriction (R) and two without root restriction (UR). The treatment combinations therefore were: AR, AUR, FR, and FUR. Roots were restricted by placing a plastic net (0.1 mm mesh size) at the bottom of each plug, thus allowing nutrient solution flow inside the plug while physically restricting roots from expansion outside each plug. The UR plants were in plugs that had holes on sides and bottom thus allowing root expansion into the Hoagland solution. The solutions were changed weekly, using aerated or anaerobically prepared nutrient solutions depending on the treatment, to prevent depletion of nutrients.

Plant gas exchange responses to various treatments were measured using a porometer *LI-1600* (*LiCor*, Lincoln, Nebraska, USA) and a portable photosynthetic system (*ADC* model *A120* Infrared Gas Analyzer, *Analytical Development Co.*, Hodesdon, England). The measurements were conducted on five sample leaves per treatment (one leaf per each plant) on the first fully developed leaf from the shoot apex. Gas exchange measurements were conducted at 2 h-intervals between 10:00 to

16:00 h during each sample day. There were nine sample days during Phase I including days 3, 4, 5, 8, 9, 13, 15, 22, and 30.

After the experiment had been in progress for six weeks (Phase I), half of the plants were harvested. The harvested plants were divided into shoot (above-ground) and root (belowground) components and dried in an oven at 80 °C to a constant mass. The remaining half were allowed to continue for additional six weeks (Phase II) under various treatments except plants that had restricted roots were freed from the physical restriction by removing the net. The treatment combinations during Phase II therefore were: aerated previously root restricted (APR), AUR, anaerobic previously root restricted (FPR), and FUR. During Phase II, plant gas exchange was measured on days 4 and 19, and after it the corresponding dry biomass components were recorded. Growth of seedlings in response to various treatments was analyzed using classical growth analysis techniques (Radford 1967, Ledig *et al.* 1970). Root to shoot ratio (RSR) was calculated from dry masses. The General Linear Models (GLM) procedure of SAS (*SAS Institute*, Cary, NC, USA, 1985) was used to detect significant differences among the variable means across treatments.

Results

During Phase I, some influence of oxygen deficiency and root physical restrictions on plant gas exchange parameters was evident (Fig. 1*A,B*). In the aerated treatment, there were no significant differences in g_s between root restricted (AR) and unrestricted (AUR) plants while P_N was significantly ($p<0.05$) higher in AUR plants than AR plants. In the anaerobic treatment, FUR plants showed significantly higher ($p<0.05$) g_s and P_N than FR plants. Plants under AUR and FUR had comparable g_s and P_N. Although g_s was not affected by AR treatment significantly, the FR plants had significantly lower g_s as compared to AUR and FUR plants (Fig. 1*B*). P_N was reduced significantly in response to AR and FR treatments.

The first biomass harvest at the conclusion of Phase I showed differences in plant responses to various treatments (Fig. 1*C,D*). Shoot and root biomasses were reduced significantly under R but biomasses of AR and FR plants were not significantly different which indicated the inhibitory effects of root physical restriction on biomass accumulation irrespective of aeration. However, both shoot and root biomasses were significantly greater in AUR plants than FUR plants indicating the inhibitory effects of anaerobiosis on biomass accumulation. In FUR plants, shoot and root biomass were substantially lower, 57.0 and 30.6 %, than in AUR plants, respectively. Within the aerated treatment, AUR plants showed significantly greater ($p<0.05$) shoot biomass (3.3 times) and root biomass (3.8 times) as compared to AR plants. Under anaerobiosis, there were no significant differences in the shoot and root biomass due to root restriction. At the end of Phase I, both shoot and root components of total biomass were significantly lower ($p<0.05$) in all treatments as compared to control (AUR) plants.

At the beginning of Phase II, the root physical restrictions on AR and FR plants were removed, and their roots grew freely (APR and FPR). Following root release

from physical restriction (Fig. 2), P_N recovered more rapidly in A seedlings (AR : AUR : APR = 69 : 100 : 123) than in F seedlings (FR : AUR : FPR = 70 : 100 : 91). P_N in FUR plants was similar during Phase I and Phase II (Fig. 2).

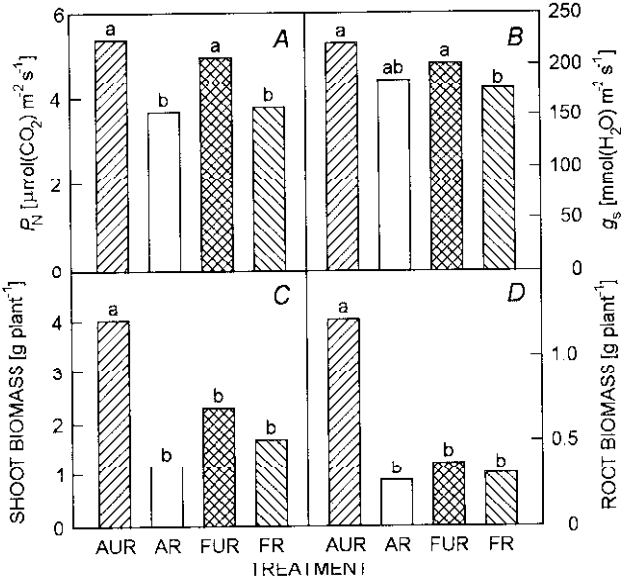

Fig. 1. Responses of (*A*) net photosynthetic rate, P_N, (*B*) stomatal conductance, g_s, and (*C*) above-ground and (*D*) below-ground biomass in AUR (aerated root unrestricted), AR (aerated root restricted), FUR (anaerobic root unrestricted), and FR (anaerobic root restricted) baldcypress seedlings during Phase I of the experiment. Values followed by different letters represent significant differences among the means across treatments at the 0.05 level.

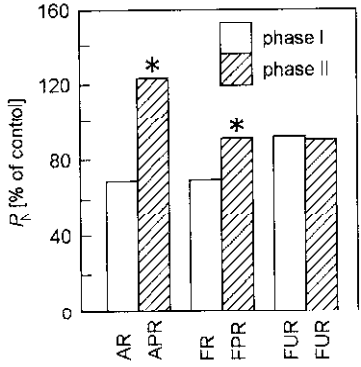

Fig. 2. Relative net photosynthetic rate, P_N, in baldcypress seedlings in response to aeration-root restriction combinations during Phase I and Phase II of the experiment. P_N of aerated root unrestricted plants was taken for 100 % control. APR means aerobic previously root restricted plants of Phase II, FPR anaerobic previously root restricted plants. For other abbreviations see Fig. 1. *Significant differences between the means of the two phases at respective treatment.

Shoot and root biomasses at the end of Phase II were significantly different between A and F treatments (Table 1): they were 2.1 and 3.8 times greater in APR than FPR plants, and 2.7 and 5.2 times greater in AUR than FUR plants, respectively. There were no significant differences in shoot and root biomasses in APR and AUR plants and in root biomass in FPR and FUR plants (Table 1). Nevertheless, shoot biomass was significantly greater in FPR compared to FUR plants.

Table 1. Changes in shoot and root dry mass [g per plant] of baldcypress plants during Phase I (first harvest) and Phase II (final harvest) of the experiment. AUR (aerated root unrestricted), AR (aerated root restricted), FUR (anaerobic root unrestricted), FR (anaerobic root restricted), APR (aerated previously root restricted), FPR (anaerobic previously root restricted). Each value represents the means for eight plants.

Biomass	Harvest first				final			
	AUR	AR	FUR	FR	AUR	APR	FUR	FPR
Shoot	3.972a	1.196b	2.255b	1.664b	11.094a	12.657a	4.086c	6.038b
Root	1.208a	0.258b	0.367b	0.298b	3.895a	3.831a	0.749b	1.022b

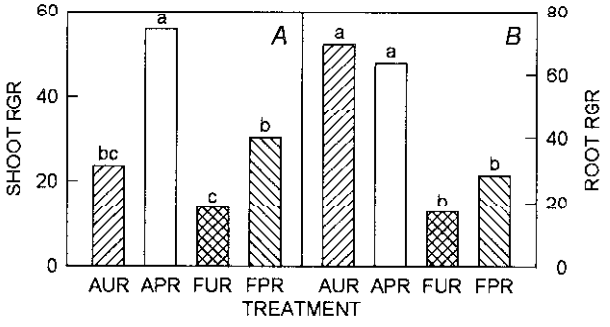

Fig. 3. Changes in relative growth rates, RGR [g(d.m.) kg^{-1}(d.m.) d^{-1}] for (*A*) shoot and (*B*) root biomass in AUR (aerated root unrestricted), APR (aerated previously root restricted), FUR (anaerobic root unrestricted), and FPR (anaerobic previously root restricted) baldcypress seedlings at the end of Phase II of the experiment. Values followed by different letters represent significant differences among the means across treatments at the 0.05 level.

The removal of physical root restriction under both A and F conditions resulted in rapid shoot and root growth in baldcypress seedlings (Fig. 3*A,B*). The shoot RGR for APR plants recovered rapidly surpassing the RGR for AUR plants, and RGR for roots was also high for APR plants. This recovery resulted in a comparable final root and shoot biomass values for APR and AUR plants by the end of Phase II (Table 1). However, the RGR for F plants remained significantly lower than their respective counterparts under A conditions. This response was attributed to the adverse effects of anaerobiosis that continued and maintained throughout Phase II for these plants.

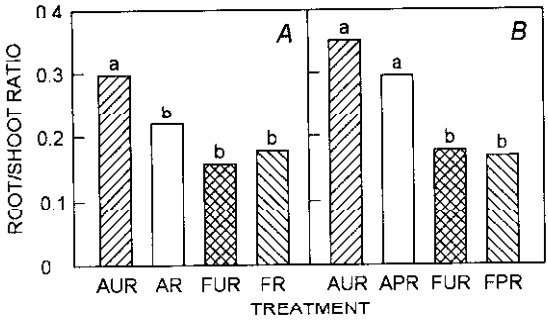

Fig. 4. Changes in root:shoot biomass ratios in baldcypress seedlings in response to aeration/root restriction combinations during Phase I (*A*) and Phase II (*B*) of the experiment. For abbreviations see legends to Figs. 1 and 2. Values followed by different letters represent significant differences among the means across treatments at the 0.05 level.

The effects of treatments on biomass partitioning were further apparent from root-shoot ratios. After Phase I, they were significantly reduced for plants under root restriction and/or root hypoxia compared to AUR plants (Fig. 4*A*). The observed changes in root:shoot ratios were attributed to the non-uniform effects of various treatments on biomass accumulation in root or shoot that had its greatest impact on root biomass. After Phase II, the root:shoot ratios were also reduced in FPR and FUR plants as compared to APR and AUR plants (Fig. 4*B*), but the difference between AUR and APR plants was not significant.

Discussion

In the present study, both root restriction and root-zone oxygen deficiency resulted in stunted root growth thus limiting root capacity as a major sink for saccharides. Gas exchange rates in bald cypress were affected by rhizosphere oxygen deficiency, physical root restriction, and the combination treatment. Baldcypress is a woody species that possesses many flood-tolerance characteristics (Pezeshki 1991). However, both g_s and P_N in this species were reduced by soil anaerobiosis, at least during the initial period of treatment. The gas exchange rates, however, recovered subsequently in FUR plants as has been reported previously (Pezeshki 1994).

Root restriction, in absence of anaerobiosis, had adversely affected P_N rates in baldcypress seedlings. For instance, P_N in AR plants was significantly reduced as compared to AUR plants (Fig. 1*A*). Root restriction alone, however, did not affect g_s significantly (Fig. 1*B*). In contrast, Carmi *et al.* (1983) found lower g_s in bean plants with restricted roots. The proposed negative feed-back inhibition of photosynthesis in response to sink size (Neales and Incoll 1968) assumes that photosynthetic inhibition occurs through a feedback inhibition mechanism that responds to the accumulation of photosynthates in the sink organs. The reduction in leaf P_N may also be due to accumulation of photosynthates in the mesophyll cells (Neales and Incoll 1968). In addition, reduced growth may be attributed to a diminished ability of the plants to transport photosynthates to the sink organs including roots. However, the growth

decreases due to the growth regulator imbalance may also result from a lower supply of growth substances translocated from roots to leaves as a result of root restriction. Therefore, limitation of photosynthesis by restricting the growth of sink organs in turn may affect the eventual growth and productivity of plants.

Although high P_N and photosynthate production have been associated with high growth rates and biomass production, such relationship has not been reported in all cases (Carmi and Heuer 1981). Thus previous works have not shown a clear relationship between P_N and root restriction. Carmi *et al.* (1983) reported continued high P_N for plants of *Phaseolus vulgaris* with restricted roots; however, such high P_N did not lead to high plant growth rates as was expected. They concluded that suppression of root growth does not necessarily limit photosynthesis, as the feedback inhibition theory assumes.

Several factors influence the efficiency with which saccharides are used for growth. One is that a portion of the saccharides may accumulate in the leaves, and another that the allocation of saccharides among different plant organs will affect the rate of growth (Stitt and Schulze 1994). In addition, plant ability to use assimilates may be more limiting to growth than the supply of saccharides (Barta 1987, 1988a,b). Carmi *et al.* (1983) demonstrated that high P_N continued in bean plants under root restriction without any growth promotion thus leading to photosynthates' accumulation. In the present study, we found lower P_N that was associated with periods of reduced RGR in baldcypress plants subjected to root restriction or anaerobiosis. We also found improved photosynthetic activities associated with the resumption of root growth during the post-release period. In addition, compensatory mechanism/s might also exist as was evident from the substantial increase in P_N in APR plants (as compared to AUR plants) during Phase II. During this period, average P_N increased by 23 % in APR plants as compared to AUR plants (Fig. 2).

In Phase I there were significant reductions in shoot and root biomass in plants due to root restriction. Biomass measurements conducted six weeks after removal of root restriction showed no significant differences in shoot biomass between APR and AUR plants (Table 1). Since APR plants started Phase II with much smaller initial root and shoot biomass than AUR plants, the final biomass indicated that APR plants accumulated biomass at greater rates than AUR plants during the post-release period. In contrast, there were significant differences in final biomass between FPR and FUR plants. In the latter case, the plant dry mass accumulation rates did not recover as quickly as in plants under aerated treatment due to the continuous adverse effects of low-oxygen stress. Rhizosphere oxygen deficiency reduces plant growth in both flood-sensitive and flood-tolerant species (Pezeshki 1991, 1993). Root growth in certain woody species is more sensitive to root-zone oxygen deficiency than growth of other organs (Pezeshki 1994).

There were also indications of changes in biomass partitioning patterns in response to various treatments as shown by the root:shoot ratios. In Phase I, these were significantly reduced for plants under root restriction and/or root hypoxia compared to AUR plants (Fig. 4*A*). The changes may be attributed to different effects on biomass accumulation patterns in root or shoot, but the reduction in the ratios were primarily due to the greater relative reductions in root biomass. In contrast, root

restrictions resulted in uniform reduction of root and shoot growth in several cultivars of summer squash (NeSmith 1993). Other studies have shown no root restriction effect on root/shoot ratios (Krizek *et al.* 1985, Robbins and Pharr 1988). Cook *et al.* (1996) found no evidence of changes in carbon allocation to the roots for plants under physical restrictions as compared to non-stressed plants. On the other hand, both increased (Carmi *et al.* 1983, Ruff *et al.* 1987) and decreased (Peterson *et al.* 1984) root:shoot ratios have been reported. Reduced shoot growth in plants subjected to root restriction has been attributed to many factors including small root volume and the subsequent reduction in the capacity for water and nutrient uptake (Boone and Veen 1982, Atwell 1990, Oussible *et al.* 1992). However, shoot growth reduction may occur under root restriction in absence of water or nutrient deficits (Carmi and Heuer 1981, Carmi *et al.* 1983, Krizek *et al.* 1985, Cook *et al.* 1996). Such response has been attributed to reduction or changes in balance among growth regulators (Carmi and Heuer 1981, Carmi *et al.* 1983).

In addition to the reports that plants can regulate the fate of photoassimilates (Carmi *et al.* 1983) and our results, there are evidences that support the proposed feed-back inhibition of photosynthesis (see Neales and Incoll 1968): (*1*) the significant P_N reductions in plants with restricted roots (AR, FR plants) during Phase I (Fig. 1*A*), (*2*) the remarkable recovery of P_N during the post-release period (Phase II) in APR plants, and (*3*) the accumulation of significantly greater biomass in APR plants during the period following root release. Such increase in biomass accumulation was associated with enhanced photosynthetic activity. The lack of parallel response to root release was attributed to the persistent inhibitory effects of continuous anaerobiosis on root growth that also provided the feedback inhibition of photosynthesis. We demonstrate that in baldcypress seedlings, there are close relationships between the root restriction or root-zone anaerobiosis and reductions in P_N as well as between root release from restriction and photosynthetic recovery. Present results support the previously proposed source-sink feed-back inhibition of photosynthesis in plants subjected to root-zone oxygen deficiency or physical restriction.

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