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Effects of flooding depth on growth, morphology and photosynthesis in *Alnus japonica* species

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Abstract The present study deals with effects of flooding depth on growth, morphology and photosynthesis in *Alnus japonica* species thorough one field study and two controlled experiments. In the field study performed in Kushiro Mire, Hokkaido Island, Japan, tree heights and stem diameters decreased with an increase in water depth accompanied with the reduction of soil redox potential. In contrast, the rate of multiple stems per individual tree increased. In the controlled experiments for seedlings flooding suppressed the shoot elongation and biomass increment in roots. However, diameter increment around water levels, epicormic shoot development and adventitious root formation were enhanced in flooded seedlings. The photosynthetic rate and stomatal conductance of flooded seedlings also were lowered with an increase in flooding depth. The recovery of the reduced photosynthetic rate and stomatal conductance occurred simultaneously with the advancement of adventitious root formation in the flooded seedlings. These results indicate the importance of a series of morphological changes occurring on stems around water levels in flood tolerance in *A. japonica* species.

Keywords Adventitious roots · *Alnus japonica* · Flooding depth · Photosynthesis

Introduction

Flooding results in poor soil aeration and depletion of oxygen in rhizosphere of plants (Kozlowski et al. 1991). The declined gas diffusion by flooding induces chemical reduction. Decrease in soil Eh under flooding condition indicates progressive increase in demand for oxygen and accumulation of phytotoxic compounds in soil (Ponnamperuma 1984;

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Pezeshki 2001). Those compounds including reduced form of Fe and Mn, ethanol, lactic acid, acetaldehyde, aliphatic acids and cyanogenic compounds cause injury in root metabolism and inhibition of shoot and root growth in plants (Jackson and Drew 1984; Armstrong and Armstrong 1999; Armstrong et al. 1996; Pezeshki 2001). Such declined root system by low soil Eh condition affects shoot growth and physiological activity through inhibition of water and mineral uptake, and their transport (Pezeshki 2001).

There are many examples for effects of flooding such as inhibition of shoot elongation, leaf expansion, senescence and abscission of leaves and lowered photosynthetic activity (Kozlowski et al. 1991). Flood-tolerant species respond to flooding by morphological changes such as the development of intercellular spaces in lenticels, increase in stem growth, formation of adventitious roots and aerenchyma development (Yamamoto et al. 1995a, b; Kozlowski et al. 1996; Pezeshki 2001; Dat et al. 2004).

Alnus japonica (Thunb.) Steud. is native to swamp area along rivers and lakes and widely distributed in northeast Asia (Fujita and Kikuchi 1986). This species has high flood-tolerance and a dominant species in swamp forests of Kushiro Mire, Hokkaido, Japan (Grosse et al. 1993; Nakamura et al. 2002). In swamp forest of Kushiro Mire, *A. japonica* trees assume the form of shrubs consisting of multiple stems derived from regeneration system by coppicing in deeply flooded areas, in contrast, they can grow up to 20–15 m in shallowly flooded areas (Shinshoh 1985). Such phenomenon suggests that changeable flooding depth may affect expression of stress adaptability relating to modification of various physiological processes in plants. However, there is little information about effects of depth of flooding on growth, morphology and physiology of this species.

In the present report we examined development and distribution of *A. japonica* trees in wetland forests at Kushiro Mire in relation to environmental factors including soil redox potentials. We also investigated the effect of flooding depth on size, growth and morphology in controlled experiments using *A. japonica* seedlings. On the results of these two different studies, the stress adaptability of this species to flooding was discussed (Fig. 1).

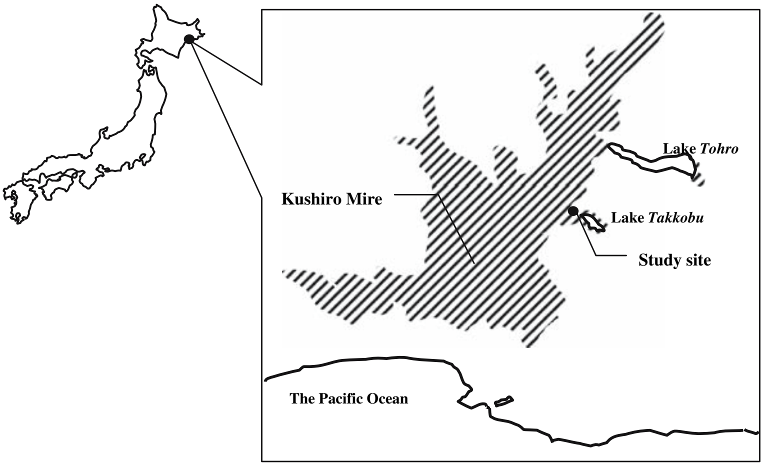

Fig. 1 Location of the study site at Kushiro Mire

Materials and methods

Field studies

Field studies were performed in a swamp forest of *Alnus japonica* species in Kushiro Mire, Hokkaido Island, Japan (Fig. 2). In September, 1998, a 10 m wide and 200 m long rectangular plot extended from the edge of Lake Takkobu, a lagoon of the mire, toward a deep area of it was made at 43°04́ N and 144°29́ W. Locations of *A. japonica* trees in the plot were recorded and their heights and stem diameters at 130 cm above the ground level (DBH) were measured with a measuring stick and a diameter tape, respectively. The number of stems including epicormic shoots was counted in each *A. japonica* tree. Ground heights from the water level of Lake Takkobu were surveyed with a levelling instrument (Automatic level 10316, Sokkisha Co. Ltd.) from the shore edge to another edge in the plot at 10 m intervals. On 22 September 2001, values of soil redox potential (Eh) were determined with a portable pH/conductivity meter (D-24S, Horiba, Ltd.) in the plot at 20 m intervals. The values were taken for three times at each measuring point.

Experimental studies

Plant materials

Two different experiments were performed using 3-year-old *Alnus japonica* seedlings in 2001 and 2003, respectively. About 2 months before the beginning of experiments, the seedlings grown from seeds obtained from the Makunbetsu Marsh in a basin of Ishikari river, Hokkaido, were transplanted in plastic pots (φ19.5 × 14.5 cm) containing one part vermiculite, one part bark compost and three parts sandy loam and grown under outdoor condition. The seedlings were watered daily with tap water and fertilized every 2 weeks with 200 ml of a 1/500 Hyponex solution (Hyponex: 10N-3P-3K-0.05Mg-0.001Mn-0.005B, HYPONeX Japan, Co. Ltd.) until the initiation of treatments.

Experiment 1

On 15 June 2001, 18 seedlings were selected for uniformity in size and development. Average seedling heights and stem diameters at 1 cm above the ground level (GL) were 134.1 ± 2.9 cm and 14.6 ± 0.6 mm, respectively. The seedlings were submitted to three treatments: (1) six seedlings unflooded and watered daily as control, (2) six seedlings flooded at 1 cm above the GL and (3) six seedlings flooded at 30 cm above the GL. In flooding treatments water was periodically added to keep each water level. Those flooding conditions were maintained until September 4 for 80 days.

During the experimental period, terminal shoot elongation and diameter growth at 1 cm and 30 cm above the GL were measured once a week with a ruler and a microcaliper, respectively. The number of adventitious roots and epicormic shoots developing on stems and stocks were counted every week. At the end of experiments, heights of developing positions and lengths of epicormic shoots were measured with a ruler. Then, the seedlings were harvested, separated into leaves, stems, epicormic shoots, roots and adventitious roots and their dry weights were determined separately after drying at 80°C for 48 h.

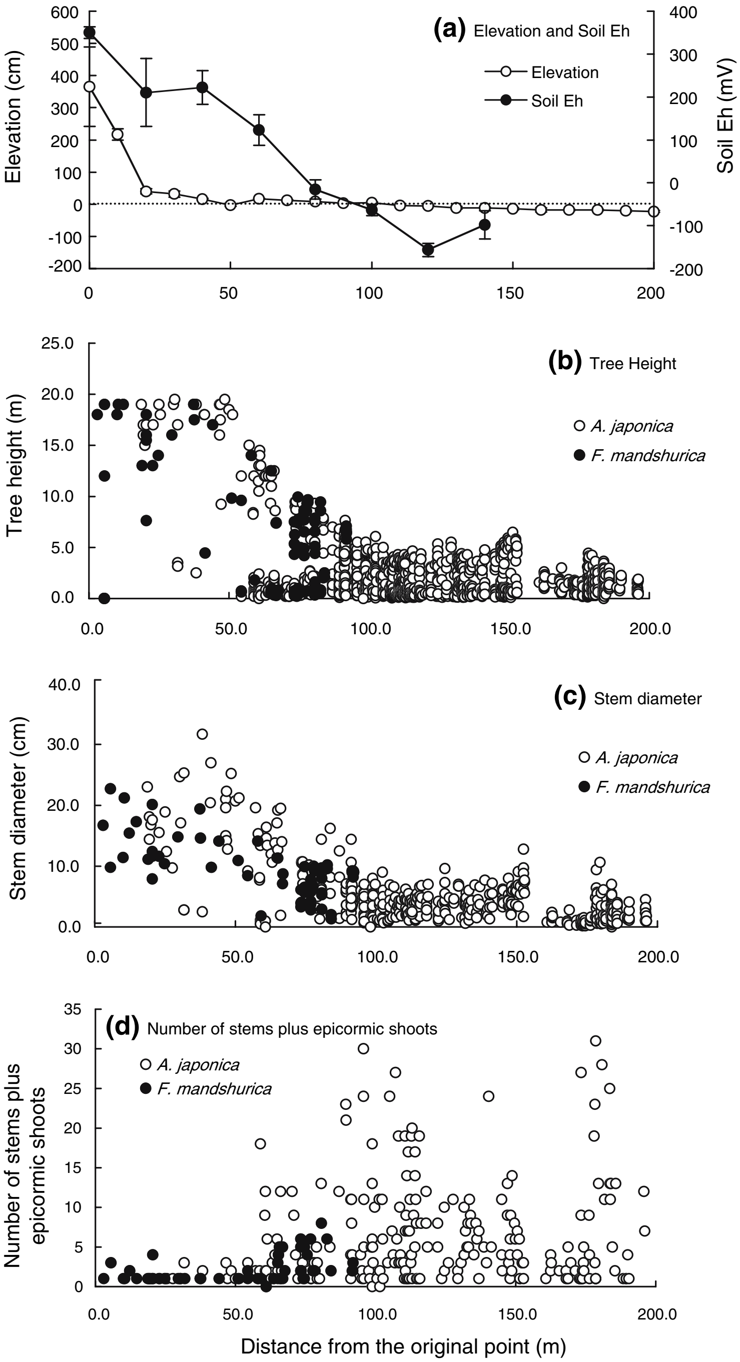

Fig. 2 Ground heights, soil redox potential (Eh), tree heights, stem diameters (DBH) and total number of stems and epicormic shoots in *Alnus japonica* trees growing at Kushiro Mire

Experiment 2

On the basis of the results in the field study and the experimental study 1, photosynthetic rates of flooded *A. japonica* seedlings were determined in this experiment. On 6 May 2003, the seedlings were selected for uniformity in size and development as: heights, 96.1 ± 1.6 cm; stem diameters at the 1 cm above the GL, 11.6 ± 0.2 mm. The seedlings were transferred to the greenhouse of Arid Land Research Center, Tottori University. At the beginning of the experiment on 20 May 2003, five seedlings were harvested, separated into leaves, branches, stems and roots and their dry weights were determined separately after drying at 80°C for 48 h.

In this experiment 15 seedlings were submitted to three treatments. Five seedlings unflooded were watered daily, as control. The remaining seedlings were divided into two groups: (1) five seedlings flooded at 1 cm at the GL and (2) five seedlings flooded at 30 cm above the GL. Water was periodically added to keep each water level, but the water was not changed. These flooding treatments were performed for 42 days.

Measurements of photosynthetic rates and stomatal conductance were made at a photosynthesis photon flux density (PPFD) of 1,100 μmol m^{-2} s^{-1} determined from light-saturated photosynthetic rates using the photosynthesis-PPFD response curve. To obtain photosynthesis-PPFD response curve, photosynthetic rates at different PPFD were measured on three leaves from different seedlings prior to the initiation of treatments. The CO_2 concentration, temperature and vapour pressure deficit in leaf surface were not controlled. The photosynthesis measurements were conducted from 8:00 to 9:30 a.m. to avoid midday depression of photosynthesis and made on well expanded, matured and developed leaves positioned on the fourth or fifth node from shoot apices. Air temperature (AT), relative humidity (RH) and CO_2 concentration during photosynthesis measurements were recorded as follows: AT ± SE, 30.2 ± 0.5 °C; RH ± SE, 44.8 ± 2.8%; CO_2 concentration ± SE, 381.2 ± 3.0 ± mol m^{-2} s^{-1}. Every week during the experimental period, terminal shoot elongation, stem diameters, number of adventitious roots and epicormic shoots and biomass were measured as described above. The statistical analysis of variance was applied to each data set. To compare mean values of treatments, *t*-test was used. Multiple comparisons among treatments were performed by the method of Scheffe's test. To test the relationships between number of adventitious roots and photosynthetic rates, simple regression analysis were performed (Excel software).

Results

Field studies

Figure 2 indicates ground heights, soil redox potential (Eh), tree heights, stem diameters (DBH) and number of stems and epicormic shoots in *A. japonica* trees growing at the study site. The total of *A. japonica* trees surveyed was 1,495 individuals. The ground height above the water level descended slowly toward Lake Takkobu. Values of soil Eh decreased as a decrease in ground heights. The values gradually reduced and reached about 150 mV at the point of 120 m from the shore edge of the plot. The heights and stem diameters of *A. japonica* trees indicated the same tendency to increase as the changes in the values of soil Eh. Meanwhile, the total number of stems and epicormic shoots per tree (Figs. 2 and 3) increased with the decrease of soil Eh.

Fig. 3 Multiple stems and epicormic shoots appearing on flooded *A. japonica* saplings. The arrow shows the water level

Experimental studies

Experiment 1: development of epicormic shoots

Flooding at 30 cm above the GL suppressed shoot elongation in the seedlings (Table 1). In the flooded seedlings diameter increments were enhanced around the water levels. Flooding at 1 cm above the GL caused rapid diameter increment at the stem base, whereas 30 cm-flooding increased stem diameter at 30 cm above the GL (Table 1). Flooding at 30 cm reduced the dry weight increment of roots and total plants. The 1 cm-flooding reduced dry weights of roots only. Flooding did not change the dry weights of stems and leaves (Table 1).

Formation of adventitious roots was observed in the flooded seedlings (Table 1). The number of adventitious roots in the 30 cm-flooded seedlings was greater than those of the 1 cm-flooded seedling. Epicormic shoot development also was observed on the stems of the flooded and unflooded seedlings (Table 1), however, more epicormic shoots in the

Table 1 Effects of flooding depth on growth, biomass and morphology of *A. japonica* seedlings in Experiment 1

	Treatments	Unflooded	F-1 cm	F-30 cm
Growth	Shoot elongation (cm)	32.33 ± 4.07 a	14.07 ± 1.73 ab	8.55 ± 1.81 b
	Diameter increment (cm)			
	At 1 cm	2.72 ± 0.37 a	6.91 ± 1.13 b	1.51 ± 0.71 a
	At 30 cm	2.92 ± 0.34 a	3.27 ± 0.50 a	6.18 ± 0.66 b
Biomass	Total plants (g)	68.01 ± 7.79 a	47.60 ± 5.25 ab	36.62 ± 5.35 b
	Leaves (g)	23.42 ± 1.73 a	19.41 ± 2.95 a	14.79 ± 2.54 a
	Stems (g)	5.92 ± 0.69 a	6.57 ± 0.80 a	4.90 ± 0.74 a
	Roots (g)	38.68 ± 6.15 a	21.62 ± 2.81 b	16.93 ± 2.41 b
	T/R	0.81 ± 0.09 a	1.28 ± 0.17 a	1.17 ± 0.10 a
Morphology	Number of adventitious roots	0.0 ± 0.0 a	5.0 ± 2.0 b	20.7 ± 7.3 b
	Number of epicormic shoots	4.5 ± 1.1a	14.8 ± 3.0 b	8.2 ± 1.9 ab

The seedlings were flooded at 1 cm (F-1 cm) or 30 cm (F-30 cm) above the GL. Values without common superscripts in each line are significantly different at $P < 0.05$ using Scheffe's test flooded seedlings were observed than those of unflooded seedlings. The number of epicormic shoots in the flooded seedlings kept increasing during the experimental term (Fig. 4). The dry weights of epicormic shoots in the 1 cm-flooded seedlings were greater than those of the unflooded and the 30 cm-flooded seedlings as well as the number of epicormic shoots (Table 1). Developing positions of epicormic shoots as well as adventitious roots were heightened as water levels increased (Figs. 5 and 6). The epicormic shoots of the 1 cm-flooded seedling were comparatively larger than those of other seedlings (Fig. 5). The average lengths of epicormic shoots in the 1 cm-flooded, 30 cm-flooded and the unflooded seedlings were 8.75 ± 0.83, 1.76 ± 0.26 and 3.10 ± 0.89 cm, respectively (Table 1).

Experiment 2: photosynthesis and adventitious root formation

Table 2 indicates effects of flooding depth on growth, biomass and morphology of the flooded seedlings in Experiment 2. The same tendency was observed in this experiment as the data obtained in Experiment 1 (Table 1). Dry weights of leaves in the flooded seedlings were significantly lower than those of the unflooded seedlings (Table 2), whereas flooding

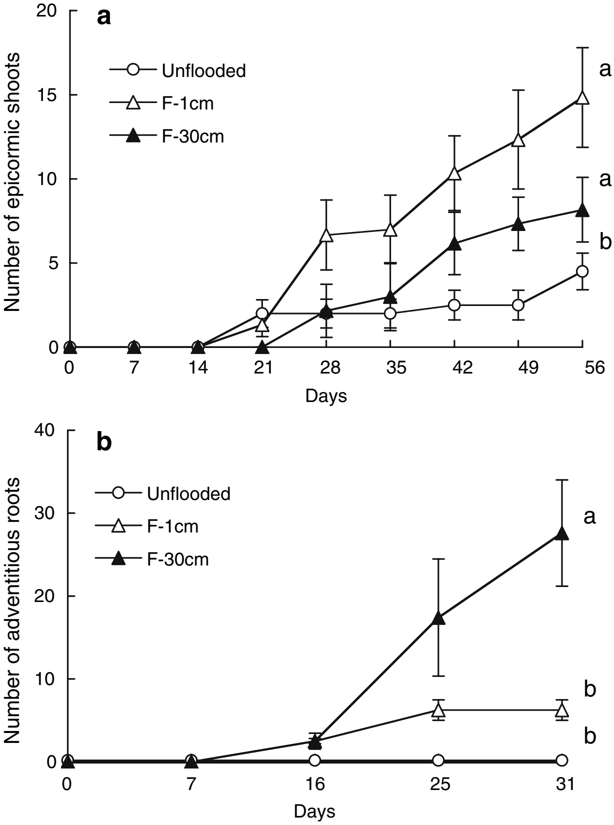

Fig. 4 Effects of flooding depth on changes in number of epicormic shoots (**a**) in Experiment 1 and adventitious roots (**b**) in Experiment 2: □, flooded at 1 cm above the GL; ▲, flooded at 30 cm; ○, unflooded. Values without common superscripts are significantly different at $P < 0.05$ using Scheffe's test

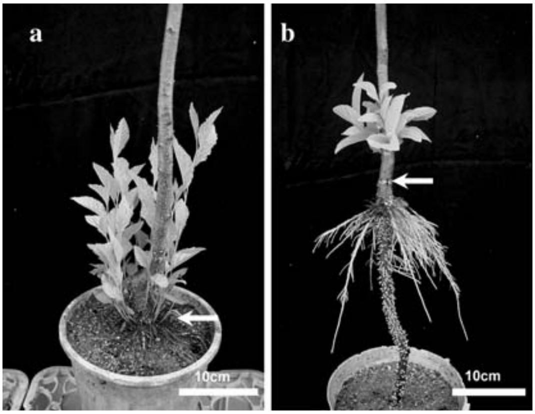

Fig. 5 *A. japonica* seedlings flooded at 1 cm (**a**) and 30 cm (**b**) above the GL. Arrows in each figure indicate water levels

did not change them in Experiment 1 (Table 1). Although flooding enhanced the formation of adventitious roots, there was no significant difference in the number of epicormic shoots between the flooded and the unflooded seedlings (Table 2).

The rates of photosynthesis in the unflooded seedlings were continuously higher than those of the flooded seedlings (Fig. 7). Within 25 days after flooding initiated, the photosynthetic rates of the 30 cm-flooded seedlings were lower than those of the unflooded seedlings. On the 56th day after flooding was initiated, there was no significant difference in photosynthetic rate among the treatments although flooding treatment caused consistently lower photosynthetic rates (Fig. 7). The tendency of changes in stomatal conductance was similar to that of photosynthetic rate. The recovering process of photosynthesis was highly related to changes in the number of adventitious roots (Fig. 8). In the 30 cm-flooded seedlings the decreased rates of photosynthesis recovered with an increase in the number of adventitious roots (Figs. 7 and 8). The dry weights of adventitious roots in the 30 cm-flooded seedlings were less than those of the 1 cm-flooded seedling whereas more adventitious roots were observed in the 30 cm-flooded seedlings (Table 2).

Discussion

Under flooding condition in Kushiro Mire, distribution and development of *A. japonica* trees declined with decrease in the value of soil Eh. This phenomenon may be explained by the negative effects of the low soil Eh condition on growth and physiology. For instance, soil Eh significantly affects energy condition through inhibitory effects on various woody plants (DeLaune et al. 1998; Anderson and Pezeshki 2001; Pezeshki 2001). Flooded *Quercus nuttallii*, *Q. michauxii* and *Taxodium distichum* seedlings showed decrease in photosynthetic rates and stomatal conductance under reduced condition with about −200 mV soil Eh (Anderson and Pezeshki 2001). According to Pennington and Walters (2006), inhibitory effects of low soil Eh condition are greater than those of hydrology on growth and photosynthesis of several woody species.

In general, flooding suppresses height growth, formation and expansion of leaves and root growth in many upland species (Kozlowski 1984a). Our controlled experiments indicated that deep flooding apparently inhibits shoot growth, total biomass increment and photosynthetic activity of *A. japonica* seedlings, as well as declined development and distribution of this species in Kushiro Mire. In contrast, flooding stimulated many kinds of

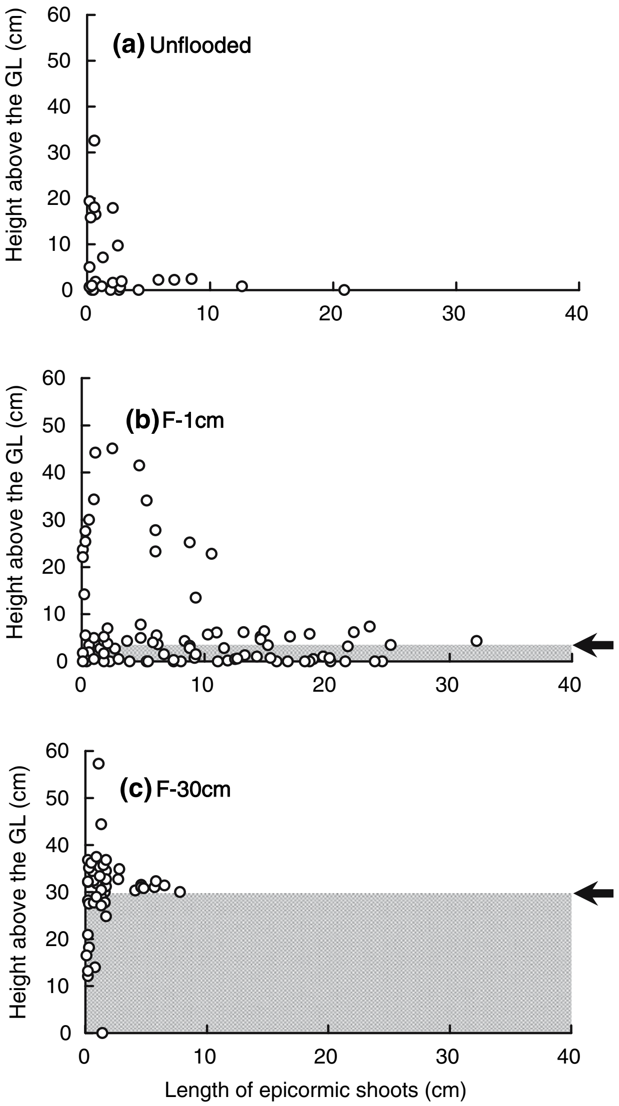

Fig. 6 Positions of epicormic shoot development and shoot lengths in the seedlings unflooded, (**a**) looded at 1 cm (**b**) and 30 cm (**c**) above the GL. Arrows indicate each water level

visible change in stem portions of flooded seedlings around water levels. In a few days after initiation of flooding, stem lenticels on submerged portions showed hypertrophic development. Lenticels are the important pathway of gas exchange between atmosphere and internal tissues in stems and roots (Kozlowski 1984b; Buchel and Grosse 1990; Schaffer 1998). Hypertrophied lenticels having abundant intercellular spaces in flooded plants enhance gas diffusion by thermo-osmotic activity (Buchel and Grosse 1990) and contribute oxygen supply to submerged roots (Kozlowski and Pallardy 1997; Grosse et al. 1992; Yamamoto et al. 1995a, b; Angelov et al. 1996).

Table 2 Effects of flooding depth on growth, biomass and morphology of the seedlings in Experiment 2

	Treatments	Unflooded	F-1 cm	F-30 cm
Growth	Shoot elongation (cm)	30.23 ± 6.79 a	12.80 ± 3.26 ab	8.00 ± 2.01 b
	Diameter increment (cm)			
	At 1 cm	2.34 ± 0.80 a	7.51 ± 1.03 b	0.66 ± 0.11 a
	At 30 cm	1.80 ± 0.14 a	2.60 ± 0.37 ab	3.20 ± 0.17 b
Biomass	Total plants (g)	90.92 ± 5.00 a	75.80 ± 6.30 ab	57.69 ± 8.32 b
	Leaves (g)	17.45 ± 0.92 a	12.94 ± 0.52 b	7.91 ± 1.21 c
	Stems (g)	26.23 ± 2.22 a	26.25 ± 5.96 a	24.55 ± 4.00 a
	Roots (g)	46.17 ± 4.50 a	32.46 ± 3.77 ab	25.10 ± 5.02 b
	T/R	1.02 ± 0.14 a	1.43 ± 0.27 a	1.51 ± 0.39 a
Morphology	Number of adventitious roots	0.0 ± 0.0 a	6.3 ± 1.2 b	27.6 ± 6.4 b
	Number of epicormic shoots	4.2 ± 1.0 a	5.0 ± 1.5 a	2.4 ± 0.9 a

Values without common superscripts in each line are significantly different at $P < 0.05$ using Scheffe's test

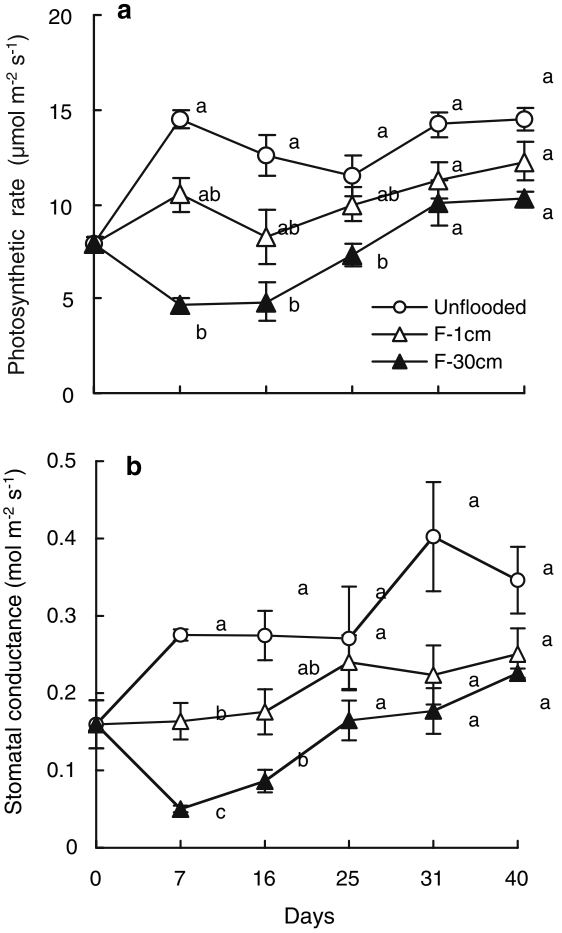

Fig. 7 Changes in photosynthetic rate (**a**) and stomatal conductance (**b**) in leaves of the seedlings. Symbols with common superscripts on the same day are not different at the 5% level using Scheffe's test

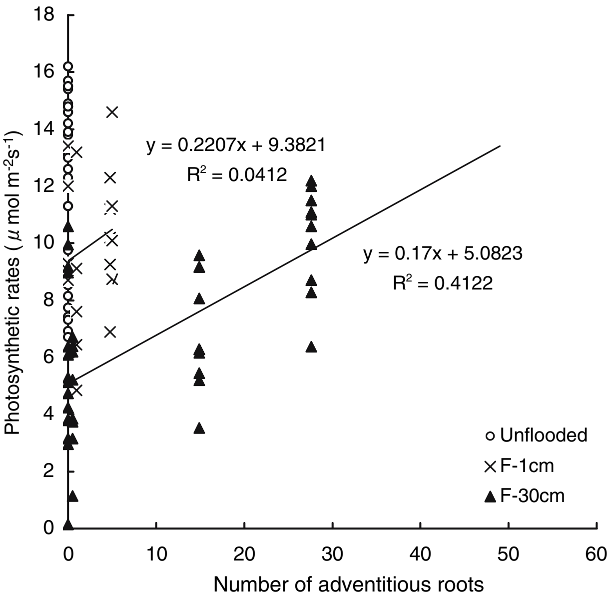

Fig. 8 Linear regression relationships between photosynthetic rates and number of adventitious roots in flooded *A. japonica* seedlings of Experiment 2 ($P < 0.05$)

Numerous adventitious roots began to develop on submerged stems about 3 weeks after the initiation of flooding. The root formation occurred coincidently with the increment of stomatal conductance and photosynthetic rates. Several investigations reported the close relationships between adventitious root formation and stomatal reopening in flooded plants (SenaGomes and Kozlowski 1980; Kozlowski 1984b; Topa and Cheeseman 1992). In flooded *Fraxinus pennsylvanica*, for instance, adventitious root formation lowered leaf diffusion resistance (SenaGomes and Kozlowski 1980). The function of adventitious roots is regarded as the support for shoot growth during prolonged soil waterlogging by supplying water, minerals and hormones (SenaGomes and Kozlowski 1980; Jackson and Drew 1984; Tsukahara and Kozlowski 1985; Vartapetian and Jackson 1997; Islam and MacDonald 2004). Furthermore, Terazawa et al. (1989) found the oxidization of rhizosphere occurred around adventitious roots of flooded *A. japonica* seedlings.

The importance of adventitious rooting on growth in flooded woody plants would vary with species. Removing adventitious roots from submerged portions of stems reduced height and diameter growth in flooded *Platanus occidentalis* seedlings (Tsukahara and Kozlowski 1985). In contrast, there was no significant effect on height growth in flooded *A. glutinosa* seedlings (Gill 1975). However, the present experiments on *A. japonica* species indicated the coincidental relationship between adventitious root formation and recovery of reduced photosynthetic rate, suggesting the importance of this phenomenon for the survival of this species in wetland. Most of flood-tolerant woody plants showed reduced diameter growth by prolonged flooding (Kozlowski 1997), whereas the occurrence of stem hyperplasia also was observed in flooded *Nyssa aquatica* (Hook 1984), *Fraxinus mandshurica* (Yamamoto et al. 1995b) and *A. japonica* (Terazawa and Kikuzawa 1994; Yamamoto et al. 1995a). Such enlarged stems had lower density and abundant intercellular spaces in woody plants (Hook 1984; Yamamoto 1987, 1995a, b), although the increase in stem diameter of *A. japonica* resulted largely from both increased number and size of xylem cells consisting mainly of libriform wood fibers (Yamamoto et al. 1995a).

In our field studies, most of the flooded *A. japonica* trees at Kushiro Mire had multiple stems presumably derived from epicormic shoots (Shinshoh 1985). Flooded *A. japonica* seedlings also showed acceleration of epicormic shoot development in controlled experiments. Under anaerobic condition causing decline of shoot and root growth, regeneration system by coppicing is efficient for the maintenance, existence and development of individual tree. Rapid development of epicormic shoots in flooding environment would give a substantial advantage to *A. japonica* species for survival.

The epicormic shoots are produced from dormant buds on the main stems or branches of the trees (Kozlowski and Pallardy 1997). The dormant bud is dominated by the terminal shoot and released by thinning or partial cutting of the shoot (Zimmermann and Brown 1971; Kozlowski and Pallardy 1997). Suppressed growth in roots and shoots of flooded plants may affect the balance of plant hormones in relation to apical dominance. In our previous experiments, the flooded *A. japonica* seedlings girdled or applied with 1-naphthylphthalamic acid (NPA), an auxin transport inhibitor, indicated more epicormic shoot developments than those of untreated seedlings, suggesting that the reduced shoot growth caused by flooding condition is one of the direct factors for promoting epicormic shoot formation in *A. japonica* growing in mires (Iwanaga and Yamamoto unpublished data).

In the experimental studies the depth of flooding controlled positions of epicormic shoot development, adventitious root formation and stem hyperplasia. Grinchko and Glick (2001) mentioned regulatory roles of plant hormones including auxin and ethylene in both stem hyperplasia and adventitious root formation. Yamamoto et al. (1995a) also suggested that such morphological changes in flooded *A. japonica* seedling were highly related to flood-induced ethylene. Elevated levels of ethylene in some portions of stems in flooded plants may cause auxin accumulation at the same point. For instance, Eklund and Little (1996) reported that auxin accumulation in stems was enhanced by the application of ethrel, an ethylene-generating compound, in *Abies balsamea* seedlings. In woody plants auxin is regarded as a promoter of both xylem production (Little and Pharis 1995; Eklund and Little 1996) and adventitious root formation (Kozlowski et al. 1996). The present results suggest that changes in water levels may shift positions of both rapid ethylene production and auxin accumulation in stems, causing hypertrophic stem growth and adventitious root formation. However, more direct information about the relationship between roles of plant hormones and morphological changes is needed to clarify physiological mechanisms and function of morphological changes in *A. japonica* under flooding condition.

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