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Response of *Pinus taeda* L to soil flooding and salinity

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Summary — Seedlings of *Pinus taeda* L were subjected to soil flooding alone (F) and combined with salinity (FS) of 50 mol m^{-3}. The flooding effects on soil were quantified by measuring soil redox potential. Soil redox potential remained in the range of +400 to +450 mV in control pots while it was reduced to –50 to –140 mV in flooded pots. Stomatal conductance (g) and net carbon assimilation (A) were reduced significantly under flooding alone and flood/salt combination treatments. Stomatal conductance averaged 120 mmol H_2O m^{-2} s^{-1} for control plants, while it averaged 51 and 45 mmol H_2O m^{-2} s^{-1} for flooded (F) and flooded plus salt (FS) treatments, respectively. Net carbon assimilation was reduced from 5.82 μmol CO_2 m^{-2} s^{-1} (control plants) to 2.22 and 0.09 μmol CO_2 $m^{-2}s^{-1}$ in F and FS plants, respectively. The reductions in g and A were statistically significant. Dry weight increment per plant was reduced from 24.38 g in control to 10.09 and 8.22 g per plant in F and FS treatments, respectively. The reduction represents 59% reduction in F and 66% reduction in FS treatment. Based on the present results, it is concluded that : 1), *P taeda* showed considerable sensitivity to saltwater treatment within the range of soil anaerobiosis and salinity tested; and 2), in areas where saltwater intrusion occurs frequently, regeneration and survival of this species will be adversely affected. The severity of such an impact is partially dependent upon the intensity of soil reduction and the concentration of salt in floodwater.

flooding / forested wetlands / loblolly pine / photosynthesis / salt stress / stomatal conductance

Résumé — Réponse de *Pinus taeda* L à l'inondation et à la salinité. *L'effet d'une inondation (F) seule ou accompagnée par la salinité (50 mol/m^3) sur le semis de* Pinus taeda *L a été déterminé. L'effet de l'inondation a été évalué en mesurant le potentiel d'oxydation et de réduction* (Eh) *du sol. Le potentiel d'oxydation et de réduction dans les pots témoins était compris entre +400 et +450 mV alors qu'il était réduit de –50 à –140 mV dans les pots inondés (fig 1). La conductance stomatique* (g) *et l'assimilation nette du carbone* (A) *ont été réduites de façon significative dans les pots soumis à l'inondation* (F) *d'une part et l'inondation/salinité* (FS) *d'autre part. La conductance stomatique moyenne était de 120 mmol H_2O $m^{-2}s^{-1}$ dans les témoins et de 51 et 45 mmol H_2O $m^{-2}s^{-1}$ pour les pots seulements inondés ou accompagnés par la salinité, respectivement. L'assimilation du carbone était réduite de 5,82 mol CO_2 m^{-2} s^{-1} dans les témoins à 2,22 et 0,9 mol CO_2 m^{-2} s–1 pour les pots F et FS, respectivement. La relation A-Ci indique que l'inondation seul ou accompagnée par la salinité affecte la capacité de la photosynthèse du* P taeda *L par un puissant effet non stomatique, mais aussi de façon significative par la régulation stomatique (fig 4). L'augmentation du poids sec par plant a été significativement réduite de 24,38 g dans les témoins à 10,9 et 8,22 g dans les F et FS, respectivement (tableau II). Ces réductions représentent 59% et 66% pour les F et FS. Ces résultats suggèrent que :*

– le P taeda *L montre une sensibilité considérable à l'eau salée dans les intervalles testés;*
– la régénération et la survie de cette espèce sont sérieusement affectées dans les endroits où l'intrusion de l'eau salée est assez fréquente. La sévérité de cet impact dépend partiellement de la diminution du potentiel de réduction du sol et du degré de salinité de l'eau.

inondation / photosynthèse / forêt inondée / salinité

INTRODUCTION

Pinus taeda L is a mesophytic, moderately flood-tolerant species (Hook, 1984). This species grows on a wide range of soils including flat, poorly drained areas of the lower coastal plain in pure as well as mixed stands (USDA, Forest Service 1965). On wet site sites it is associated with *Liquidambar styraciflua, Nyssa sylvatica, Quercus nigra* and *Fraxinus pennsylvanica.* On drier sites, it is found with *Q falcata* var *falcata, Q alba* as well as with *P echinata* and *P palustris.* Portions of these forests in areas adjacent to the coast experience flooding and, in some cases, periodic saltwater intrusion as a result of subsidence and/or high tidal events caused by tropical storms.

The adverse effects of flooding on survival and growth of *P taeda* seedlings has been documented in several reports (Hunt, 1951; Topa and McLeod, 1986). Flooding for 3 months with stagnant water reduced growth of *P taeda* (Hunt, 1951). Significant reduction in biomass of *P taeda* after 2 months of exposure to soil flooding was found by Topa and McLeod (1986). Permanent root injury has been reported when *P taeda* seedlings were flooded for 10 months (Hunt, 1951). Flood-induced conditions substantially reduced root biomass of several southern US pine species (Hook *et al,* 1983; McKee *et al,* 1984).

Along the US Gulf Coast, high tidal events caused by tropical storms have previously been associated with mortality of various salt-sensitive species including *P taeda* (Little *et al,* 1958; Land, 1974). While the growth response of *P taeda* to various durations of flooding (but not intensity as determined by soil redox potential, Eh) has been documented, little is known about the threshold levels of soil hypoxia and sublethal salinity which triggers various responses of this species.

Several important areas of research which needed to be addressed included quantifying such terms as "flooding". As pointed out by DeLaune *et al* (1990), to evaluate the threshold levels of physiological responses of plants to soil flooding, it is important to quantify oxygen demand in the root environment. Additionally, common responses of trees to root hypoxia include stomatal closure (Kozlowski, 1982, 1984; Tang and Kozlowski, 1982) and reduction in net photosynthesis even in highly flood-tolerant species such as *Taxodium distichum* (Pezeshki *et al,* 1986, 1987). However, little information is available on the physiological responses of *P taeda* to increases in salinity levels in the presence of flooding. Assessment of physiological response of *P taeda* seedlings to salt stress is of great importance in order to identify the possible adaptation and (or) acclimation to saline conditions. Maintenance of positive net photosynthesis is an important factor contributing to the survival and growth of a given species under nonlethal salinity conditions. Reports of stomatal and photosynthetic behavior of *P taeda* to individual and combined flooding and salinity stresses is limited. The present study was conducted to investigate the effect of floodwater salinity on gas exchange in

P taeda. The effects of individual and combined hypoxia and salinity on net carbon assimilation of this species and the subsequent effects of these stresses on growth and biomass partitioning was evaluated.

MATERIALS AND METHODS

Pinus taeda L seedlings obtained from the Louisiana Department of Forestry were grown in plastic nursery pots 25 cm in diameter and 30 cm tall. A potting mix of equal parts of sand, vermiculite, and peat was used to fill the pots. Seedlings were kept in the nursery under natural conditions of 20–30 °C temperature range and photosynthetic photon flux density maxima of approximately 2 000 μmol m^{-2} s^{-1}. Plants were watered daily and fertilized with a commercial (23–19–17% N, P, K respectively) water-soluble fertilizer once per month. In early spring, 36 plants were selected for uniformity and transferred to a greenhouse. Plants averaged 31.0 ± 3.3 cm in height, and were randomly assigned to 1 of 3 treatments (12 plants per treatment). Treatments consisted of a well-watered control with no flooding or salt stress (C), flooded with salt water containing 50 mol m^{-3} NaCl (FS), and flooded with tap water containing no salt (F).

Salt solutions were prepared using Instant Ocean Synthetic Sea Salt (Aquarium Systems Inc, Mentor, OH, USA), with major ionic components of Cl (47%), Na (26%), SO_4 (6%), Mg (3%), Ca (1%), and K (1%) as percentage of dry weight. Treatment F and FS began by flooding the pots and maintaining the water level approximately 5 cm above soil surface in each pot. In treatment FS, salt was added over a 2-week period, *ie*, plants were subjected to salt level of 17 mol m^{-3} (1 part per 1 000) during the first day. Salinity level was then increased to 34 mol m^{-3} on the 7th day and to 50 mol m^{-3} on the 14th day of the experiment. A YSI Model 33 meter (Yellow Springs Instrument Co, Yellow Springs, OH, USA) was used for measurements of salt levels in all pots throughout the experiment.

On 8 sample days during the experiment, beginning day 61 and ending day 180, diurnal patterns of changes in environmental parameters and plant responses were measured. Measurements of air temperature, relative humidity, photosynthetic photon flux density (PPFD), needle temperature (T_1), and stomatal conductance (g) were made on 1 sample fascicle per replication per treatment every 3 h beginning at 0800 h until 1800 h on each sample day.

Stomatal conductance was measured using a steady state porometer (LI-1600, LiCor Inc, Lincoln, NE). After recording g, the same fascicle was used for net carbon assimilation (A) measurement. A portable gas exchange system (Model A120, ADC, Field Analytical System, PK Morgan Inst Co, Dallas, TX) was used to provide rapid measurement of A. The fascicle was enclosed in the chamber and PPFD and differential CO_2 levels were recorded. Net carbon assimilation rates were calculated from the flow rate of air through the chamber and from the CO_2 partial pressure differences between the incoming and the outgoing air, as outlined by Caemmerer and Farquhar (1981). The internal CO_2 concentration pressure (Ci) was calculated from g and A values using the equations described by Sharkey *et al* (1982). Needle surface area was calculated according to a model described in detail by Fites and Teskey (1988).

The intensity of soil reduction was quantified by measuring changes in oxidation-reduction of soil (redox potential, Eh). Eh was measured using a Digi-Sense meter, model 5985-00 (Cole Parmer Instrument Co, Chicago, IL), a calomel probe, and platinum electrodes. The procedure was similar to that described in detail by Patrick and DeLaune (1972, 1977). In summary, Eh was measured each sample day after allowing the electrodes to equilibrate in place for 12 h. Eh measurements were then made on 6 platinum electrodes per treatment (1 per pot). The probes were installed 5 cm below the soil surface. Corrections were made as descried by Patrick and DeLaune (1972, 1977).

At the beginning of the experiment, 12 plants were used for destructive sampling. Plants were separated into root, stem, and needle components and their respective dry weights determined after drying at 70 °C to a constant weight. At the conclusion of the study, the dry weight increments were determined by subtracting mean initial dry weight values from the final dry weights for each biomass component.

The General Linear Models (GLM) procedure of the SAS System (SAS Institutde, Inc, Cary, NC, USA) was used to test for differences in g and A among the treatment means using a repeated measures design including the day and the hour of measurement according to Moser *et al* (1990).

RESULTS

Shortly after flooding, Eh began to decrease in flooded (F) and flood plus salt (FS) treatments (fig 1). Three weeks after the initiation of flooding, soil Eh averaged +420 mV in treatment C while Eh was in the range of –50 to –140 mV in treatments F and FS. The Eh data indicated availability of oxygen in treatment C, while it showed oxygen disappearance and moderately reduced conditions in treatments FS and F.

Flooding alone and combined with salinity resulted in a substantial reduction of g and A. Figure 2 presents diurnal responses of g and A for days #100 and 160 following treatment initiation. Both g and A in treatment F and FS remained lower than control plants throughout the day. Maximum g and A for control plants were measured around 1200–1400 h; however, in treatments F and FS, maximum g and A were recorded earlier in the day followed by a declining pattern throughout the day. During each day, g and A values remained substantially lower in F and FS treatments as compared to control plants.

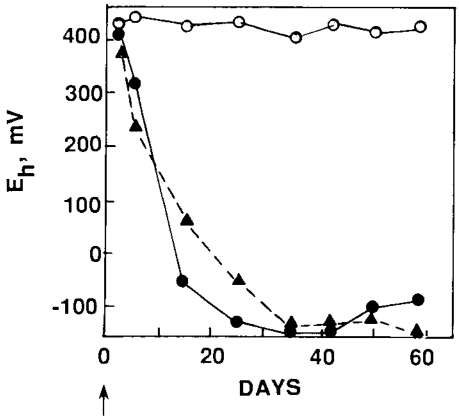

Fig 1. Changes in soil redox potential (Eh) following flood treatment initiation. Each point is the mean for 6 redox electrodes. Symbol designation: control (open circles), flooded only (closed circles) and flood plus salt (closed triangles). Arrow represents treatment initiation.

The time course responses of g and A to various treatments are presented in figure 3. Over the period of study, both g and A (mean daily values) remained lower in F and FS treatments as compared to control plants with the greatest reduction noted in FS treatment. While the reduction in g and A for treatment F and FS was significant (table I), the difference in g between treatment F and FS was not statistically significant. In addition, no significant improvement in g or A was observed for either F or FS treatment with progression of the experiment (fig 3).

The A–Ci relationship is used to examine stomatal contribution to control of photosynthetic rates. The relationships between intercellular CO_2 concentration (Ci) and A is presented in figure 4. In control plants, A increased as Ci increased. In contrast, in F and FS plants, A showed less response to increase in Ci. For a given Ci level, A decreased from control to F and FS plants. The relationship indicated that both F and FS treatments affected photosynthetic capacity in *P taeda.* While there was a direct response of A to Ci for control plants, the relationship was altered for plants in F and FS treatment indicating strong, non-stomatal limitations of A. These findings suggest that in addition to stomatal closure, both F and FS treatment had affected the plant's photosynthetic capacity through non-stomatal effects.

The effect of different treatments on various biomass components is illustrated in table II. Needle dry weight and root dry weight increment were reduced significant-

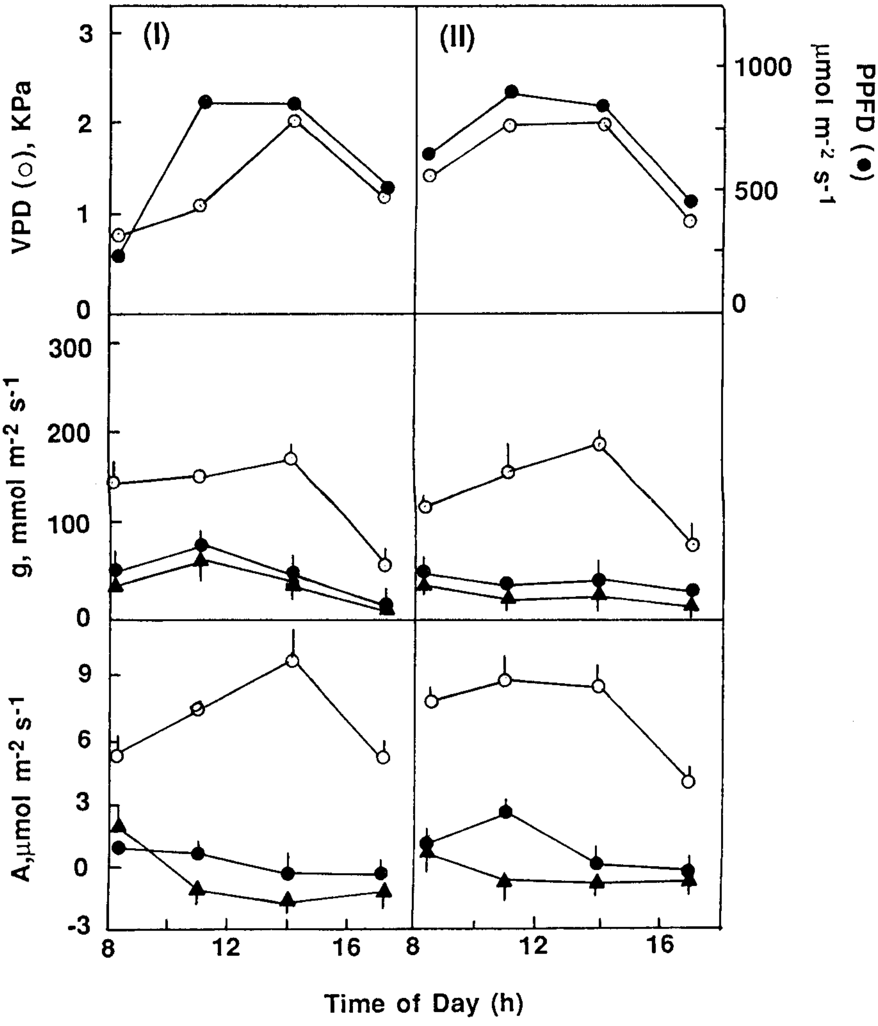

Fig 2. Diurnal patterns of net carbon assimilation (A), stomatal conductance (g), vapor pressure difference from leaf to air (VPD) and photosynthetic photon flux density (PPFD) for *Pinus taeda* seedlings. Symbol designation: control (open circles), flooded (closed circles) and flooded plus salt treatment (closed triangles). (I) represents day #100, while (II) represents day #160. Each point is the mean of 12 measurements. Bars represent SE.

ly ($P \leq 0.05$) for plants in treatment F and FS as compared to the control plants. The overall dry matter increment was also reduced significantly ($P \leq 0.05$) for plants in treatments F and FS compared to control plants.

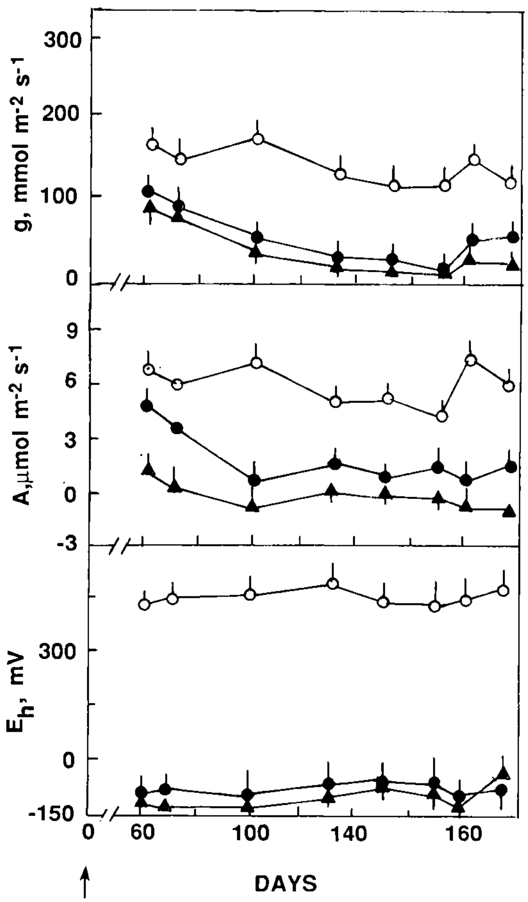

Fig 3. Changes in soil redox potential (Eh), net carbon assimilation (A) and stomatal conductance (g) of *Pinus taeda* plants grown under control (open circles), flooded only (closed circles) and flooded plus salt treatment (closed triangles). Arrow represents treatment initiation.

DISCUSSION

Waterlogging alone and combined with salt resulted in a substantial reduction of g, A and biomass in *P taeda* plants. Flooding, salinity and a combination of these 2 cause reduction in g and A in many woody species (Kozlowski, 1984; Pezeshki *et al,* 1986; Dreyer *et al,* 1991). Downton (1977), Longstreth and Strain (1977), Kemp and Cunningham (1981), Longstreth *et al* (1984) and Pezeshki *et al* (1986, 1987) have reported reduced g in response to salinity for many species. For instance, reduction in A under increased soil salinity has been reported in *Acer pseudoplatanus, Tilia cordata, P sylvestris* (Cornelius, 1980) and in *P ponderosa* seedlings (Bedunah and Talica, 1979). Ball and Farquhar (1984a,b) noted a decrease in A for 2 mangroves, *Aegiceras corniculatum* and *Avicennia marina.* Pezeshki and Chambers (1986) observed up to 86% reduction in A for *F pennsylvanica* seedlings subjected to soil salinity.

In glycophytes, the net effect of salt stress is a reduction in growth which has been partially attributed to the reduction in net A. The effect of excess salt on various plant biochemical and structural changes which can cause changes in photosynthetic capacity has been documented by Chimikilis and Karlander (1973), Helal and Mengel (1981), Longstreth *et al* (1984), Rouxel *et al* (1989), Hajibagheri *et al* (1989), Rawson *et al* (1988), Werner and Stelzer (1990), and Chow *et al* (1990). Generally, the photosynthetic capacity decreases under saline conditions partially because of reduction in stomatal conductance imposing diffusional limitations and the subsequent decline in intercellular CO_2 concentration (Downton *et al,* 1985; Seemann and Critchley, 1985; Flanagan and Jeffries, 1988). In addition to diffusional limitations, a portion of the reduction has also been attributed to metabolic inhibition of photosynthesis (Walker *et al,* 1982; Ball and Farquhar, 1984a, b; Seemann and Critchley, 1985; Seemann and Sharkey, 1986; Flanagan and Jeffries, 1988). Metabolic reductions are caused by changes in leaf content of photosynthetic systems

Table I. Statistical significance of different treatments on stomatal conductance (g) and net carbon assimilation (A) of *Pinus taeda*. Each value is the mean for 384 measurements conducted every 3 h on 8 sample days. Values in horizontal sequence not followed by the same letter are significantly different at the 0.05 level.

Variable	*Control (C)*	*Flood (F)*	*Flood and salt (FS)*
g, (mmol H_2O m^{-2} s^{-1})	120 ^{a}	51 ^{b}	45 ^{b}
A, (μmol CO_2 m^{-2} s^{-1})	5.82 ^{a}	2.22 ^{b}	0.09 ^{c}

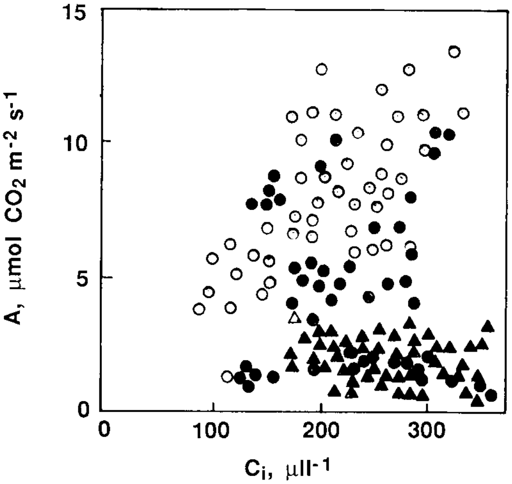

Fig 4. Net carbon assimilation (A) *versus* intercellular CO_2 concentration (Ci) for *Pinus taeda* under different treatments. Measurements were made between 800 and 1800 h during 8 sampling days at atmospheric CO_2 levels in a greenhouse. Symbols are the same as in figure 1.

and/or alteration in the efficiency in system operations (Seemann and Critchley, 1985; Sharkey, 1985; Seemann and Sharkey, 1986). Reduced stomatal conductance and photosynthesis in response to salinity is a common response found in flood/salt-sensitive woody species (Kozlowski, 1982, 1984).

The relationship between A and Ci (fig 4) was altered for F and FS plants, *ie* lower A rates were associated with higher Ci which indicates decrease in capacity of chloroplasts for depletion of CO_2 resulting in maintenance of high intercellular CO_2 concentration. The present data indicates a strong, non-stomatal limitation of A in *P taeda* under F and FS treatments (fig 4). However, use of this approach has been questioned and appears to be somewhat controversial (Wise *et al*, 1990). Recently documented evidence showing non-homogeneities and stomatal patchiness across leaves in some species (Terashima *et al*, 1988) and an apparent potential non-

Table II. Biomass components (increments) of *Pinus taeda* under various treatments. Values in horizontal sequence not followed by the same letter are significantly different at the 0.05 level.

Variable		*Control (C)*	*Treatment* *Flood (F)*	*Flood + salt (FS)*
Root dry weight	(g)	5.06 A	2.56 B	2.19 B
Needle dry weight	(g)	11.82 A	4.39 B	3.32 B
Total dry weight	(g)	24.38 A	10.09 B	8.22 B

uniform photosynthetic capacity across a leaf under stress conditions (Sharkey and Seemann, 1989). Such non-homogeneities in leaf conductance if present result in overestimation of calculated Ci, leading to erroneous conclusions regarding non-stomatal inhibition of photosynthesis (Terashima *et al,* 1988). Nevertheless, there are no indications of stomatal patchiness and/or such non-homogeneities in *P taeda.* Teskey *et al* (1986) demonstrated that water stress affected photosynthesis in *P taeda* primarily through direct effects in mesophyll rather than its effects on stomatal conductance.

The reduction in g and A in *P taeda* seedlings observed in the present study may have been partially caused by the development of water stress following salt application. There is direct evidence, however, suggesting that high internal Cl^- or Na^+ concentration affects different plant processes independently of water stress (Greenway and Munns, 1980). Sands and Clarke (1977) found that salt damage to *P radiata* seedlings was not a result of water stress. The damage was attributed instead to excess Cl^- accumulation. Land (1974) reported similar results for seedlings of *P taeda.* Both water stress and excess foliage ion concentrations at higher salinity treatment may have contributed to the observed g and A responses.

The reduced growth rates under flooded conditions found in the present study are consistent with previous reports indicating inhibition of growth of tree species under stagnant water which can impose anaerobic conditions (low Eh) in the soil. For example, Harms (1973) noted reduced height growth in highly flood-tolerant, *N sylvatica* var *biflora* and *N aquatica* seedlings when grown in stagnant water. Shanklin and Kozlowski (1985) reported a substantial growth reduction in *T distichum* seedlings, another highly flood-tolerant tree species, when flooded with stagnant water.

In the present study, the addition of salt to flooding further reduced net photosynthesis to a greater degree compared to flooding alone and an additional 8% reduction in overall dry matter increment compared to flooding alone. Among the factors which contribute to the slow growth under saline conditions are root water deficits and growth regulator imbalances (Munns and Termaat, 1986). It is important to note, however, that the salinity of 50 mol m^{-3} imposed in this study was not lethal for the duration of this study and that higher salinity and/or longer exposure to saline conditions may change the observed responses.

CONCLUSIONS

P taeda is a moderately flood-tolerant tree species growing on diverse natural habitats in the southeastern US (Hook, 1984). The impact of different treatments on net carbon assimilation and growth was greater in *P taeda* plants exposed to saltwater treatment than those flooded with tapwater. This indicated that the addition of salt to floodwater will cause an additional stress condition resulting in further reduction of photosynthetic activity and growth. Such changes could adversely affect survival, productivity and species composition of these forests.

In light of the present findings, severe inhibition of net carbon assimilation and growth of *P taeda* seedlings is expected in those areas subject to saltwater intrusion which results in saline conditions accompanied by soil anaerobiosis. The extrapolation of these results to that of mature trees requires careful evaluation. It is likely that *P taeda* trees under field conditions encounter somewhat different conditions than seedlings did in this study. For instance, both salinity and water levels (soil anaerobiosis) in the field can change rapidly providing intermittent periods of aerobic and/or non-saline conditions. However, in areas where saltwater intrusion occurs frequently, regeneration and survival of *P taeda* will be severely affected through the adverse effects of both flooding and salinity on physiological functioning of the seedling. The severity of such an impact is partially dependent upon the water depth (and the subsequent soil redox intensity) and the concentrations of salt in the floodwater.

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