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Original article

Growth response of *Populus* hybrids to flooding

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Summary — The growth responses to flooding of 19 *Populus* clones representing crosses among 7 species from 3 sections were studied under controlled conditions. Softwood cuttings were grown in a greenhouse and subjected to three treatments, well watered and flooded to 10 or 5 cm below the soil surface, for 12 weeks from July to November. Root growth was severely reduced by flooding and stem growth was unaffected for some clones and increased in others. Consequently, clonal mean dry matter production for flooded soils ranged from 107 percent to 62 percent of the control. The capacity to grow roots in waterlogged soil was associated with dry weight production in flooded soil. *Aigeiros* hybrids and the intersectional hybrids *Tacamahaca* x *Aigeiros* showed higher resistance to waterlogged soils than *Tacamahaca* hybrids. *Leuce* hybrids showed a wide range of responses and the *P. tremula* x *P. tremuloides* hybrids ranked high for capacity to grow roots below the water table. Flooding caused all the clones to develop morphological traits associated with oxygen transport to submerged roots : stem hypertrophy, hypertrophied lenticels on the stem and roots, oxidation of the rhizosphere and increased root porosity.

waterlogged soil – root porosity – resistance – roots – morphology

Résumé — Comportement d'hybrides de *Populus* en sol ennoyé. *L'objectif de l'étude était de comparer le développement et l'adaptation de clones de* Populus *dans des conditions simulées d'hydromorphie édaphique, pour apporter aux sélectionneurs une technique précoce de prédiction de l'adaptation des clones aux sols hydromorphes.*

Dix-neuf clones, hybrides interspécifiques, dont les parents appartiennent à 7 espèces des 3 sections principales utilisées en populiculture – Aigeiros, Tacamahaca *et* Leuce *–, ont été utilisés (Tableau I). L'essai s'est déroulé en serre. Des boutures herbacées ont été installées dans un substrat de texture limoneuse, inclus dans des conteneurs d'un volume intérieur d'un litre. Elles ont été soumises à 3 régimes hydriques : bon drainage (témoin), niveau d'eau à 10 cm de la surface du sol, niveau à 5 cm. L'ennoiement a été maintenu pendant 12 semaines, de mi-juillet à mi-novembre. A l'issue de cette période, les observations suivantes ont été réalisées : accroissement aérien et souterrain, modifications morphologiques et porosité racinaire. Du fait d'une différence de croissance, avant l'ennoiement, les clones ont été séparés en deux groupes, pour l'analyse des résultats. Le premier contenait les clones à enracinement rapide. Le second, ceux dont l'enracinement était retardé d'environ une semaine par rapport aux premiers.*

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Les clones ont montré une tolérance remarquable à l'excès d'eau. Ils n'ont eu aucune mortalité. La croissance de certains d'entre eux a été augmentée, ou, à la rigueur, seulement légèrement diminuée, par rapport au témoin (Tableau II). En majorité, les clones ont modifié la répartition de leur biomasse. Si leur développement était réduit, ils l'ont équilibré en augmentant la biomasse de leur partie aérienne et des boutures originelles (Figs 1 et 3). En conséquence, la biomasse sèche totale n'a pas été affectée par l'ennoiement pour les clones du Groupe 1. Pour ceux du Groupe 2, la réduction de biomasse a été moins importante que prévu, malgré la forte diminution de la croissance racinaire.

En général, la productivité des clones était directement liée à l'aptitude de leurs racines à croître dans les horizons ennoyés (Tableaux II et III, Fig. 3). Dans le Groupe 1, un clone de P. alba *(clone 1) et les hybrides intersectionnaux Unal et Beaupré (clones 5 et 4), considérés comme peu adaptés aux sols hydromorphes, ont eu une croissance racinaire exceptionnelle sous le niveau d'eau et sont classés parmi les meilleurs sur le plan de la biomasse produite en milieu ennoyé. A l'opposé, des clones souvent recommandés pour des sols insuffisamment drainés, comme les clones de la section* Tacamahaca, *Fritzi Pauley et Androscoggin (clones 2 et 3) se sont mal comportés en sol ennoyé.*

Dans le Groupe 2, les clones Aigeiros *Robusta et I 214 (clones 6 et 7) se sont comportés d'une façon exceptionnelle en sol ennoyé. Pourtant ils ne sont pas connus pour leur adaptation aux sols hydromorphes. Les 4 hybrides de la section* Leuce, *chez lesquels* P. tremuloides *a été croisé avec* P. alba *(clones 13 et 14) ou* P. tremula *(clones 15 et 16) se sont très bien comportés en sol ennoyé. Ceci est en parfaite concordance avec ce que l'on sait de leurs performances en sol hydromorphe. Comme dans le Groupe 1, les clones de la section* Tacamahaca, P. trichocarpa *et* P. maximowiczii *(clones 17 et 18) ont eu un mauvais comportement en sol ennoyé.*

L'ennoiement a provoqué, chez tous les clones, des développements morphologiques associés au transport de l'oxygène vers les racines noyées : hypertrophie de la tige et des lenticelles de tiges et de racines, oxydation de la rhizosphère et augmentation de la porosité racinaire.

Ces travaux devraient être complétés pour déterminer comment les clones se comportent en milieu forestier dont l'hydromorphie due à l'excès d'eau hivernal est souvent combinée à une sécheresse estivale.

sol hydromorphe – porosité racinaire – résistance – racine – morphologie – test précoce

INTRODUCTION

Millions of hectares of land have management restrictions due to excess soil water; these areas are not only along rivers but also in uplands with poor drainage. Such land is usually managed for forestry purposes, as it is inappropriate for agriculture. The problems caused by flooding place severe restrictions on forest productivity, and the success of forestry in flood-prone areas depends on selection of the right species and silvicultural treatments for the site.

The most important constraint for trees growing in waterlogged soils is the lack of oxygen which can become complete within hours of flooding due to displacement of gas by water, reduced diffusion of oxygen and depletion of oxygen by microorganisms (Scott & Evans, 1955; Coutts & Armstrong, 1976). Secondary effects of flooding are the production by roots of toxic substances such as ethanol (Fulton & Erickson, 1964; Keeley, 1979) and cyanogenic compounds (Rowe & Catlin, 1971) and the development of soil toxins due to reducing conditions (Jones, 1972; Ponnamperuma, 1972). The type and degree of damage depends on the tree species, age, and phenological state and on the soil type (Coutts & Armstrong, 1976; Kozlowski, 1982). Some tree species are killed by as little as 24 hours of flooding and others can withstand continuous flooding for as long as 4 years (Crawford, 1982). Adaptations to flooding include development of aerenchyma (Yu *et al.*, 1969; Jat *et al.*, 1975; Coutts & Armstrong, 1976; Harrington, 1987) for maintenance of oxygen supply to flooded roots and alternative metabolism for growth and maintenance under anoxia (Keeley, 1979; Crawford, 1982).

Several species of *Populus* are recommended for forestry in areas that have poor drainage or are subject to flooding because they are recognized as being tolerant to waterlogged soils (Food and Agriculture Organization of the United Nations, 1980; Soulères, 1984). However, the nature of the tolerance to flooded soils has not been studied and there is little information about which species or clones perform best under flooding. The objective of the present study was to compare the adaptation and development of various *Populus* clones under controlled conditions of simulated waterlogged soils. The ultimate goal was to provide information concerning resistance to waterlogged soils that could be used to develop selection criteria for tree improvement programs.

MATERIALS AND METHODS

A total of 19 clones representing 7 species from 3 sections (Table I) were included in the study. They represent a range of capacity to withstand waterlogged soils based on empirical knowledge, and there is interest in using them in forest plantations where flooding occurs. Some of the clones are already widely used in intensive culture.

Softwood cuttings were taken from new growth in early June and trimmed to a length of 10 to 15 cm and a constant leaf area (one to two leaves depending on the clone). The stem cuttings were poked into flats of a peat-vermiculite mixture and placed in a greenhouse until roots developed. When most of the stem cuttings for a clone developed roots they were separated and transplanted into 1.5 litre (diameter 9 cm and height 26 cm) plastic bottles (1 cutting per bottle) from which the tops had been removed. The bottles had three drainage holes and 2 cm of gravel in the bottom and were enclosed in black plastic. They were filled with a loamy sand collected along a stream on the property of the Centre de Recherche d'Orléans. Particle size distribution for the soil was 6% clay, 17% silt, and 77% sand. The organic matter content was 6.7%. The transplants were transferred to a greenhouse where the treatments were applied. As each clone developed roots at a different rate, 9 days were required to transplant all the clones.

Flooding treatments were begun 15 days after the last clone had been transplanted. Therefore, the period of establishment in the bottles ranged from 23 to 22 days for 5 clones to 15 to 17 days for 14 clones. The treatments consisted of an unflooded control and flooding to 10 cm and 5 cm below the sol surface (-10 cm and -5 cm). The bottles were placed in waterproof containers that were filled with water to the specified level by an automatic irrigation system. In order to replace water lost to evaporation and transpiration the water level was brought up to the treatment level 3 times each day. The entire experiment was watered with a sprinkler as needed to maintain adequate moisture in the unflooded control.

Treatments were arranged in a split-plot design with flooding treatments as the whole plots and clones as sub-plots. There were three replicates. Each clonal sub-plot contained 3 bottles. Treatments were begun on July 18th and terminated when the seedlings were harvested in October and early November.

Each of the plants was measured for dry weight of the new stem, original stem cutting and roots. The leaves had already begun to fall and were not measured. The bottles were cut horizontally into 5 cm long sections. Roots were extracted from the soil for each 5 cm increment of soil depth and measured for dry weight. Observations were made of the condition of the roots and stems of each plant, including discoloration, oxidation of the rhizosphere, lenticel development and stem hypertrophy.

Root porosity was measured for the portion of roots in the 10 to 15 cm deep soil segment for the control and the -10 cm flooding treatment according to established techniques (Jensen *et al.*, 1969; Yu *et al.*, 1969; Luxmoore

Table I. Identification numbers and parents of *Populus* clones evaluated in the study (1).

	Clone Number	*Section*	*Species or Hybrid*	*Cultivar*
Group 1	1	*Leuce*	*P. alba*	605-3B8
	2	*Tacamahaca*	*P. trichocarpa*	Fritzi Pauley
	3		*P. maximowiczii* x *P. trichocarpa*	Androscoggin
	4	*Tacamahaca* x *Aigeiros*	*P. trichocarpa* x *P. deltoides*	Beaupré
	5			Unal
Group 2	6	*Aigeiros*	*P. deltoides* x *P. nigra*	Robusta
	7			I214
	8	*Leuce*	*P. alba*	602-1
	9		*P. tremula*	117-50-1
	10		*P. tremuloides*	212-66
	11		*P. tremula* x *P. alba*	710-23
	12			706-10
	13		*P. alba* x *P. tremuloides*	812-1-6
	14		*P. tremuloides* x *P. alba*	808-111-6
	15		*P. tremula* x *P. tremuloides*	327-1
	16			310-8
	17	*Tacamahaca*	*P. trichocarpa*	36-134
	18		*P. maximowiczii*	12-150
	19	*Aigeiros* x *Tacamahaca*	*P. nigra* x *P. trichocarpa*	Roxbury

(1) Cultivar numbers provided by the station d'amélioration des arbres forestiers, INRA, Ardon 45160 Olivet, France.

et al., 1972). Root porosity measurements were only made for clones 2, 4, 12, 15, and 19.

Response indices for total dry weight and for the dry weight of roots below and above the water table were calculated as the plot mean for a flooding treatment divided by the plot means for its control. Preliminary analysis showed that the clonal response index for total dry weight for the -5 cm treatment was significantly correlated with date of transplanting; therefore, the data were divided into two groups for separate analyses. Group 1 comprised clones 1-5 with 22 to 23 days of establishment and Group 2 comprised clones 6-19 with 15 to 17 days of establishment before beginning treatments. Analysis of variance was used to test the significance of treatment and clonal effects. The least significant difference test and Duncan's multiple range test were used to test for significant differences at the 5 percent level among treatments and clonal means, respectively (Steel & Torrie, 1980).

RESULTS

Dry Matter Allocation

Clones in Group 1 showed flooding to −10 cm significantly reduce root weight by 14% and increased both the original stem

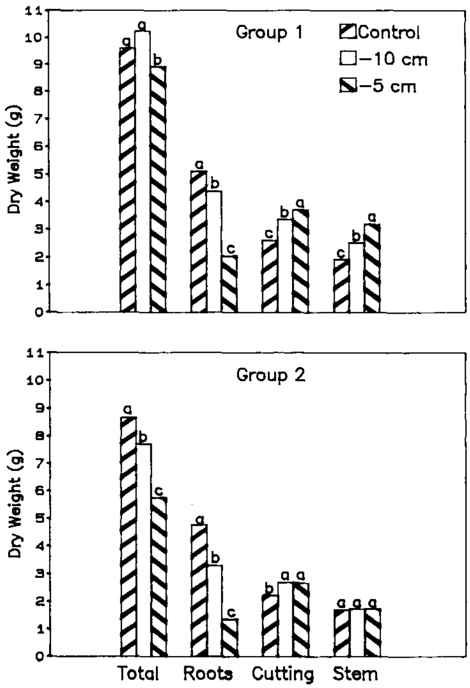

Fig. 1. Effects of flooding to −10 cm and −5 cm on dry weight of the total plant, roots, original cutting and new stem for Groups 1 and 2. Different letters ont top of the bars indicate treatment means that are different at the 5 % level.

cutting and new stem dry weight by 30% (Fig. 1). Flooding to −5 cm reduced root weight by 60%, and increased to original stem cutting and new stem weight by 43 and 60%, respectively. In contrast, Group 2 clones showed flooding to −10 cm reduced total plant weight by 11% and root weight by 31%. Flooding to −5 cm reduced total plant by 34% and root weight by 72%. Both flooding treatments increased the original stem cutting dry weight by 21%.

The height growth response to the flooding treatment was essentially the same as the response of stem dry weight. At the start of the treatment average height was 15.3 and 21.6 cm for Groups 1 and 2. Treatment effects on height growth were significant in Group 1. Average height growth was 25.5, 29.8 and 34.3 cm for the control, −10 cm and −5 cm treatments, respectively. In Group 2 the average height growth was 26.3 cm and the treatment showed no effect.

Flooding altered the allocation of dry weight to roots, original stem cutting and new stems (Fig. 2). In both groups of clones the proportion of dry weight allocated to roots declined from 54% in the control to 23% in the most severe flooding treatment. Correspondingly, mean allocation to the original stem cutting and to the new shoot was increased under flooding.

The response index for total dry weight was significantly different among clones in Group 2 but not in Group 1. As the response index did not show a significant

Table II. Clonal differences in response of total dry weight to flooding (1).

	Clone	*Response index for total dry weight*
Group 1	1	1.07 A
	4	1.06 A
	5	1.06 A
	3	0.92 A
	2	0.89 A
Group 2	13	0.95 a
	6	0.89 ab
	14	0.86 abc
	8	0.85 abc
	15	0.84 abc
	7	0.82 abcd
	12	0.81 abcd
	17	0.76 abcd
	16	0.73 bcd
	19	0.71 bcd
	18	0.69 bcd
	10	0.68 bcd
	11	0.65 cd
	9	0.62 d

(1) Within-groups means followed by the same letter are not different at the 5% level. (See Table I for clone identification).

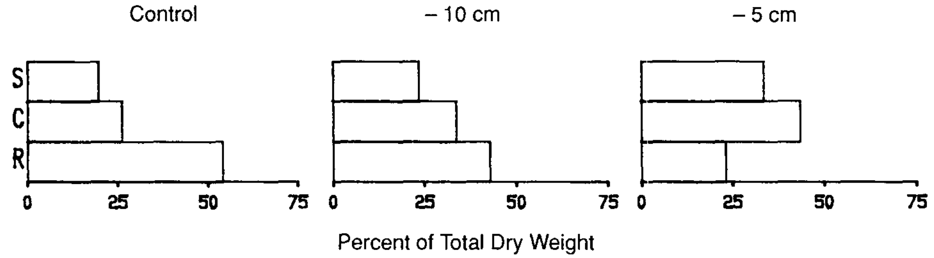

Fig. 2. Effects of flooding to –10 and –5 cm on allocation of dry matter to roots (R), original cutting (C) and stem (S) for all clones combined.

interaction between treatment and clone for either group, indexes were averaged over both flooding treatments to show clonal differences (Table II). The average response index ranged from 1.07 to 0.89 for Group 1 and from 0.95 to 0.62 for Group 2 (Table II). The *Aigeiros* hybrids Robusta and I214 (clones 6 and 7) showed above average performance while the *Tacamahaca* clones 36-134 and 12-150 (clones 17 and 18) showed below average performance. Among the *Leuce* hybrids (clones 8-16 in Group 2), which showed the full range of response indices, both *P. alba* x *P. tremuloides* hybrids (clones 13 and 14) showed high performance. The response indices for the intersectional hybrids *(Tacamahaca* x *Aigeiros)* were high for Beaupré and Unal (clones 4 and 5) in Group 1 and low for Roxbury (clone 19) in Group 2.

Root Growth

Root growth in the soil below the water table was greatly reduced by flooding. The average response index for root dry weight below the water table for both groups was 0.12 and 0.08 for the –10 and –5 cm treatments. In contrast, root growth above the water table was increased. Group 1 clones showed an average response index for root dry weight above the water table of 1.72 and 1.96 for the –10 and –5 cm treatments. Corresponding values for Group 2 were 1.24 and 1.31.

Clonal differences in response index for root dry weight above and below the water table were similar for the two flooding treatments and consequently only the values for the –10 cm treatment are reported here (Table III). Clones in Group 1 showed significant differences in root growth response index below the water table but not above. In contrast, Group 2 clones showed significant differences below and above the water table.

Clonal values for the response index for root dry weight below the water table ranged from 0.01 to 0.22 (Table III). The *Aigeiros* hybrids Robusta and I214 (clones 6 and 7) ranked highest in Group 2. The *Tacamahaca* hybrids Fritzi Pauley and Androscoggin (clones 2 and 3) ranked lowest in Group 1. Also, in Group 2 the *Tacamahaca* clones 36-134 and 12-150 (clones 17 and 18) showed poor performance. *Leuce* hybrids showed a wide range of responses. In Group 1 the *P. alba* clone 605-3B8 (clone 1) ranked highest. In Group 2 two *P. tremula* x *P. tremuloides* hybrids 327-1 and 310-8 (clones 15 and 16) ranked high; Again the response indexes for the intersectional hybrids ranged from high for Unal (clone 5) to low for Roxbury (clone 19).

Table III. Clonal differences in root growth response to flooding above and below the water table (1).

	Clone	Response Index for Dry Weight of Roots Below Water Table at −10 cm	Clone	Above Water Table at −10 cm
Group 1	1	0.22 A	5	2.07 A
	5	0.19 AB	2	2.00 A
	4	0.09 BC	4	1.62 A
	2	0.07 C	1	1.52 A
	3	0.03 C	3	1.41 A
Group 2	6	0.22 a	13	1.80 a
	7	0.19 ab	6	1.60 ab
	16	0.15 abc	14	1.48 abc
	15	0.13 bc	16	1.46 abc
	13	0.10 cd	8	1.40 abc
	12	0.08 cde	17	1.37 bc
	8	0.08 cde	15	1.36 bc
	11	0.05 de	7	1.19 bcd
	9	0.05 de	10	1.19 bcd
	10	0.04 de	12	1.09 cd
	14	0.03 de	19	1.07 cde
	17	0.03 de	18	0.92 de
	19	0.03 de	9	0.76 e
	18	0.01 e	11	0.72 e

(1) Within-groups means followed by the same letter are not different at the 5% level. (See Table I for clone identification).

The rankings of the clones were somewhat different for the response index for root dry weight above the water table (Table III). Nonetheless, in Group 2 the *Aigeiros* hybrid Robusta (clone 6) ranked among the highest and the *Tacamahaca* clone 12-150 (clone 18) ranked low. The *Leuce* hybrids again showed a wide range of responses.

Flooding altered the distribution of roots with depth (Fig. 3). Root growth in the control treatment was well distributed through the entire soil depth. In contrast, flooding severely limited root penetration below the water table. Deep root penetration below the water table was shown by the intersectional hybrid Unal (clone 5) in Group 1 and *Leuce* and *Aigeiros* hybrids 310-8 and Robusta (clones 16 and 6) in Group 2. Root penetration was severely limited for the *Tacamahaca* hybrids 12-150 and Androscoggin (clones 18 and 3) in both groups.

Morphology

Flooding did not cause any mortality, but it did result in yellowing of the leaves and early leaf fall in all clones. The original stem cutting extended below the water table and in all clones it became hypertrophied and showed hypertrophied lenticels. The increased diameter of the cuttings with flooding was due primarily to increased bark thickness. Hypertrophied lenticels were also numerous on the roots. All clones showed evidence of oxidation of the rhizosphere : blackening of roots and a black halo in the soil around the roots as

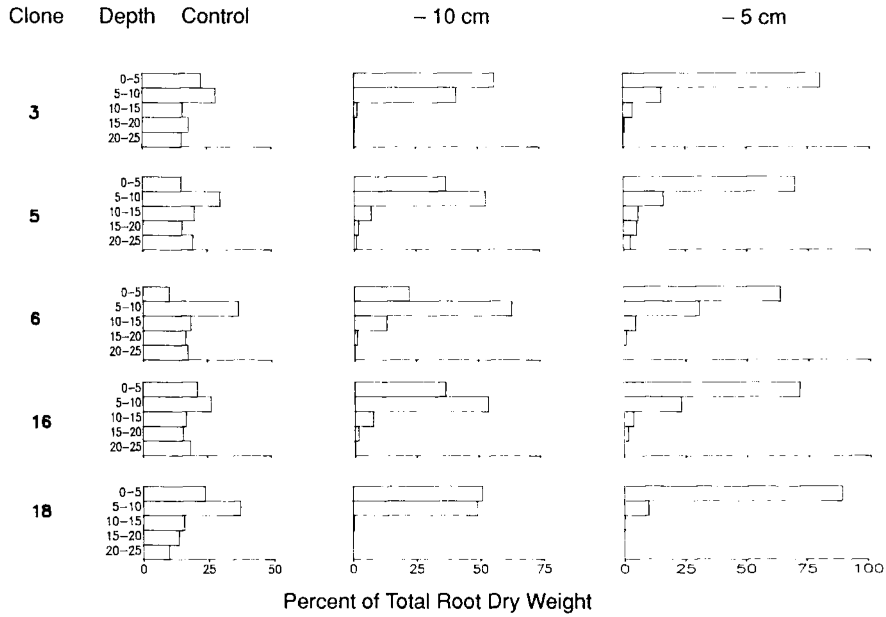

Fig. 3. Effects of floodig to –10 cm and –5 cm on distribution of roots in the soil for selected clones. See Table I for clone identification.

well as reddish brown iron oxides encrusting and cementing soil particles in a sheath around the roots (Levan, 1985).

It was not possible to determine if adventitious roots developed because the flooding treatments were below the soil surface. Flooding significantly increased root porosity from 2.80 to 7.45%. Clonal differences in root porosity were not significant and the interaction between clone and treatment was not significant.

DISCUSSION

The *Populus* clones included in this study showed remarkable tolerance to flooded soils; they experienced no mortality and some clones showed increased growth or only a slight reduction in growth following flooding for over 12 weeks (Table II). The greatest damage from flooding usually occurs during the growing season and dormant season flooding frequently has little effect (Minore, 1968; Kozlowski, 1982). However, 100% survival has been shown previously for short-term flooding of *Populus trichocarpa* during the growing season (Harrington, 1987; Smit, 1988).

Most of the clones showed the capacity to alter the allocation of growth to favor the stem and cutting when root growth was restricted (Fig. 1). The average response of Group 1 was to increase cutting and stem dry weight enough to compensate for reduced root growth and as a consequence total dry weight showed little effect of flooding. Group 2 clones increased cutting dry weight due to flooding but not enough to offset the much greater reduction in root dry weight.

The most frequently reported response to flooding of trees is reduced growth which is more severe for the roots than the stems and leaves (Newsome *et al.*, 1982; Tang & Kozlowski, 1982a, 1982b, 1983; Hook *et al.*, 1983; Osonubi & Osundina, 1987). On the other hand, well adapted species such as *Nyssa sylvatica* may show reduced root growth and no effect on shoot growth (Keeley, 1979). Previous studies have also shown top growth to be stimulated by flooding in *Nyssa aquatica* (Hook & Brown, 1973; Dickson & Broyer, 1972), *Taxodium disticum* (Dickson a Broyer, 1972) and *Alnus rubra* (Harrington, 1987). In the current study the stimulation of top growth in Group 1 increased with the severity of flooding which suggests that the effect was not due simply to increased water supply in the flooded treatments, but to restricted root growth.

The allocation of dry matter to the roots and shoots is generally believed to be under control of a sensitive feedback system that maintains an adaptive balance between the different plant organs despite seasonal imbalances (Drew & Ledig, 1980). Flooding greatly altered the allocation of dry matter between roots and shoots. Roots depend on carbohydrates from leaves for growth. Evidence suggests that root and shoot growth compete for carbohydrates and that use of carbohydrates for shoot growth can restrict root growth (Eliasson, 1968, 1971). Perhaps when root growth is restricted by flooding the supply of carbohydrates and consequently shoot growth are increased. The reduced root system apparently supplies adequate moisture and nutrients for increased top growth. It has been suggested that basipetal transport of auxin in plants is impeded by flooding, resulting in high levels in tissues above the water line and deficient levels below (Kramer, 1951). This may explain in part the increased growth of the tops.

The original stem cuttings, which were partially submerged in the flooding treatments, became swollen and covered with hypertrophied lenticels. This response was reflected in their greater dry weight. Hypertrophy of stem tissue, as shown by the stem cutting, under flooded conditions has been frequently reported (Newsome *et al.,* 1982; Tang & Kozlowski, 1982a; Osonubi & Osundina, 1987) and has been attributed to increased bark development (Yamamoto *et al.,* 1987) as it was in this study. The thicker bark is composed of abundant low density cells and extensive intercellular spaces and has been shown to be associated with increased ethylene production in flooded plants (Yamamota *et al.*, 1987).

Group 1 clones tended to show a smaller reduction in total growth due to flooding than Group 2 clones (Table II), probably because they were better established prior to the flooding treatments. Thus, it is not correct to compare clones in the different groups. Nonetheless, it is worth noting some trends in clonal responses that are evident.

In general clones that ranked high in the amount of roots produced under flooded conditions also ranked high in total dry weight production (tables II and III). Both *Aigeiros* clones Robusta and I214 in Group 2 showed exceptional root growth below the water table which is somewhat surprising, as they are not considered the best choice for waterlogged soils. In contrast, *Tacamahaca* hybrids, especially the cultivar Fritzi, which are frequently recommended for waterlogged soils (Teissier du Cros, 1980; Souleres, 1984) ranked low in both groups for growth in the flooding treatments. The poor performance of the *Tacamahaca* hybrids may have resulted from the study being conducted with a sandy soil, since they usually how superior growth on heavy and compact clay soils (Soulères, 1984).

The study included a high proportion of *Leuce* hybrids and they showed a wide range of responses from highest to lowest for some of the tests. Much interest has been expressed in the aspen hybrids, crosses between *P. tremula* and *P. tremuloides,* for forestry planting on waterlogged soils (Lemoine, 1973; Soulères, 1984). In the current study the clone 327-1 (clone 15) showed above average growth for both roots and total dry weight on waterlogged soil (Table III).

All of the clones showed adaptations to flooding that are associated with the capacity to transport oxygen to submerged roots : stem hypertrophy, hypertrophied lenticels, increased root porosity and oxidation of the rhizosphere (Kozlowski, 1982). Flooding caused root porosity to nearly triple from 2.80 to 7.45%. In agronomic crops such as maize, wheat, sunflower, barley and tomato, the level of root porosity and the relative increase in porosity with flooding have been found to be correlated with degree of tolerance to flooding among species and among cultivars within species (Yu *et al.,* 1969; Jat *et al.,* 1975). The level of porosity in *Populus* is lower than that reported for flooded *Salix sp.* (42%) and higher than that for *Pinus strobus* (less than 3%) (Levan, 1985). *Quercus robur,* which is considered well adapted to flooded soils, showed a root porosity of 1 to 4% in drained soil and a 2- to 4-fold increase in porosity with flooding. In contrast *Q. rubra,* which is less well adapted to flooding, showed a root porosity of less than 3% in drained soil and no increase with flooding (Belgrand, 1983).

CONCLUSIONS

Some *Populus* clones show an increase in allocation of biomass to stem tissue when grown in waterlogged soil. It remains to be determined if this response is generally found in the field and in older trees. If this effect also occurs in plantations it may contribute to explaining differences among sites in productivity of merchantable stem wood.

The clones in this study showed a wide range in capacity to grow roots into waterlogged soil that correlated with total growth in the flooding treatments. However, some clones that were expected to show high resistance to waterlogged soils, such as the *Tacamahaca* clones Fritzi Pauley, Androscoggin, 36-134 and 12-150, showed below average performance in their groups. Also, clones that were not known for their resistance to flooded soils, including Beaupré, Unal, Robusta, I214 and a *P. alba* clone (605-3B8), performed exceptionally well. The aspen hybrids 327-1 and 310-8 showed a high capacity for root growth below the water table, as expected.

The techniques employed provided an opportunity to develop preliminary information on clonal response to flooding. Further work needs to be done to determine how the various clones respond to flooding in the field at older ages. As many forest sites are subject to temporary flooding followed by summer drought, it would be interesting to determine clonal response to alternating conditions of waterlogging and drought (Levy, 1971; Soulères, 1984).

In general, the *Populus* clones in this study showed tolerance to flooding as evidenced by the lack of mortality and development of morphological traits generally considered to be adaptations for transport of oxygen to submerged roots (Kozlowski, 1982). As expression of these traits was uniform among the clones, they could not be used to determine the level of flooding tolerance. It is possible that more precise quantification of these traits could lead to methods for ranking clones by level of adaptation to flooding. In addition, a more severe flooding treatment, to the soil surface or above, might have caused mortality in some of the clones.

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