Adaptive responses of *Lepidium latifolium* to soil flooding: biomass allocation, adventitious rooting, aerenchyma formation and ethylene production

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**Abstract**

*Lepidium latifolium*, perennial pepperweed, is an exotic crucifer that has spread explosively in recent years in wetlands and riparian areas of the western United States. Adaptive responses of *L. latifolium* to different durations of 0, 3, 7, 15, 30 and 50-day soil flooding treatment were investigated. Biomass allocation, adventitious rooting, aerenchyma development and ethylene production in plants were measured. Compared with controls maintained at −20 kPa soil matric water potential, flooding stress reduced total biomass of *L. latifolium*. After 7 days of flooding, the total biomass and root/shoot ratio of flooded plants were significantly less than those of unflooded controls. The number of adventitious roots on the stem base increased with the duration of flooding. Root porosity was much higher in the flooded plants than in the unflooded controls after 3 days of treatment and rose to 43% after 50 days. Ethylene production in roots was higher in flooded plants than in the control throughout the 50-day duration of flooding and peaked at 7 days. The reduction in the root/shoot ratio, adventitious rooting, and aerenchyma development in flooded *L. latifolium* are important contributions to flood tolerance. *L. latifolium* resembled species adapted to standing water conditions in terms of having an initially high porosity, but it resembled species adapted to either saturated or occasionally flooded habitats in terms of the degree of increase in root porosity under flooded conditions. However, in growth of biomass, *L. latifolium* was more like plants that do not grow in mostly saturated conditions. Thus, *L. latifolium* appears to be a plant that exhibits plasticity to tolerate or survive saturated conditions, but not to grow well under these conditions. This may be an adaptation to arid or semiarid riparian habitats where spring flooding and summer drought are characteristic. © 2002 Elsevier Science B.V. All rights reserved.

**Keywords:** Invasive species; Flood tolerance; Aerenchyma; Adventitious rooting; Ethylene; Wetlands; Tall whitetop

1. **Introduction**

*Lepidium latifolium* L., perennial pepperweed, is an invasive exotic weed that is widely distributed in the western United States, coastal New Eng-
land, Mexico, Canada and Australia (Young et al., 1995; Rollins, 1993; Kloom, 1973). This weed is native to southeastern Europe and is extremely competitive in many habitats, especially in wetlands and riparian areas. It has only recently become a serious problem in the western United States. *L. latifolium* proliferates in lowland ecosystems to form dense monospecific stands that can crowd out more desirable native wetland species (Young et al., 1995). *L. latifolium* exhibits a wide range of ecological amplitude of adaptation to different environmental factors. It is a highly flood tolerant species and survives both exceptionally long periods of flooding and relatively dry conditions with a large perennial rhizome. This ability to survive varied flooding and dry conditions led us to investigate whether it has morphological and physiological adaptations similar to other hydrophytes.

The initial eco-physiological response of most plants to flooding is wilting and stomatal closure within a day or two following root exposure. Reduction in net photosynthesis is observed in many flooded plants (Bradford, 1983; Vu and Yelenosky, 1991; Pezeshki et al., 1996). These changes decrease shoot and root growth and even result in root damage and death in many plant species (Kozlowski, 1984). Seedlings of bald cypress (Pezeshki et al., 1999) and oaks (Pezeshki et al., 1996, 1999) exhibit a significant reduction in total biomass in response to flooding. Soil saturation also reduces biomass allocation to roots and changes biomass allocation pattern in many woody and herbaceous plants (Tang and Kozlowski, 1982; Voeseen et al., 1989; Naidoo and Naidoo, 1992; Rubio et al., 1995), which diminishes plant root metabolism and oxygen demand.

Adventitious rooting is one of the important adaptive mechanisms of wetland plants for replacing existing roots that have been killed or whose function is impaired by stressed environments (Vartapetian and Jackson, 1997; Pezeshki, 2001). Soil flooding induces adventitious rooting on submerged portions of stems above soil line (Tang and Kozlowski, 1982). The adventitious roots are important for plants under root hypoxia or anoxia to obtain oxygen from the environment because adventitious roots may directly get oxygen from the surroundings and internally transport oxygen through aerenchyma (Drew et al., 1979; Laan et al., 1989). However, little is known of the mechanism of flood-induced adventitious rooting (Pezeshki, 2001). Application of auxin induces adventitious root formation in two species of *Rumex* with different abilities of developing adventitious roots (Visser et al., 1995). In flooded *Rumex palustris* Sm., auxin delivered by basipetal transport to the shoot base is a prerequisite for rooting, but no accumulation of auxin takes place (Visser, 1995; Visser et al., 1995) as has been shown in sunflower plants (Wample and Reid, 1979). In contrast, much less certain is the role of ethylene in the formation of adventitious roots (Laan et al., 1989; Drew, 1992). Adventitious rooting is strongly enhanced by both exogenous ethylene and flood-induced accumulated ethylene in the plant tissue (Visser et al., 1995, 1996). Studies on rooting in cuttings showed that ethylene might have either a stimulative (e.g. *Picea abies* Karst. Bollmark and Eliasson, 1990) or negative (e.g. Pea Nordstrom and Eliasson, 1984) effect on the formation of adventitious roots.

Aerenchyma formation is another important adaptive response in wetland plants to soil flooding or waterlogging (Justin and Armstrong, 1987; Vartapetian and Jackson, 1997). Aerenchyma provides a low-resistance internal pathway for gas exchange between the plant parts above the water and the flooded tissues, and improves the internal supply of oxygen (Armstrong, 1979). In flood-tolerant species, such as *Senecio* (Smirnoff and Crawford, 1983) and *Rumex* (Laan et al., 1989) and flood-intolerant species, such as *Zea mays* L. and *Triticum aestivum* L. (Trought and Drew, 1980), oxygen deficiency in flooded soils increases the amount of aerenchyma formation in roots. The process is mediated by ethylene (Drew et al., 1979) that is produced in greater amounts under hypoxia (Jackson, 1985). The increase in ethylene production promoted by low levels of O2 is due to increased levels of 1-aminocyclopropane-1-carboxylic acid (ACC), a precursor of ethylene (Bradford and Yang, 1980), resulting from enhanced ACC synthase activity (Wang and Arteca, 1992). There is a close relationship between enhanced ethylene production and aerenchyma formation in some species (Drew et al., 1979; Justin...
and Armstrong, 1991). In rice, an obligate hydrophyte, however, aerenchyma formation is part of ordinary root growth and is not increased by poorly aerated conditions (John et al., 1974).

Due to the relatively recent nature of the problem with *L. latifolium* as a highly invasive exotic, little is known about the ecophysiology of *L. latifolium* and few economically feasible options exist for effective control of this weed. Our general goal was not to demonstrate new mechanisms of adaptation or the biochemical mechanisms behind them for wetland plants in general, but was to show what adaptations this very important invasive plant manifests. A thorough knowledge of the ecophysiology of invasive species is essential in understanding what habitats are subject to invasion, and the possibilities for control. Since this species is extremely competitive in wetlands and riparian areas, we hypothesized that soil flooding leads to physiological responses and further morphological adaptations that help this species tolerate flooding stress. Rapid biochemical changes are easily induced through short-term soil flooding or hypoxia, but anatomical and morphological changes are more likely to be involved in the long-term acclimation to flooding stress. Our specific hypotheses were that (1) saturated conditions decrease growth of *L. latifolium* but allow survival, compared with a moist soil condition (−20 kPa); (2) root/shoot ratios are reduced under saturated soil conditions; (3) adventitious roots develop in response to saturated soil conditions; (4) root porosity is initially low but increases rapidly in response to soil saturation; and (5) ethylene is released in *L. latifolium* in response to saturated soil conditions.

2. Materials and methods

2.1. Plant material

Seeds of *L. latifolium* were collected from the University of Nevada Farm in Reno, NV, germinated in washed sand in an aluminum tray in the greenhouse, and watered using half-strength Hoagland’s solution containing 2 mM Ca(NO$_3$)$_2$, 1.1 mM MgSO$_4$, 3.0 mM KNO$_3$, 0.5 mM KH$_2$PO$_4$, 66.7 μM EDTA–Fe, 22.5 μM H$_2$BO$_3$, 10 μM MnSO$_4$, 0.2 μM CuSO$_4$, 0.35 μM ZnSO$_4$ and 0.1 μM (NH$_4$)$_6$Mo$_7$O$_2$$_4$. Seedlings were transferred to 10 × 10 × 9 cm pots containing natural riparian soil of the Truckee Series (a fine-loamy, mixed, superactive, mesic Fluvaquentic Haploxerolls) from the University of Nevada Farm. Afterwards, 120 small plants, with 3–5 mature leaves and roots of uniform length, were selected and randomly transplanted into twenty 113 l plastic barrels containing natural riparian soils from the University of Nevada Farm. Each barrel was placed in the open air with six plants per barrel. Before initiation of the soil treatments, plants were allowed to grow in the open air and maintained under well-aerated soil conditions with a soil matric water potential of −20 kPa for 7 days, using tensiometers to monitor soil matric water potential. After the initial 7-day period, 16 of the barrels were randomly assigned to the soil flooding treatments and the soil in the other four barrels was kept at a soil matric water potential of −20 kPa as a control. Soil was flooded to about 1 cm above the soil surface. Soil flooding treatments included six durations of 0, 3, 7, 15, 30 and 50 days; six plants for controls and 18 plants for treatments for each duration. At 0, 3, 7, 15, 30, and 50 days after soil flooding, root porosity and ethylene production were measured and plant tissues samples were collected for measurement of root, stem and leaf biomass. Samples for biomass were dried at 70 °C for 72 h. Analysis of all samples was performed in triplicate except where indicated.

2.2. Aerenchyma formation and adventitious rooting

On days 0, 3, 7, 15, 30, 40 and 50 after soil flooding, root porosity (aerenchyma) was measured in four replicates by the pycnometer method (Jensen et al., 1969). Adventitious roots above the soil surface per plant in the flooded treatments were also counted and plant morphology was noted.
2.3. Ethylene production

Ethylene in fine roots and mature leaves was determined by gas chromatography. Flooded and unflooded plants were sampled at 0, 3, 7, 15, 30 and 50 days after the initiation of soil flooding. Leaf and root samples were taken from plants. Roots were washed and immediately gently blotted dry using paper towel. Leaf and root samples then were transferred to 25 ml vials with filter paper moistened with 1 ml of distilled water. Vials were immediately sealed with gas-tight septa caps. Ethylene was allowed to diffuse from the roots and accumulated in the headspace for 2 h at 25 °C. Then 1 ml of gas sample from the headspace was withdrawn with a gas-tight syringe and was injected into a HP 5790A gas chromatograph equipped with CP-Pora PLOT Q Capillary column: 0.53 mm id; 25 m length; 20 μm df; 250/250 T-Max and a flame ionization detector. Column, injection and detector temperatures were 45, 175 and 275 °C, respectively, using helium as carrier gas. Identification of ethylene was confirmed by analysis of a certified ethylene standard (Alltech Assoc., Inc.). The amount of released ethylene was expressed as μmol kg−1 h−1.

2.4. Experimental design and statistical analysis

The experiment consisted of two factors (two flooding treatments and six durations of flooding). Data on biomass, root/shoot ratio, root porosity and ethylene production were analyzed with the analysis of covariance, using the general linear model (GLM) procedure of the Statistical Analysis System (SAS Institute Inc., Cary, NC). Variation was partitioned into flooding treatment (a categorical variable) and the duration of flooding (a continuous variable) as main effects, and interaction. Differences between flooded and control treatments on individual dates were also indicated using the Student’s t-test. Changes in the number of adventitious roots were tested with one-way ANOVA (analysis of variance) supplemented with a multiple comparison of means using Duncan’s multiple range test at $P < 0.05$.

3. Results

3.1. Plant growth and biomass

After only 3 days of flooding, leaves of *L. latifolium* exhibited chlorosis, an increasingly reddish-green color, and the original root systems stopped growing downwards. Compared with the control plants, observations showed that root penetration and leaf expansion of flooded plants appeared to be inhibited. On day 7 after initiation of flooding, we observed the emergence of a few adventitious roots, and some damage of the original root system, as well as the re-direction to horizontal growth of existing roots. Some roots that grew to the water surface turned green and some new shoots emerged from those roots. After 30 days of flooding, the damage and death of many original root systems was observed in most flooded plants. Some 83% of the flooded plants and 17% of the control plants began to flower and exhibited markedly senescent symptoms after 35 days of flooding (data not shown). Despite the observed effects of flooding, all flooded plants survived.

Soil flooding led to a significant reduction in total biomass of *L. latifolium*, compared with the control plants (Fig. 1). On day 50 after initiation of flooding, total, root, stem and shoot biomass of flooded plants was 80, 85, 48 and 85% less than controls, respectively. Also, the duration of flooding greatly changed biomass allocation pattern in the plants (Fig. 1). In the flooded plants, the root/shoot ratio ranged from about 0.5 to 0.7 throughout the duration of flooding. The root/shoot ratio in the control plants increased significantly as they grew. On day 50 after initiation of flooding, the root/shoot ratio in flooded plants was only 53% of the control plants.

Analysis of covariance indicated that flooding treatment had a significant effect on total biomass ($P < 0.0001$) and root/shoot ratio ($P < 0.002$). Also, the interaction of flooding treatment and the duration of flooding had a significant effect on total biomass ($P < 0.0001$) and root/shoot ratio ($P = 0.007$) of *L. latifolium*. Thus, these results show that the growth curve of total biomass or the root/shoot ratio for flooded plants was signifi-
cantly different from that for the control plants because their slopes of growth curves (their interactions) were significantly different (Fig. 1).

3.2. Aerenchyma formation and adventitious rooting

In the present study, *L. latifolium* showed a fairly high root porosity of about 26% in unfllooded plants (Table 1). After flooding, root porosity significantly increased up to 52% in flooded plants and was much higher in the flooded plants than in the control plants throughout the 50-day duration of flooding (Table 1). An analysis of covariance, using $y = \text{root porosity}$; $x_1 = \text{duration}$, $x_2 = (\text{duration})^2$, $x_3 = \text{flood treatment}$, showed a significant effect of treatment ($P < 0.001$) and duration ($P < 0.01$). In flooded plants, the number of adventitious roots emerging on the stem base significantly increased with the duration of flooding as tested by an analysis of variance ($P < 0.05$) (Table 1). No adventitious roots were found on the control plants.

3.3. Ethylene production

Ethylene production in roots was higher in the treatment than in the control throughout the 50-day duration of flooding and peaked at 7 days (Fig. 2A). An analysis of covariance using $y = \text{ethylene production}$, $x_1 = \text{duration}$, $x_2 = (\text{duration})^2$, $x_3 = \text{flood treatment}$, showed a significant effect of treatment ($P < 0.01$) and duration ($P < 0.05$). Ethylene production in the roots of all flooded plants was markedly higher than that in the leaves (Fig. 2A vs. B). In contrast to the results for roots, ethylene production in leaves of flooded plants was lower than in the control plants for the duration of flooding except for that at 30 days of flooding (Fig. 2B). However, an analysis of covariance showed an overall significant effect of duration ($P < 0.05$) but treatment was not significant ($P = 0.3$). There was a significant positive correlation ($r = 0.53$, $P < 0.01$, $n = 23$) of ethylene production in roots to root porosity in flooded plants (not shown). There was a significant negative correlation of ethylene production in roots to the number of adventitious roots in flooded plants ($r = 0.78$, $P < 0.01$, $n = 20$) (Fig. 3).

4. Discussion

Extended flooding greatly reduced growth and inhibited the increase in root/shoot ratio observed in the control plants (Fig. 1). These results confirm our first hypothesis that saturated conditions decrease growth of *L. latifolium*, while allowing it to survive, and our second hypothesis that they decrease the root/shoot ratio. Tang and Kozlowski (1982) also reported that after 30 days of flooding, leaf, stem and root biomass in flooded *Quercus macrocarpa* Michx. seedlings was 95, 60 and 42% of the control plants, respectively, and the ratio of root to shoot in flooded seedlings was less than 50% of unflooded plants. In many species, inhibition of root growth in response to soil flooding has been reported (Kozlowski, 1984;
Table 1
Responses of adventitious rooting and aerenchyma development (root porosity) in *L. latifolium* to the different durations of soil flooding

<table>
<thead>
<tr>
<th>Duration (days)</th>
<th>Adventitious roots (Number per plant)</th>
<th>Root porosity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Flooded</td>
<td>Control</td>
</tr>
<tr>
<td>0</td>
<td>0 d*</td>
<td>26.3 ± 2.0</td>
</tr>
<tr>
<td>3</td>
<td>0 d</td>
<td>27.7 ± 2.6</td>
</tr>
<tr>
<td>7</td>
<td>0.4 ± 0.2 d</td>
<td>26.4 ± 2.6</td>
</tr>
<tr>
<td>15</td>
<td>3.1 ± 0.4 d</td>
<td>29.3 ± 4.0</td>
</tr>
<tr>
<td>30</td>
<td>9.3 ± 0.9 c</td>
<td>27.6 ± 4.2</td>
</tr>
<tr>
<td>40</td>
<td>14.4 ± 2.0 b</td>
<td>n.d. b</td>
</tr>
<tr>
<td>50</td>
<td>18.6 ± 2.2 a</td>
<td>21.4 ± 3.8</td>
</tr>
</tbody>
</table>

No adventitious roots were found on control plants. One-way ANOVA (analysis of variance) showed a significant effect of the duration of flooding on the number of adventitious roots (*P* < 0.05). Analysis of covariance showed a significant effect of treatment (*P* < 0.001) and the duration of flooding (*P* < 0.01) on root porosity. Data are the mean ± S.E. of 18 plants for adventitious roots and are the mean ± S.E. of four plants for root porosity. * And ** represent the significant difference between the flooded and control plants at *P* < 0.05 and 0.01 by *t*-tests, respectively.

*Means within a column followed by the different letters indicated a significant difference at *P* < 0.05 by Duncan’s multiple range test.*

Rubio et al., 1995; Pezeshki et al., 1996). In flooded conditions, this biomass allocation pattern and the shallow distribution of roots in *L. latifolium* are an adaptive mechanism to soil flooding, because a decrease in biomass allocation in roots diminishes the metabolic requirement of stressed roots for oxygen, water and nutrient uptake (Naidoo and Naidoo, 1992; Joly, 1994). In addition, plants may be tolerant of prolonged flooding if they can develop a shallow root system that utilizes the oxygen present near the soil surface (Justin and Armstrong, 1987).

In response to soil flooding, adventitious roots on the stem base began to emerge after only 3 days of flooding and the number increased with the duration of flooding (Table 1), confirming our third hypothesis. This increase in adventitious roots was accompanied by an increase in the damage and death of original roots. A number of other herbaceous and woody species exhibit growth of adventitious roots (Jackson and Drew, 1984; Sena Gomes and Kozlowski, 1980), but to our knowledge it has not been reported in crucifers. These replacement roots usually emerge from the flooded stem base and reach the water surface above the flooded soil line, where a relatively high content of oxygen is available (Jackson and Drew, 1984). These new roots have a positive role in supporting shoot growth during prolonged flooding (Jackson, 1985; Armstrong et al., 1994). Ameliorating effects of adventitious roots are suggested by the positive relationship between flooding tolerance and the amount of rooting in several species of *Rumex* in response to soil flooding (Blom et al., 1994). The mechanisms by which flooding promotes adventitious rooting are not clear (Vartapetian and Jackson, 1997; Pezeshki, 2001). Many studies describe an important role for ethylene in the process of adventitious rooting (Tang and Kozlowski, 1982, 1984; Voesenek et al., 1990; Visser et al., 1996). Liu and Reid (1992) demonstrated for cuttings of sunflower seedlings that enhanced ethylene production by waterlogging involved in increasing the tissue sensitivity towards the existing auxin concentration to induce adventitious rooting. Our results (Fig. 3) showed that there was a significant negative correlation between the number of adventitious roots and ethylene concentration in flooded roots after 3-day flooding. Further study is needed concerning the role of ethylene in adventitious roots in flooded *L. latifolium*.

In our study, *L. latifolium* exhibited a high root porosity of 26% in unflooded plants, and it re-
Fig. 2. Time-course of responses of ethylene production in roots (A) and leaves (B) of *L. latifolium* to soil flooding. Each bar represents the means and S.E. of three plants. Analysis of covariance showed the effect of flooding treatment (roots, \( P < 0.01 \); leaves, \( P = 0.3 \)) and the duration of flooding (roots, \( P < 0.05 \); leaves, \( P < 0.05 \)) on ethylene production. Asterisks *, ** and *** represent the difference between flooded and control plants at \( P < 0.05 \), 0.01 and 0.001 by *t*-test, respectively. Note the different scales.

We have compared root porosity, and yield ratio (final shoot biomass under flooded conditions/shoot biomass under drained conditions) for our experiment with data for a large number of European species from experiments of Justin and Armstrong (1987) (Table 2). We grouped species using the habitat categories of Fitter (1978). Species in category 1 (standing water above soil surface) had a high porosity, even growing under drained conditions, and tended to have very little increase in porosity under flooded conditions. Their yield was much greater under flooded conditions. Species in categories 2 and 3 had (on average) much lower porosity under drained conditions, but the porosity approximately doubled (on average) under flooded conditions. In species of category 2, their yield averaged about the same
Table 2
Comparison of root porosity and yield ratio for our experiment with data for 91 of European species from experiments of Justin and Armstrong (1987)

<table>
<thead>
<tr>
<th>Habitat preferencea</th>
<th>Root porosity(%)</th>
<th>Ratio</th>
<th>Yield ratiob</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Flooded</td>
<td>Unflooded</td>
<td>Flooded/unflooded</td>
</tr>
<tr>
<td>1</td>
<td>29.6</td>
<td>24.1</td>
<td>1.5</td>
</tr>
<tr>
<td>2</td>
<td>13.8</td>
<td>8.1</td>
<td>1.9</td>
</tr>
<tr>
<td>3</td>
<td>8.3</td>
<td>6.5</td>
<td>2.2</td>
</tr>
<tr>
<td>4</td>
<td>4.0</td>
<td>2.6</td>
<td>2.0</td>
</tr>
<tr>
<td><em>L. latifolium</em></td>
<td>43.6</td>
<td>21.4</td>
<td>2.0</td>
</tr>
</tbody>
</table>

Data were calculated based on Table 2 of Justin and Armstrong (1987).

a Category 1 included species whose habitat preference included those with standing water above the soil surface for all or most of the year; category 2 included species whose habitat preference included habitats that were saturated for most of the year but not with water standing above the soil surface; category 3 included species whose habitat preference included habitats that were damp or occasionally wet, but not saturated as in categories 1 or 2; category 4 includes species whose habitat preference includes ‘normally moist soils’ but not wetter habitats. Species classification after Fitter (1978).

b Yield ratio was the ratio of final shoot biomass under flooded conditions to final shoot biomass under drained conditions.

under flooded and drained conditions, but in species of category 3, flooding was detrimental to the yield. Thus plants in categories 2 and 3 were more ‘plastic’ in terms of modifying morphology to fit changing conditions of saturation. In our experiment *L. latifolium* resembled species in category 1 in terms of having an initially high porosity, but it had a higher than average increase in porosity under flooded conditions. However, in terms of yield, *L. latifolium* was more like plants that did not grow in mostly saturated conditions. Many weeds have been shown to be relatively plastic in their responses to the environment through flexibility in germination, phenology, temperature, etc. Thus, *L. latifolium* appears to be a plant that exhibits plasticity to tolerate or survive saturated conditions, but not to grow well under these conditions. This may be an adaptation to arid or semi-arid riparian habitats where spring flooding and summer drought is characteristic.

In summary, *L. latifolium* exhibited morphological and anatomical adaptations to flooding stress typical of facultative hydrophyte species, although this species is classified as an intermediate species in Europe, based on the classification of wetness–dryness of habits (Fitter, 1978). Plants of *L. latifolium* survived 50 days and had some limited reproductive capacity under soil flooding. However, unlike most true hydrophytes, growth was severely inhibited. *L. latifolium* allocated a high proportion of its biomass to roots under aerated conditions while it significantly reduced biomass allocation in roots under flooded conditions. This species also had high root porosity even in aerated soil and developed significantly higher porosity in flooded soil (Table 1). These adaptive features and the ability to tolerate an extremely wide range of soil moisture conditions for survival has allowed this exotic crucifer to spread explosively in recent years in wetlands and riparian areas of the western United States.

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