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Importance of adventitious roots to growth of flooded *Platanus occidentalis* seedlings*

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Summary Flooding of soil with standing water for 50 or 110 days drastically reduced growth of 178-day-old *Platanus occidentalis* seedlings, with growth inhibited more as the duration of flooding was increased. Flooding reduced the rate of height and diameter growth, leaf initiation and expansion, and dry weight increment and relative growth rates of leaves, stems, and roots. Flooding also induced leaf epinasty, leaf necrosis, and formation of hypertrophied lenticels and many adventitious roots on submerged portions of stems. Severing of adventitious roots after 50 and 95 days from the submerged portions of stems of continuously flooded seedlings reduced several growth parameters including height and stem diameter growth and relative growth rates of leaves and roots. Evidence for the physiological importance of flood induced adventitious roots is discussed.

Introduction

Platanus occidentalis L. is highly prized as an ornamental and forest tree. It is the predominant species in the *Betula nigra-Platanus occidentalis* forest type in the northeastern United States and southward into Oklahoma, Missouri, and Tennessee. This forest type also occurs in the Alleghany and Piedmont Plateaus of the Appalachian Mountains. The species is rated as intermediately flood tolerant and occurs most frequently and achieves its largest size along streams and on bottomlands[14]. Its tolerance of wet soils is also shown by its occurrence in small depressions with poor drainage, muck lands, and shallow peat soils[4].

Adaptation of this species to flooding has been linked to production on submerged stems of hypertrophied lenticels which may assist in exchange of dissolved gases in flood water, and in production of adventitious roots (AR) on stems which may increase absorption of water[31]. However, since the adaptive significance of flood induced AR has been questioned[6,35] additional experiments were conducted to quantify the importance of such roots to growth of seedlings.

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Materials and methods

Platanus occidentalis seedlings were grown in the greenhouse from seeds. When the seedlings were 167 days old they were transplanted into 14 cm pots containing two parts sand and three parts loam. Environmental conditions during the experiment were: average high and low temperatures, 31.1 and 16.3°C, respectively; relative humidity 75% ± 5%.

When the seedlings were 178 days old, 48 were selected for uniformity. Height, stem diameter (measured with a microcaliper) at four cm above the soil surface, and the number of fully expanded leaves more than two cm long were determined for each seedling. Eight randomly selected seedlings were then harvested and separated into roots, stems, and leaves. Leaf area per plant (measured with a Licor leaf area meter), and dry weights of leaves, stems and roots were determined separately for each seedling after drying at 70°C for 48 hours.

The remaining 40 seedlings were divided into 2 groups: 8 unflooded seedlings and 32 seedlings flooded in trays, with the water level maintained at 2 cm above the soil surface. Unflooded plants were watered to excess once every two days. Both groups were grown for 50 days. They were then divided into the following treatment groups:

(A) U + U – unflooded for 110 days

(B) F + U – flooded for 50 days and unflooded for an additional 60 days

(C) F + F – flooded for 110 days

(D) F + ARC + U – flooded for 50 days and unflooded for an additional 60 days; flood-induced adventitious roots (AR) severed from the stem at 50 days

(E) F + ARC + F – flooded for 110 days; flood-induced adventitious roots (AR) severed from the stem at 50 days and subsequently-formed AR severed from the stem at 95 days

Seedling heights and stem diameters were determined for all seedlings at 0, 15, 30, 50, 65, 80, 95 and 110 days. At 110 days the 8 seedlings in each of groups A through E were harvested and the same observations were made for each seedling that were made for the set harvested for initial measurements. For flooded plants with AR, relative growth rate ($\overline{RGR}$) was determined for each seedling for 0–110 days. $\overline{RGR}$ was determined separately for increment in dry weight of leaves, stems and roots by the equation:

$$\overline{RGR} = \frac{\ln(\text{final dry weight}) - \ln(\text{mean initial dry weight})}{\text{weeks}}$$

The data for effects of treatments on seedling height, stem diameter, and dry weights of leaves, stems, and roots, as well as number of attached and shed leaves, leaf area, and size of the average leaf, were subjected to analysis of variance. Multiple comparisons were made using honestly significant differences (HSD).

Significant differences among $\overline{RGR}$ values were identified by HSD multiple comparisons. Variances of $\overline{RGR}$ values were calculated in accordance with the principles outlined by Ku[23]:

$$\mathrm{VAR}\ \overline{RGR} = \frac{1}{n(t_2 - t_1)^2} \left[\frac{S_1^2}{\overline{X}_1^2} + \frac{S_2^2}{\overline{X}_2^2}\right]$$

Variances of $\overline{RGR}$ values were pooled for calculation of HSDs.

Results

Flooding greatly reduced growth of *Platanus occidentalis* seedlings, with inhibition greater as the duration of flooding was increased (Tables 1–4).

Within six days some leaves on each flooded plant had turned light red. Shortly thereafter the leaves of flooded plants developed necrotic lesions. Within 15 days 3 to 27% of the leaves of individual flooded plants, particularly the lower leaves, were dead. After 50 and 110 days 33% and 85%, respectively, of the leaves of flooded seedlings were dead.

Flooding decreased the rate of height growth of seedlings within 15 days. After 50 and 110 days the height of unflooded seedlings increased by 184 and 246%, respectively; of flooded plants by only 59 and 91% (Table 1). Increase in stem diameter was also inhibited by flooding, with a significant effect apparent within 15 days. Whereas diameters of unflooded plants increased by 148% and 195%, after 50 and 110 days, respectively, in flooded plants they increased by only 56% and 93%.

Table 1. Effect of flooding and flood-induced adventitious roots on height and stem diameter of *Platanus occidentalis* seedlings. Data are means and standard deviations. Original seedling height averaged 20.2 cm and stem diameter 2.56 mm. For explanation of treatments see text

	Height (cm)			Stem diameter (mm)		
Treatment	50 days	110 days	% increase	50 days	110 days	% increase
U + U	57.29^a	69.94^a	22.1^b	6.34^a	7.79^a	23.0^c
F + U	33.69^b	52.63^b	56.5^a	4.12^b	6.12^b	50.3^a
F + F	32.11^b	38.64^c	20.4^b	3.99^b	4.93^c	23.4^c
F + ARC + U	33.73^b	50.90^b	51.5^a	4.29^b	5.92^b	39.3^b
F + ARC + F	32.79^b	37.13^c	13.3^c	4.36^b	4.89^c	11.4^d

Means within columns lacking or followed by the same letter are not significantly different.

Flooding for 50 or 110 days decreased the leaf area and size of the average leaf (Table 2). After 110 days leaf areas of unflooded seedlings increased by 419% and of flooded seedlings by only 89%. The size of the average leaf of unflooded plants increased by more than 246%; that of flooded plants by only 11%. The number of leaves was not reduced by flooding and it appeared that the reduction in leaf area of flooded plants was entirely the result of lowered leaf expansion. However, during the latter stages of the experiment the unflooded seedlings with their extensive leaf areas more rapidly depleted soil moisture and showed significantly more abscission of lower leaves than was the case with the flooded plants. It also appears likely that leaf initiation may have been inhibited by water deficits in the unflooded plants during the latter part of the experiment, by which time the leaves were fully expanded. Hence the data on effects of flooding on leaf expansion probably are more reliable than those on leaf initiation.

Flooding also decreased dry weight increment and RGR of seedlings and various plant parts (Tables 3, 4). After 110 days the increase in dry weight was about five times as great in unflooded seedlings as in flooded seedlings. Percent increase in dry weight of unflooded plants varied in the following order: stems > roots > leaves. In continuously flooded plants the order was: stems > leaves > roots. The very low dry weights of root systems of flooded plants reflected both cessation of root initiation and growth as well as death of many of the original roots. The remaining original roots of flooded plants had darkened conspicuously and were sparely branched.

Flooding also induced leaf epinasty and morphological changes. Within five days after flooding was initiated, hypertrophied lenticels were observed on the submerged portion of the stem above the soil surface. Within 10 days a few AR had formed and some of these emerged through lenticels. Within 13 days AR were present on submerged portions of stems of all flooded plants. The dry weights of AR severed from stems at 50 days after initiation of flooding averaged near 34% of the weight of non-adventitious roots of the initially harvested plants. The AR that formed between 50 and 95 days in flooded plants averaged 26% of the dry weight of non-adventitious roots present at 95 days.

Severing of AR from the submerged portions of the stems reduced height growth and stem diameter growth of flooded and unflooded plants (Table 1, compare % increase for treatments F + F *vs* F + ARC + F for plant height; also compare % increase for treatments F + U *vs* F + ARC + U and F + F *vs* F + ARC + F for stem diameter. Severing of AR did not reduce dry weight increment of leaves, stems

Table 2. Effect of flooding and flood-induced adventitious roots on number of attached and shed leaves, leaf area, and size of leaves of *Platanus occidentalis* seedlings. For explanation of treatments see text

Days	Treatment	Number of attached leaves	Number of shed leaves	Total number of leaves	Leaf area (cm^2)	Size of average leaf (cm^2)
0	–	7.5 ± 0.9	–	7.5 ± 0.9	238 ± 39	31.8 ± 3.8
110	U + U	11.6 ± 3.2	10.2 ± 1.8^b	21.8 ± 3.7	1237 ± 213^c	110.0 ± 19.5^c
110	F + U	13.9 ± 5.6	8.0 ± 2.2^a	21.9 ± 4.4	796 ± 152^b	61.8 ± 16.4^{ab}
110	F + F	12.4 ± 2.8	6.4 ± 2.3^a	18.8 ± 3.0	450 ± 168^a	35.2 ± 8.6^a
110	F + ARC + U	14.0 ± 3.1	6.6 ± 2.6^a	20.6 ± 1.3	1016 ± 266^{bc}	77.1 ± 34.9^b
110	F + ARC + F	11.4 ± 2.1	6.6 ± 1.6^a	18.0 ± 1.6	393 ± 152^a	34.0 ± 8.9^a
Significance		ns	*	ns	**	**

** significant at the 1% level; * significant at the 5% level; ns not significant. Means within columns and harvest date lacking or followed by the same letter are not significantly different.

Table 3. Effect of flooding and flood-induced adventitious roots on dry weight increment and root-shoot ratio of *Platanus occidentalis* seedlings. For explanation of treatments see text

		Dry weight (g)						
Days	Treatment	Leaves	Stem	Non-adv. roots	Adventitious roots	Total roots	Seedlings	Root-shoot ratio
0		0.69 ± 0.11	0.29 ± 0.05	0.59 ± 0.09	0	0.59 ± 0.09	1.57 ± 0.22	0.60 ± 0.08
	U + U	6.82^a	8.03^a	13.27^a	0^a	13.27^a	28.1^a	0.92^a
	F + U	4.50^b	2.98^b	4.49^b	1.25^b	5.74^b	13.2^b	0.78^{ab}
110	F + F	2.47^c	1.61^c	1.34^c	0.39^a	1.73^c	5.8^c	0.42^c
	F + ARC + U	4.10^b	3.04^b	4.72^b	0.17^a	4.89^b	12.0^b	0.69^b
	F + ARC + F	1.85^c	1.50^c	1.10^c	0.38^a	1.48^c	4.8^c	0.45^c
Significance		**	**	**	**	**	**	**

** Significant at the 1% level. Means followed by the same letters within columns are not significantly different.

Table 4. Effect of flooding and flood-induced adventitious roots on relative growth rate ($\overline{RGR}$) of *Platanus occidentalis* seedlings. Data are in gm/gm dry weight/week for 110 days. For explanation of treatments see text

Treatment	Seedling	Leaves	Stems	Non-adventitious roots	Total roots
U + U	0.184^{a}	0.146^{a}	0.211^{a}	0.198^{a}	0.198^{a}
F + U	0.135^{b}	0.119^{b}	0.148^{b}	0.129^{b}	0.145^{b}
F + F	0.083^{c}	0.081^{c}	0.109^{c}	0.052^{c}	0.068^{d}
F + ARC + U	0.129^{b}	0.113^{b}	0.150^{b}	0.132^{b}	0.135^{c}
F + ARC + F	0.071^{c}	0.063^{d}	0.105^{c}	0.040^{c}	0.059^{e}
Significance	*	*	*	*	*

* Significant at the 5% level. Means followed by the same letters within columns are not significantly different.

or roots of seedlings flooded for 110 days (Table 3, compare treatments F + F *vs* F + ARC + F). Severing of AR also reduced $\overline{RGR}$ of leaves of flooded and unflooded plants (Table 4, compare treatments F + F *vs* F + ARC + F) and $\overline{RGR}$ of total roots in both additionally flooded and unflooded plants (Table 4, compare treatments F + U *vs* F + ARC + U and F + F *vs* F + ARC + F).

Discussion

Growth of *Platanus occidentalis* seedlings was drastically reduced when the roots were inundated by standing water. These observations reinforce studies showing that growth of other flood tolerant species is also reduced by flooding with stagnant water[9]. Observations of the present study are consistent with studies by Hosner[13], Hosner and Boyce[14], Dickson, Hosner, and Hosley[3], Hook and Brown[10], and Tang and Kozlowski[31].

Although its growth was reduced by flooding, *Platanus occidentalis* exhibited considerable morphological adaptation to flooding by producing hypertrophied lenticels and abundant adventitious roots on submerged portions of stems. Such lenticels may assist in aeration of the stem and roots and in oxidation of the rhizosphere. They may also serve as openings through which toxic compounds associated with anaerobiosis are released[7,18].

Severing of flood-induced adventitious roots from submerged stems of *Platanus occidentalis* seedlings significantly reduced seedling growth, providing evidence of an important physiological role of AR in flooded plants. In our study only very few of the newly regenerated roots were removed from the flooded seedlings. In addition to producing AR on submerged portions of stems (those removed in the present study) flood tolerant woody plants regenerate new roots at the points to which the original roots die back to major secondary roots or the primary roots[7]. Furthermore, in the present study the AR on submerged stems began to form after 10 days but were severed from the stem only after 50 and 95 days. Hence, these roots were functional for an appreciable portion of the experimental period. Growth reduction probably would have been greater if all of the flood-induced roots could have been removed as soon as they formed.

There has been some controversy about whether flood induced AR have beneficial effects on growth of flooded plants or whether they are merely non-functional expressions of flooding injury. Flooding of soil was very harmful to sunflower plants even though they produced many AR in response to flooding[35]. Gill[6] found that excision of flood-induced AR had a relatively minor effect on leaf growth of *Alnus glutinosa* and attributed little adaptive significance to such roots. Tripepi and Mitchell[34] deemphasized the importance of AR for flood tolerance when they concluded that such roots were not required for survival of flooded *Acer rubrum* and *Betula nigra* seedlings. By comparison, the present study as well as the following lines of evidence indicate that flood-induced AR are physiologically important and confer some degree of flood tolerance to plants that have the capacity to form such roots: (1) Production of AR and flood tolerance of both herbaceous and woody plants often are related. For example, herbaceous plants (*e.g.*, melon, eggplant, peas) which lack the capacity to produce AR in response to flooding are less flood-tolerant than tomato and cucumber which readily produce AR[15,22]. Flood tolerant cultivars of sugar cane and corn produced most adventitious roots[17,26]. In flooded *Lycopersicon esculentum* plants the formation of adventitious roots was correlated with recovery from flooding and resumption of leaf growth[1,20]. Many flood-intolerant woody plants (*e.g.*, *Pinus halepensis*, *P. banksiana*, *P. resinosa*, and *Betula papyrifera*) also have limited capacity to produce adventitious roots when flooded[30,32,33]. Relative flood tolerance of three Eucalyptus species (*E. grandis*, *E. robusta*, and *E. saligna*) was correlated with differences among them in production of AR[2]. Both flood tolerance and capacity to produce adventitious roots on submerged portions of stems were greater in *Eucalyptus camaldulensis* than in *E. globulus* seedlings[29]. Abundant production of AR by *Melaleuca quinquenervia* seedlings was correlated with the high degree of flood tolerance of this species[28]; (2) Flood induced AR increase the capacity for absorption of water and nutrients by flood tolerant plants and thereby compensate for loss of absorbing capacity through decay of a portion of the original root system[11,16].

The fibrous roots of flood tolerant plants may be sustained by anaerobic respiration until AR develop and absorb water and minerals[34]. The AR that form on stems proliferate most in the upper well-aerated portions of submerged soils and in the water layer above. Hence the optimal environment for uptake of minerals is exploited[12,19]. Absorption of water by flooded *Fraxinus pennsylvanica* seedlings was 80 to 90% higher in plants with flood-induced AR on stems than in plants from which such roots had been removed. In addition increased production of AR with time after flooding was highly correlated with reopening of stomata which had closed shortly after flooding was initiated[27]. In flooded *Zea mays* plants leaf water deficits declined when AR emerged[36]. The increased absorption of water associated with the presence of AR increases availability of mineral nutrients to shoots because appreciable amounts of salts are carried upward in the transpiration stream. As the more rapid flow of water through the root xylem sweeps out the salt the decreased concentration of minerals increases active uptake of minerals by roots[20]. Jackson and Drew[16] emphasized that the AR of flood tolerant herbaceous plants often float and grow horizontally. Both characteristics keep such roots close to the air-water interface where enough dissolved O_2 is present to support growth and increase total uptake of mineral nutrients; (3) Flood-induced AR of flood-tolerant species play an important role in oxidizing the rhizosphere and transforming soil-borne toxins to less harmful products. For example, the flood-induced roots of *Nyssa sylvatica* var. *biflora* plants oxidized the rhizosphere whereas unflooded roots of this species did not[8,12]. The flood-induced new roots of the flood-tolerant species, *Fraxinus pennsylvanica* and *Nyssa aquatica*, exhibited greater capacity for oxidizing the rhizosphere than did the new roots of the less flood-tolerant *Platanus occidentalis*[10]; and (4) Flood-induced AR increase the availability of root-synthesized growth hormones, especially gibberellins and cytokinins, to shoots[24,25].

References

1 Aloni B and Rosenshtein G 1982 Effects of flooding on tomato cultivars: the relationship between proline accumulation and other morphological and physiological changes. Physiol. Plant. 56, 513–517.

2 Clemens J, Kirk A M and Mills R D 1978 The resistance to waterlogging of three *Eucalyptus* species, effect of flooding and on ethylene-releasing growth substances on *E. robusta*, *E. grandis*, and *E. saligna*. Oecologia 34, 125–131.

3 Dickson R E, Hosner J F and Hosley N W 1965 The effects of four water regimes upon the growth of four bottomland species. For. Sci. 11, 299–305.

4 Fowells H A 1965 Silvics of forest trees of the United States. U.S. Dept. Agric., Agric. Handb. No. 271.

5 Gill C J 1970 The flooding tolerance of woody species – a review. For Abstr. 31, 671–688.

6 Gill C J 1975 The ecological significance of adventitious rooting as a response to flooding in woody species, with special reference to *Alnus glutinosa* L. Gaertn. Flora 164, 85–97.
7 Hook D D 1984 Adaptations to flooding with fresh water. *In* Flooding and Plant Growth. Ed. T T Kozlowski, pp 265–294. Academic Press, New York.
8 Hook D D, Brown C L and Kormanik P P 1970 Lenticels and water root development of swamp tupelo under various flooding conditions. Bot. Gaz. 131, 217–224.
9 Hook D D, Langdon O G, Stubbs J and Brown C L 1970 Effect of water regimes on the survival, growth, and morphology of tupelo seedlings. For. Sci. 16, 304–311.
10 Hook D D and Brown C L 1973 Root adaptations and relative flood tolerance of five hardwood species. For. Sci. 19, 225–229.
11 Hook D D and Scholtens J R 1978 Adaptations and flood tolerance of tree species. *In* Plant Life in Anaerobic Environments. Eds. D D Hook and R M M Crawford, pp 299–331. Ann Arbor Science Publ. Ann Arbor, Michigan.
12 Hook D D, Brown C L and Kormanik P P 1971 Inductive flood tolerance in swamp tupelo [*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.]. J. Exp. Bot. 22, 78–89.
13 Hosner J F 1959 Survival, root and shoot growth of six bottomland species following flooding. J. For. 57, 927–928.
14 Hosner J F and Boyce S G 1962 Relative tolerance to water saturated soil of various bottomland hardwoods. For. Sci. 8, 180–186.
15 Jackson M B 1979 Rapid injury to peas by soil waterlogging. J. Sci. Food Agric. 30, 143–152.
16 Jackson M B and Drew M C 1984 Effects of flooding on growth and metabolism of herbaceous plants. *In* Flooding and Plant Growth. Ed. T T Kozlowski, pp 47–128. Academic Press, New York.
17 Jat R L, Dravid M S, Das D K and Goswami N N 1975 Effect of flooding and high soil water condition on root porosity and growth of maize. J. Indian Soc. Soil Sci. 23, 291–297.
18 Kozlowski T T 1984 Responses of woody plants to flooding. *In* Flooding and Plant Growth. Ed. T T Kozlowski, pp 129–164. Academic Press, New York.
19 Kozlowski T T and Pallardy S G 1984 Effect of flooding on water, carbohydrates, and mineral relations. *In* Flooding and Plant Growth. Ed. T T Kozlowski, pp 165–193. Academic Press, New York.
20 Kramer P J 1951 Causes of injury to plants resulting from flooding of the soil. Plant Physiol. 26, 722–736.
21 Kramer P J and Kozlowski T T 1979 Physiology of Woody Plants. Academic Press, New York.
22 Krizek D T 1982 Plant response to atmospheric stress caused by waterlogging. *In* Breeding Plants for Less Favorable Environments. Ed. M N Christiansen, pp 293–334. Wiley, New York.
23 Ku K H 1966 Notes on the use of propagation of error formulas. J. Res. Natl. Bur. Standards 70C, 331–341.
24 Reid D M and Crozier A 1971 Effects of waterlogging on the gibberellin content and growth of tomato plants. J. Exp. Bot. 22, 39–48.
25 Reid D M and Bradford K J 1984 Effects of flooding on hormone relations. *In* Flooding and Plant Growth. Ed. T T Kozlowski, pp 195–219. Academic Press, New York.
26 Sartoris G B and Belcher B A 1949 The effect of flooding on flowering and survival of sugar cane. Sugar 44, 36–39.
27 Sena Gomes A R and Kozlowski T T 1980a Growth responses and adaptation of *Fraxinus pennsylvanica* seedlings to flooding. Plant Physiol. 66, 267–271.
28 Sena Gomes A R and Kozlowski T T 1980b Responses of *Melaleuca quinquenervia* seedlings to flooding. Physiol. Plant. 49, 373–377.
29 Sena Gomes A R and Kozlowski T T 1980c Effect of flooding on *Eucalyptus camaldulensis* and *Eucalyptus globulus* seedlings. Oecologia 64, 139–142.
30 Sena Gomes A R and Kozlowski T T 1980d Response of *Pinus halepensis* seedlings to flooding. Can. J. For. Res. 10, 308–311.

31 Tang Z C and Kozlowski T T 1982a Physiological, morphological and growth responses of *Platanus occidentalis* seedlings to flooding. Plant and Soil 6, 243–255.

32 Tang Z C and Kozlowski T T 1982b Some physiological and growth responses of *Betula papyrifera* seedlings to flooding. Physiol. Plant. 55, 415–420.

33 Tang Z C and Kozlowski T T 1983 Further studies in flood tolerance of *Betula papyrifera.* Physiol. Plant. 59, 218–222.

34 Tripepi R R and Mitchell C A 1984 Stem hypoxia and root respiration of flooded maple and birch seedlings. Physiol. Plant. 60, 567–571.

35 Wample R L and Reid D M 1978 Control of adventitious root production and hypocotyl hypertrophy of sunflower (*Helianthus annuus*) in response to flooding. Physiol. Plant. 44, 351–358.

36 Wenkert W, Fausey N R and Watters H D 1981 Flooding responses in *Zea mays* L. Plant and Soil 62, 351–366.