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SHORT COMMUNICATION

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# Effects of flooding on growth of seedlings of woody riparian species

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**Abstract** The effects of flooding on growth of seedlings were compared over a 7-month period (April–November) among six different woody species: *Aesculus turbinata*, *Cercidiphyllum japonicum*, *Fraxinus platypoda*, *Pterocarya rhoifolia*, *Pterostyrax hispida*, and *Quercus mongolica* var. *grosseserrata*. Flooding reduced the shoot length of *F. platypoda*, *P. rhoifolia*, *C. japonicum*, *P. hispida*, and *Q. mongolica* var. *grosseserrata* seedlings but did not affect that of *A. turbinata* seedlings. Among control seedlings, shoot elongation occurred once in *A. turbinata* and twice in *F. platypoda* and *Q. mongolica* var. *grosseserrata*; the other species continued to grow from April to August. Among the flooded plants of all species, shoot elongation occurred only once at the beginning of the growing season. On August 25, flooding significantly reduced the number of developed leaves as compared with control plants except for *A. turbinata*. In the flooded plants except for *F. platypoda*, leaf fall began on June 30; in controls, by contrast, the number of developed leaves increased until August 25. Flooding reduced the total dry weight increment in all species. The survival ratio of flooded plants after the experiment differed with species. All of the *F. platypoda* and *A. turbinata* seedlings survived the flooding treatment, while only 20% of *P. hispida* and 30% of *Q. mongolica* var. *grosseserrata* survived. Flooding seriously affected the growth of riparian pioneer species including *P. rhoifolia*, *C. japonicum*, *P. hispida*, and *Q. mongolica* var. *grosseserrata*. The effects of flooding on growth of the seedlings differed with the tree species because of differences in leaf-emergence pattern and physiological flood tolerance. The responses of tree seedlings to flooding reflected species habitats and growth patterns.

**Key words** Dry weight increment · Flooding · Leaf development · Seedlings · Shoot growth

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## Introduction

Woody plants in swampy areas along lowland rivers and lakes are highly tolerant to flooding, even under anaerobic soil conditions. These plants are morphologically well adapted to flooding; they respond by growing hypertrophic stems, forming adventitious roots (Hook 1984; Kozlowski 1984; Kozlowski et al. 1991), and sprouting shoots (Terazawa et al. 1989; Yamamoto et al. 1995a).

The growth of flooded trees is often retarded and sometimes the trees do not survive. Reports of the physiological, morphological and anatomical responses of tree seedlings to flooding are many (Yamamoto and Kozlowski 1987a,b; Yamamoto et al. 1995a,b). Effects of flooding on leaf dynamics have been reported by Terazawa and Kikuzawa (1994) and Nagasaka (2001). Some studies have described the effects of flooding on the photosynthesis rate of tree seedlings (Takahashi et al. 1988; Terazawa et al. 1992; Terazawa 1994). Flooding inhibits oxygen supply to roots and reduces water and nutrient supplies, as well as the photosynthetic rate (Pezeshki 1994).

In mountainous regions, the distribution of woody plants within each climate zone is limited by topography (i.e., ridges, slopes, and valleys) (Maeda and Yoshioka 1952). Habitat conditions such as soil, water, and light differ with microtopography. Riparian habitat is topographically diverse owing to various disturbances that differ with respect to size, magnitude, and frequency. In the riparian zone, flooding has physical and physiological effects on plants. Some tree species coexist in riparian forests; these species differ with habitat and ecological characteristics (Sakio et al. 2002). However, the difference of reactions to flooding among riparian species in mountain regions is unclear.

In this study, the effects of flooding on seedling growth were investigated in woody riparian species in different habitats in the cool-temperate forest of the Chichibu Mountains, central Japan. Riparian species were also compared with nonriparian species. The following questions were specifically addressed: (1) How does flooding affect the growth of tree seedlings? (2) Do the effects of flooding differ with riparian tree species? (3) Are species habitat and growth pattern reflected in the responses of tree seedlings to flooding?

## Materials and methods

Six deciduous woody species were studied, all of which are distributed in natural forests of the cool-temperate zone in the Chichibu Mountains, central Japan. *Fraxinus platypoda* Oliv., *Pterocarya rhoifolia* Sieb.et Zucc., *Aesculus turbinata* Blume, *Cercidiphyllum japonicum* Sieb.et Zucc., and *Quercus mongolica* var. *grosseserrata* Rehd et Wils. are canopy species; *Pterostyrax hispida* Sieb.et Zucc. is a subcanopy species. All of these species except for *Q. mongolica* var. *grosseserrata* are riparian. Of all six species, *F. platypoda* and *A. turbinata* occupy the wettest habitat. *Pterocarya rhoifolia*, *C. japonicum*, and *P. hispida* are gap dependent and more widely distributed in the riparian zone. *Quercus mongolica* var. *grosseserrata* is distributed in the driest habitat along medium slopes and ridges.

In May 1994, seeds of six tree species from natural populations in the Chichibu Mountains were sown in the nursery of the Forest Laboratory, Saitama Prefectural Agriculture and Forestry Research Center. One-year-old seedlings were dug up from the nursery on March 23, 1995. For each species, 30 seedlings were selected and divided into three groups of 10. Seedling sizes were recorded before flooding treatment (Table 1). The size and fresh weight did not differ significantly with the groups. Seedlings of one group were separated into stems, branches and roots and the dry weights of each were determined after drying at 80°C for 48 h. Each seedling of the other two groups were separately planted in nursery soil in unglazed pots.

At the beginning of the experiment, one of the two groups of seedlings of each species planted in 30.0 × 25.0 cm pots, was flooded in tubs (100 × 150 × 40 cm) from April 6 to November 6 for 214 days. The third group was not flooded and served as a control. The flooding treatment was initiated by raising the water level to the soil surface in the unglazed pots. Water was added periodically to maintain this water level but the water was not changed. In contrast, control plants were sprinkled with water once every 1 or 2 days to prevent soil desiccation. These control pots were placed in sunny areas outdoors. Mean air temperature and annual precipitation were 13.9°C and 1102 mm, respectively, at the Yorii Regional Meteorological Station (105 m above sea level) in 1995.

After April 6, seedling heights and the number of attached leaves for all seedlings were recorded at intervals of about 1 week early in the study period and at 1-month intervals toward the end of the study period. At the end of the experiment, all seedlings were removed from the pots. After washing the roots, the seedlings were separated into stems, branches and roots. Their dry weights were determined after drying at 80°C for 48 h.

## Results and discussion

In this experiment, flooding affected the growth of tree seedlings. The flooding treatment reduced the number of attached leaves, shoot elongation, dry weight increment, and the survival ratio. The effects differed among species, and the responses of tree seedlings to flooding reflected species habitat and growth patterns.

The process of shoot elongation in the control seedlings of the six tree species was classified into three types: flush (*Aesculus turbinata*), succeeding (*Pterocarya rhoifolia*, *Cercidiphyllum japonicum*, and *Pterostyrax hispida*), and intermediate (*Fraxinus platypoda* and *Quercus mongolica* var. *grosseserrata*). Shoot elongation occurred once in the *A. turbinata* seedlings and twice in *F. platypoda* and *Q. mongolica* var. *grosseserrata* seedlings. Seedlings of the other species continued to grow from April to August (Fig. 1).

In the case of controls, shoots of *A. turbinata* appeared as a flush within 2 weeks after flushing. The shoot length was constant until autumn. After flushing, shoots of *P. rhoifolia*, *C. japonicum*, and *P. hispida* elongated successively until the end of August. Shoots of *F. platypoda* and *Q. mongolica* var. *grosseserrata* elongated as a flush in spring, stopped to grow for over 1 month, and then elongated successively until the end of August.

In the flooded plants, shoot elongation occurred in all species only once at the beginning of the growing season. The shoot length did not differ significantly between the control and flooded *A. turbinata* seedlings but did in the other five species. In particular, *P. rhoifolia*, *C. japonicum*,

**Table 1.** Initial size of seedlings of six species

| Species | Control | | Flooded | |
|---|---|---|---|---|
| | Seedling height (cm) | $D_0$ (mm) | Seedling height (cm) | $D_0$ (mm) |
| *Fraxinus platypoda* | 9.3 ± 0.9 | 2.5 ± 0.2 | 10.5 ± 0.8 | 2.5 ± 0.2 |
| *Aesculus turbinata* | 22.9 ± 1.2 | 6.5 ± 0.3 | 24.5 ± 1.0 | 6.7 ± 0.3 |
| *Pterocarya rhoifolia* | 23.9 ± 1.3 | 3.6 ± 0.3 | 21.6 ± 1.3 | 3.6 ± 0.3 |
| *Cercidiphyllum japonicum* | 7.1 ± 0.5 | 0.9 ± 0.1 | 6.6 ± 0.4 | 0.9 ± 0.1 |
| *Pterostyrax hispida* | 7.3 ± 0.9 | 1.3 ± 0.2 | 6.9 ± 0.5 | 1.1 ± 0.1 |
| *Quercus mongolica* var. *grosseserrata* | 12.7 ± 0.8 | 2.6 ± 0.2 | 13.4 ± 1.1 | 2.4 ± 0.2 |

Data are given as means and standard errors. Seedling size at the starting time did not differ significantly between control and flooded seedlings

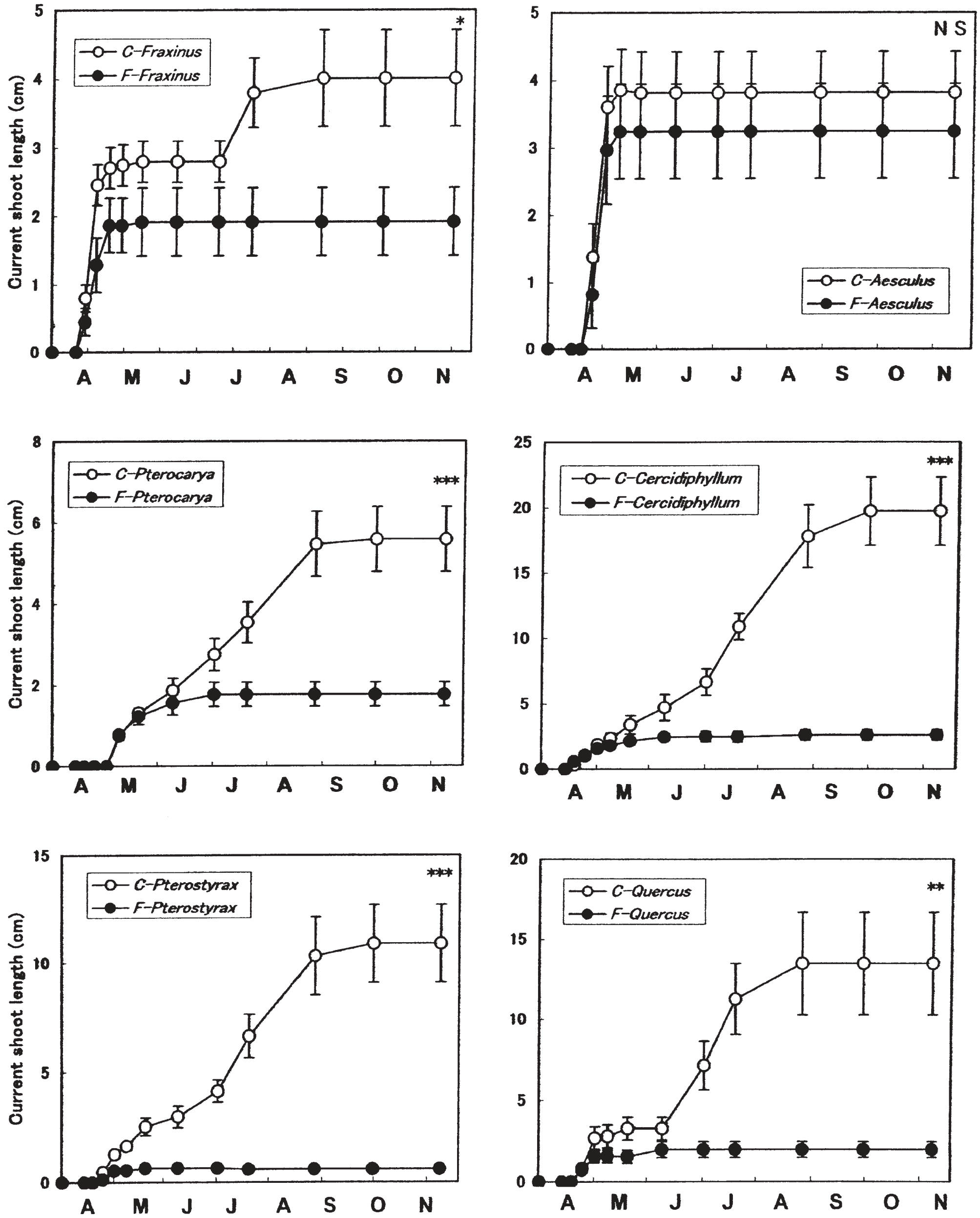


**Fig. 1.** Patterns of shoot elongation in flooded and control seedlings of the six tree species. Asterisks indicate level of significant difference from control seedlings. *Single asterisk*, 5% level; *double asterisk*, 1% level, *triple asterisk*, 0.1% level; *NS* not significant. *Vertical bars* represent standard errors

and *P. hispida* seedlings had significant differences (Welch's *t* test: $P < 0.001$).

The process of leaf development in control seedlings of the six tree species was classified into the same three types described for shoot elongation (Fig. 2). All *A. turbinata* leaves appeared as a flush within 2 weeks after flushing. Those leaves were retained on the shoots until autumn. After flushing, the *P. rhoifolia*, *C. japonicum*, and *P. hispida* seedlings developed leaves one by one, almost successively, until the end of August. The number of leaves attached to a shoot peaked at the end of August. *Fraxinus platypoda* and *Q. mongolica* var. *grosseserrata* seedlings developed several leaves as a flush in spring, stopped for over 1 month, and then developed several more leaves successively.

Flooding reduced the number of attached leaves. The number of attached leaves on flooded and control seedlings except for *A. turbinata* differed significantly on August 25 (Welch's *t* test: $P < 0.001$). In flooded seedlings except for *F. platypoda*, leaf fall began at the end of June.

Dry weights of flooded and control seedlings of all species differed significantly (Welch's *t* test). Root dry weights of flooded seedlings were less than those of control seedlings for all species (Fig. 3).

Mean values of stem and branch dry weights were lower in flooded plants than those in control plants for all species. Those dry weights did not differ significantly among control and flooded seedlings of *F. platypoda* and *A. turbinata* but they did in the gap-dependent riparian species including *P. rhoifolia*, *C. japonicum*, and *P. hispida* ($P < 0.01$); and *Q. mongolica* var. *grosseserrata* ($P < 0.05$), a nonriparian species.

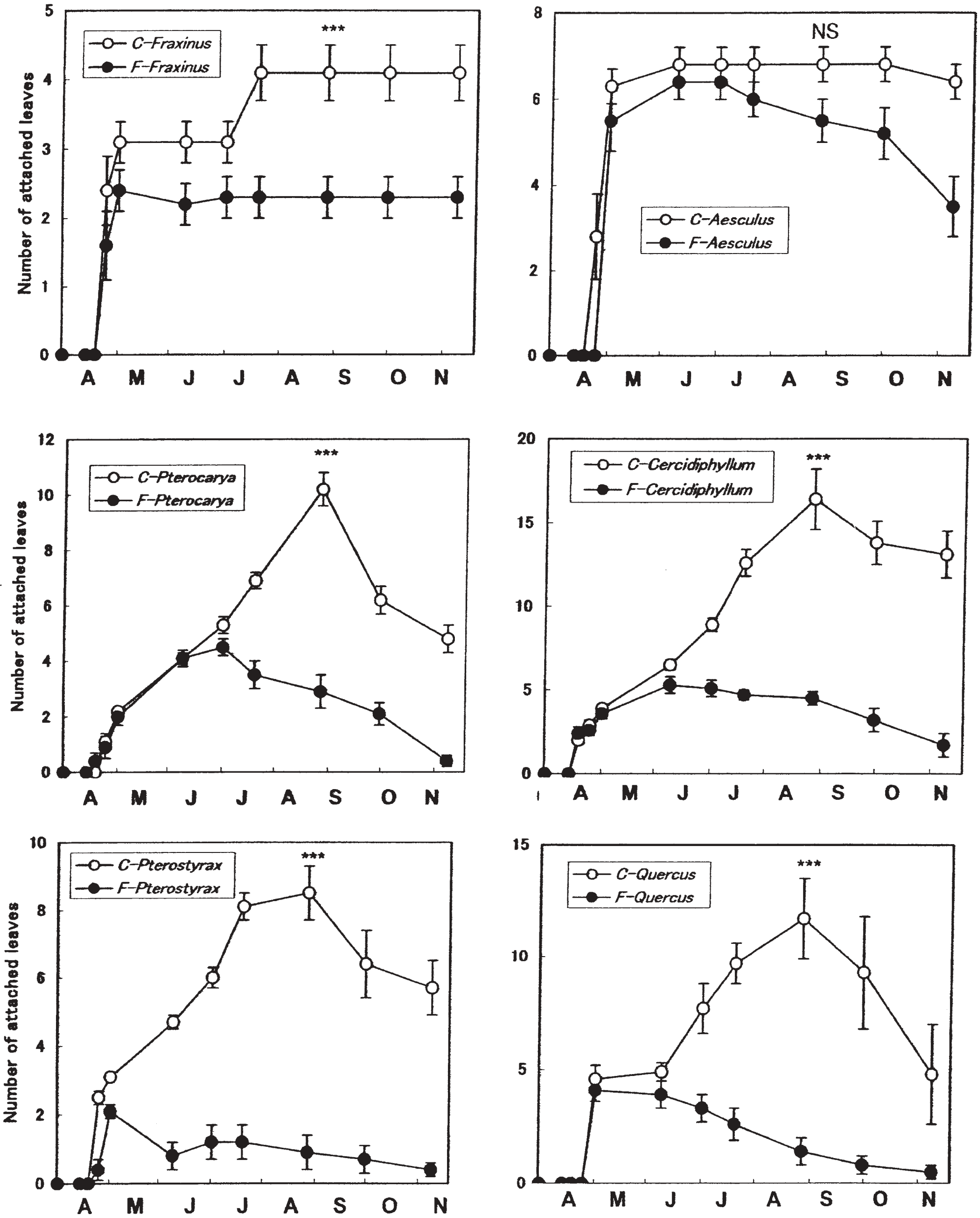


**Fig. 2.** Patterns of leaf dynamics in flooded and control seedlings of the six tree species. See Fig. 1 for explanation of symbols

The survival ratio of flooded plants after the experiment differed with species (Fig. 4). All *F. platypoda* and *A. turbinata* seedlings survived, whereas only 20% of *P. hispida* and 30% of *Q. mongolica* var. *grosseserrata* seedlings survived. The seedlings of the latter two species began to die with 1 or 2 months after the initiation of flooding treatments. The number of dead seedlings increased as the experiment progressed. Various studies have shown reductions of photosynthetic rate in flooded woody species (Takahashi et al. 1988; Terazawa et al. 1992; Pezeshki 1994). Such reduction of photosynthetic yield may be one of the causes of the decrease of the survival ratio.

*Fraxinus platypoda* and *A. turbinata* seedlings were only slightly affected by the flooding treatment. On the other hand, flooding seriously affected the growth of gap-dependent riparian species (*P. rhoifolia*, *C. japonicum*, and *P. hispida*) and *Q. mongolica* var. *grosseserrata*. The current-year growth of those species may depend on the current-year photosynthetic products as shown in *P. rhoifolia* (Sakio 1993). In gap-dependent species, growth reduction may be related to the reduction of photosynthetic rate caused by flooding (Takahashi et al. 1988; Terazawa et al. 1992; Pezeshki 1994).

In flush-type trees such as *A. turbinata*, current-year growth is driven by the previous year's photosynthetic products (Kikuzawa 1988). However, the root growth of them is limited by oxygen deficiency under a flooding environment. The leaves of *A. turbinata* seedlings turned yellow on July 18, suggesting that ethylene production stimulated by flooding stress caused a fall of chlorophyll concentration in the leaves (Abeles et al. 1992).

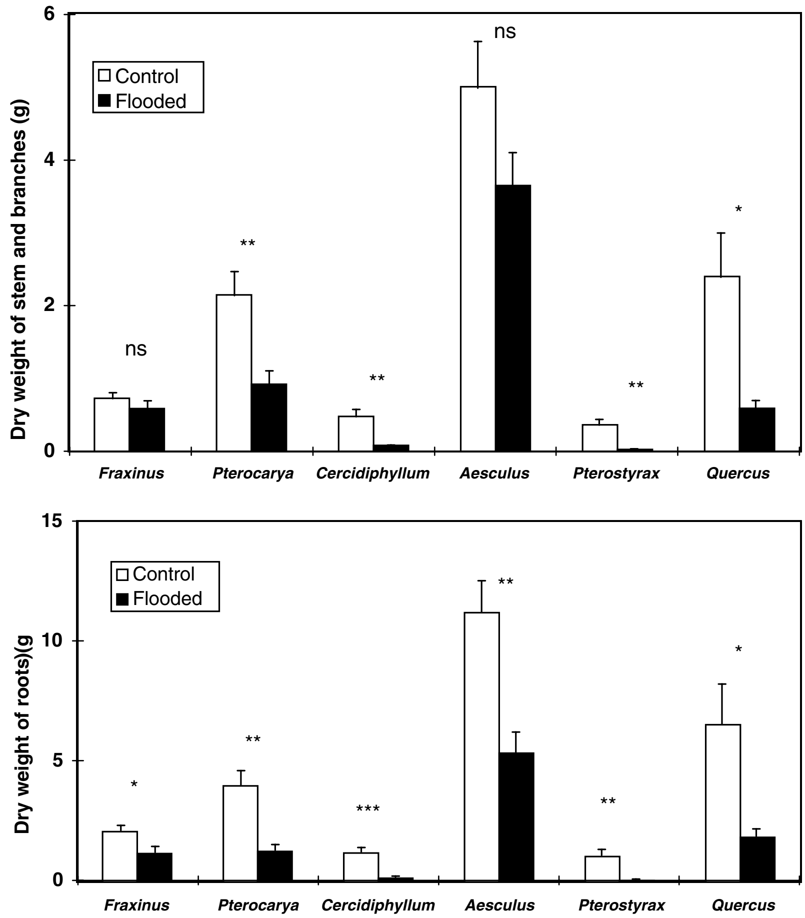


**Fig. 3.** Dry weights of flooded and control seedlings of the six tree species. See Fig. 1 for explanation of symbols

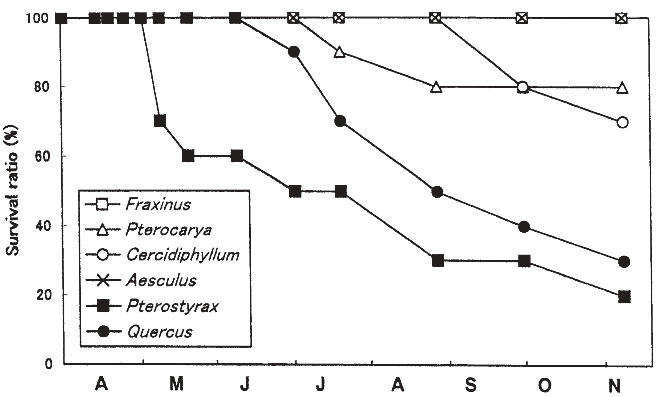


**Fig. 4.** Survival ratios in flooded seedlings of the six tree species

The difference in the effects of flooding on the survival ratio between *F. platypoda*, well adapted to various riparian disturbances (Sakio 1997), and *Q. mongolica* var. *grosseserrata*, a nonriparian species, is shown in Fig. 4. This difference may be due to physiological differences in tolerance to flooding. In the flooding treatment of the present study, leaves of *F. platypoda* seedlings did not fall by the end of growing season, whereas those of *Q. mongolica* var. *grosseserrata* began to fall immediately after leaf development. Ethylene production stimulated by flooding stress can initiate physiological responses including senescence, leaf abscission, and formation of aerenchyma (Abeles et al. 1992). *Fraxinus mandshurica* Rupr. var. *japonica* Maxim., native to swampy areas, grew adventitious roots having many aerenchyma in the bark tissue together with ethylene production during flooding treatment (Yamamoto et al. 1995b; Nagasaka 2001). Sakio (2002) demonstrated that *F. platypoda* trees planted near the stream form adventitious roots on buried stems. This species may also be adapted to flooding environment as well as *F. mandshurica*.

Nagasaka (2001) reported reduced shoot elongation, leaf number, and dry weight increment in flooded *Q. mongolica* var. *grosseserrata* seedlings. Flooding for 7 weeks reduced photosynthetic and transpiration rates of the same species (Takahashi et al. 1988). In this species, ethylene production stimulated by flooding stress may cause leaf senescence and leaf fall immediately after leaf development (Abeles et al. 1992). As a result, the effects of flooding on growth of the seedlings differed with the tree species because of differences in leaf-emergence pattern and physiological flood tolerance. The responses of tree seedlings to flooding reflected species habitats and growth patterns.

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## Literature cited

Abeles FB, Morgan PW, Saltveit Jr ME (1992) Ethylene in plant biology. Academic, San Diego, pp 56–119

Hook DD (1984) Adaptation to flooding with fresh water. In: Kozlowski TT (ed) Flooding and plant growth. Academic, New York, pp 265–294

Kikuzawa K (1988) Leaf survival of tree species in deciduous broad-leaved forests. Plant Spec Biol 3:67–76

Kozlowski TT (1984) Responses of woody plants to flooding. In: Kozlowski TT (ed) Flooding and plant growth. Academic, New York, pp 129–163

Kozlowski TT, Kramer PJ, Pallardy SG (1991) The physiological ecology of woody plants. Academic, San Diego, pp 303–337

Maeda T, Yoshioka J (1952) Studies on the vegetation of Chichibu Mountain forest (2). The plant communities of the temperate mountain zone (in Japanese with English summary). Bull Tokyo Univ For 42:129–150

Nagasaka A (2001) Effects of flooding on growth and leaf dynamics of two-year-old deciduous tree seedlings under different flooding treatments (in Japanese with English summary). Bull Hokkaido For Res Inst 38:47–55

Pezeshki SR (1994) Plant responses to flooding. In: Wilkinson RE (ed) Plant–environment interactions. Marcel Dekker, New York, pp 289–321

Sakio H (1993) Sapling growth patterns in *Fraxinus platypoda* and *Pterocarya rhoifolia* (in Japanese with English synopsis). Jpn J Ecol 43:163–167

Sakio H (1997) Effects of natural disturbance on the regeneration of riparian forests in a Chichibu Mountains, central Japan. Plant Ecol 132:181–195

Sakio H (2002) Survival and growth of planted trees in relation to the debris movement on gravel deposit of a check dam (in Japanese with English summary). J Jpn For Soc 84:26–32

Sakio H, Kubo M, Shimano K, Ohno K (2002) Coexistence of three canopy tree species in a riparian forest in the Chichibu Mountains, central Japan. Folia Geobot 37:45–61

Takahashi K, Fujimura Y, Koike T (1988) Tolerance of deciduous broad-leaved trees in Hokkaido to flooding. (II) Seasonal change of the tolerance (in Japanese). Trans Mtg Hokkaido Br Jpn For Soc 36:99–101

Terazawa K (1994) Growth and photosynthetic responses of *Fagus crenata* seedlings to continuous and periodic flooding (in Japanese). Trans Mtg Hokkaido Br Jpn For Soc 42:120–122

Terazawa K, Kikuzawa K (1994) Effects of flooding on leaf dynamics and other seedling responses in flood-tolerant *Alnus japonica* and flood-intolerant *Betula platyphylla* var. *japonica*. Tree Physiol 14:251–261

Terazawa K, Seiwa K, Usui G, Kikuzawa K (1989) Responses of some deciduous broad-leaved tree seedlings under water saturated soil condition. I. Growth and morphological changes of stem and root (in Japanese). Trans 100th Ann Meet Jpn For Soc 439–440

Terazawa K, Maruyama Y, Morikawa Y (1992) Photosynthetic and stomatal responses of *Larix kaempferi* seedlings to short-term waterlogging. Ecol Res 7:193–197

Yamamoto F, Kozlowski TT (1987a) Effect of flooding of soil on growth, stem anatomy, and ethylene production of *Cryptomeria japonica* seedlings. Scand J For Res 2:45–58

Yamamoto F, Kozlowski TT (1987b) Effects of flooding, tilting of stems, and ethrel application on growth, stem anatomy and ethylene production of *Pinus densiflora* seedlings. J Exp Bot 38:293–310

Yamamoto F, Sakata T, Terazawa K (1995a) Growth, morphology, stem anatomy, and ethylene production in flooded *Alnus japonica* seedlings. IAWA J 16:47–59

Yamamoto F, Sakata T, Terazawa K (1995b) Physiological, morphological and anatomical responses of *Fraxinus mandshurica* seedlings to flooding. Tree Physiol 15:713–719