Growth Responses to Flooding and Recovery of Deciduous Trees

Jonathan Frye* and Wolfgang Grosse

Botanisches Institut, Universität zu Köln, Gyrhofstraße 15, D-W-5000 Köln 41, Bundesrepublik Deutschland

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Tree seedling flooding tolerance for 22 species was assessed under controlled field conditions. Initial heights under control (freely draining soil, n = 20 per species) and flooded (standing water, depth = 10 cm, n = 20 per species) conditions were measured in March 1990. Survival, height and diameter growth were determined after 120 days. Recovery from flooding effects was assessed in the following growing season from March to August, 1991. *Taxodium distichum* (L.) L. C. Rich. exhibited enhanced growth when flooded. *Acer saccharinum* L., *Fraxinus excelsior* L., and *Quercus robur* L. increased diameter but not height growth. The following species exhibited reduced growth and/or survival: *Acer campestre* L., *Acer pseudoplatanus* L., *Acer rubrum* L., *Betula nigra* L., *Betula papyrifera* Marsh, *Betula pubescens* Ehrh., *Betula pendula* Roth, *Crataegus monogyna* Jacq., *Fagus grandifolia* Ehrh., *Prunus padus* L., *Prunus serotina* Ehrh., *Quercus palustris* Muenchh., *Quercus petraea* (Mattuschka) Liebl., *Rhamnus cathartica* L., *Salix purpurea* L., *Sorbus aucuparia* L., *Tilia cordata* Mill., and *Ulmus glabra* Huds. emend. Moss. Recovery from flooding in the second growing season was well established with *A. saccharinum, C. monogyna, Qu. palustris, Qu. petraea, S. purpurea, U. glabra,* while height growth relative to the flooding period was retarded in *A. rubrum, F. grandifolia, F. excelsior, Qu. robur, Rh. cathartica,* and *S. aucuparia*. Mortality increased with *B. papyrifera* and *F. grandifolia*. Flooded trees of *B. nigra, B. pendula,* and *Rh. cathartica* appeared to be strongly handicapped by losing their natural resistance against frost even in the following growing season. By decreasing shoot height growth and biomass production, long-term flooding is suggested to reduce the competitive ability of most tree species in the succession of natural forests in habitats which will be inundated more frequently in future when precipitation is increased by the predicted climatic change.

Introduction

Deciduous trees of bottomland forests are adapted to oxygen-deficient soils resulting from high water-tables and periods of dormant season flooding. At wet sites plant health and growth is affected in several ways. Because of decreased oxygen diffusion and microbial oxygen consumption, water-saturated soils become virtually anaerobic within hours to days of waterlogging and reduced phytotoxins accumulate [1–5]. These stresses alter plant metabolism, stomatal closure and phytohormonal balance, reduce photosynthesis, nutrient uptake and water absorption, and can cause death [6]. Accumulation of toxic fermentation products and lack of the enzyme superoxide dismutase (SOD) make plants susceptible to the so-called "post-anoxic injury", when plant tissues are not protected against oxygen damage on return to air [7, 8].

Tree species which are able to grow in frequently flooded bottomlands have developed low-oxygen stress avoiders. Cypress "knees", mangrove stilt roots, adventitious roots, and intumescent formations of lenticels are well know examples of morphological adaptations. Increased oxygen conductivity of roots in waterlogged soil is achieved by aerenchymatous root tissues in *Alnus glutinosa* [9] and *Nyssa sylvatica* [10, 11] or by large stelar cavities in the xylem of *Pinus contorta* roots [12]. Recently, the wetland tree species *Alnus glutinosa* [13–15], *Alnus incana* [16], *Alnus japonica, Alnus hirsuta* [17], *Betula pubescens, Populus tremula,* and *Taxodium distichum* have been identified to avoid anaerobic stress by pressurized gas transport improving oxygen transport into roots, while trees restricted to dry sites did not [18]. This physical adaption of trees to soil anoxia is based on a thermo-osmotically active partition, which is localized in the phellogen layer of the lenticels [19]. It causes pressurization of the air in the intercellular spaces

* *Present address:* Department of Environmental Sciences, University of Virginia, Charlottesville, VA22903, U.S.A.

Reprint requests to W. Grosse.

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of the stem and a gas flow down to the roots, when the temperature of the stem is a few degrees warmer than ambient air due to absorbing radiant energy as reviewed by Grosse and Schröder [20].

Besides these structural and physical features the accumulation of SOD during anoxia appears to be a highly effective biochemical adaptation to survive long-term flooding and to sustain post-anoxic injury as shown for some herbaceous monocots differently susceptive to damage by flooding and soil anoxia [8]. This biochemical adaptation is established in trees as well. Trees of the two wetland species *A. glutinosa* and *A. japonica* accumulate SOD in their root tissues during soil inundation, but *A. hirsuta* trees, which are restricted to drier sites, decrease SOD activity [17, 21].

Although wetland trees have acquired effective adaptations to flooding, their tolerance of anoxia is a relative term only. Stagnant water and flooding during the growing season are deleterious more than flowing water or dormant season flooding, even to tolerant species [6] and soil inundation should not exceed 40% of the growing season each year [5]. Survival time under constant flooding of 23 flood-tolerant trees varies from 3 years to 4 months [22], but upland or lowland tree species may be much more susceptible. When the expected heavy precipitations and sea-level rise, resulting from climatic changes and the greenhouse effect, are taken into consideration more lowland areas, which are used for timber production, will be affected by stagnant water saturation of the soil and growing season flooding. We need more data on tree responses to flooding to evaluate the situation in lowland areas, which are currently afforested by non-wetland tree species, and to understand changes of succession in natural forests in the near future. This report will survey the growth responses and resistance of seedlings of some tree species from the New and Old World, different in their optimal soil water status, to flooding in the growing season designed under identical conditions.

Materials and Methods

Plant material

Specimens of *Acer campestre* L., *Acer pseudoplatanus* L., *Acer rubrum* L., *Acer saccharinum* L., *Betula nigra* L., *Betula papyrifera* Marsh, *Betula pubescens* Ehrh., *Betula pendula* Roth, *Crataegus monogyna* Jacq., *Fagus grandifolia* Ehrh., *Fraxinus excelsior* L., *Prunus padus* L., *Prunus serotina* Ehrh., *Quercus palustris* Muenchh., *Quercus petraea* (Mattuschka) Liebl., *Quercus robur* L., *Rhamnus cathartica* L., *Salix purpurea* L., *Sorbus aucuparia* L., *Taxodium distichum* (L.) L. C. Rich., *Tilia cordata* Mill., and *Ulmus glabra* Huds. emend. Moss. were obtained as one-year-old, leafless, and unbranched seedlings from a local tree nursery in December 1989, and potted into plastic containers (13 cm × 13 cm × 13 cm) with a mixture of garden-mould and sand in a ratio 1 : 1. The trees over-wintered in individual pots in the nursery of the Botanical Institute of the University of Cologne, Germany.

Before leafing out in spring the trees were repotted into larger plastic containers (20 cm × 20 cm × 25 cm) during February 1990, randomly separated into two groups, and placed in two trenches (100 cm × 2000 cm × 30 cm) in a well drained area of the experimental garden in a south to north extension. To avoid shading the trenches were about 500 cm apart and the taller trees were positioned to the north. The control trench, containing 20 specimens of each species placed together in a 4 × 5 block and watered 3 to 7 times a week according to the seasonal variations, was allowed to drain freely. The other trench, containing an additional 20 specimens of each species, was lined with plastic and was continuously flooded for 120 days to a depth of 10 cm above the soil surface with standing water throughout the duration of the trial, but drained a few days before the trees were finally assessed for their height and diameter to eliminate swelling effects on diameter measurements. After leaf abscission in November the trees were overwintered in the nursery of the Botanical Institute and explanted finally in March of the following year in two newly designed trenches, similar to those from the year before but both well drained, for a second growth period.

Tree growth measurements

The trees were assessed by very simple methods for their height and diameter at a height of 5 cm in March 1990 and after 120 days again in July in the first, but in March and after 160 days again in August of the following year, respectively. Heights were measured to the nearest 0.5 cm using a meter T-stick. Diameters were measured to the nearest

0.01 cm using a vernier caliper. Trees were considered as dead only when they were brittle, lacked leaves, or had no green tissue visible. The fresh weight of the tree shoot with leaves included was determined gravimetrically. Two-tailed T-tests of height and diameter growth and fresh weight were made using only those data from surviving trees.

Results

Height and diameter growth

The initial heights (*i.e.* March, 1990) of the control and treatment groups for each species are presented in Table I. Statistically there was no significant difference between the initial heights of the control and treatment groups. The height and diameter of each surviving tree was re-measured after 120 days (*i.e.* July, 1990) and the height and diameter growth of the surviving trees calculated. The average height and diameter growth, and survival are presented in Table I, where the significance of the differences between control and treatment groups are also indicated.

We found considerable variation between species in their responses to flooding. *T. distichum* grew significantly better under flooded than freely drained conditions. It showed increased height and diameter growth during flooding (Fig. 1 and 2). Next to *T. distichum* four species, *F. excelsior, Qu. robur, B. nigra,* and *Qu. palustris,* are ranked with no statistically significant effect of flooding on height growth, but different in their diameter growth with a statistically significant increase in *F. excelsior* and *Qu. robur,* and no responses in *B. nigra* and *Qu. palustris.*

We found significantly reduced height growth under flooded conditions for the remaining 17 species, and reduced diameter growth with most of them. For example, height growth of the 17 tree species varied in the following order from the least to the most retarded *C. monogyna, R. cathartica, F. grandifolia* to *B. papyrifera, A. campestre,*

Table I. Effects of 120 days of flooding on 20 young trees of each species under control (C = freely draining soil control) and 20 young trees of each species under flooded (F = flooded with stagnant water to a depth of 10 cm) conditions were measured in March to July 1990. Height growth and diameter growth for each tree were determined by remeasuring each tree after 120 days. The number of survivors was also determined at that time. D = significantly decreased growth under flooded relative to control conditions (α = 0.01), d = significantly decreased growth (α = 0.05), N = no significant difference, I = significantly increased growth (α = 0.01), i = significantly increased growth (α = 0.05).

Species	Initial heights C	Initial heights F	Height growth [cm] C ± sd	Height growth [cm] F ± sd	Diameter growth [cm] C ± sd	Diameter growth [cm] F ± sd	No. trees surviving C	No. trees surviving F
Acer campestre	26.6	25.6	15.6 ± 1.65 D	3.0 ± 0.68	0.08 ± 0.01 D	0.02 ± 0.01	19	14
Acer pseudoplatanus	38.4	38.1	19.4 ± 2.20 D	3.2 ± 0.68	0.15 ± 0.01 d	0.10 ± 0.02	19	17
Acer rubrum	67.5	67.3	12.5 ± 1.30 D	5.1 ± 1.23	0.04 ± 0.08 N	0.05 ± 0.02	18	16
Acer saccharinum	83.5	82.8	26.1 ± 1.53 D	0.2 ± 0.01	0.13 ± 0.01 I	0.19 ± 0.01	20	20
Betula nigra	58.7	58.6	8.5 ± 0.90 N	9.0 ± 1.23	0.10 ± 0.01 N	0.09 ± 0.01	14	14
Betula papyrifera	75.8	70.3	29.0 ± 2.14 D	5.7 ± 1.13	0.20 ± 0.02 D	0.04 ± 0.01	20	15
Betula pubescens	17.3	20.2	12.3 ± 1.43 D	5.5 ± 0.59	0.09 ± 0.01 N	0.06 ± 0.01	18	16
Betula pendula	36.6	38.4	27.3 ± 1.78 D	9.1 ± 1.02	0.19 ± 0.01 D	0.08 ± 0.02	20	20
Crataegus monogyna	71.3	78.0	22.8 ± 2.93 d	14.7 ± 2.22	0.23 ± 0.02 D	0.12 ± 0.02	20	19
Fagus grandifolia	13.4	14.0	6.3 ± 0.76 d	3.7 ± 0.52	0.12 ± 0.02 D	0.02 ± 0.01	12	6
Fraxinus excelsior	35.0	33.2	17.3 ± 1.59 N	20.2 ± 1.88	0.14 ± 0.02 I	0.33 ± 0.01	20	20
Prunus padus	32.8	36.0	33.1 ± 2.36 D	7.1 ± 0.66	0.31 ± 0.01 D	0.09 ± 0.01	20	18
Prunus serotina	69.6	66.3	14.2 ± 1.14 D	3.0 ± 1.41	0.14 ± 0.01 D	0.01 ± 0.01	16	2
Quercus palustris	24.9	25.5	8.4 ± 1.26 N	6.7 ± 0.72	0.03 ± 0.01 N	0.02 ± 0.01	19	20
Quercus petraea	31.5	35.2	12.5 ± 2.47 d	4.8 ± 1.89	0.07 ± 0.02 N	0.04 ± 0.03	17	9
Quercus robur	49.8	50.4	9.8 ± 1.64 N	11.3 ± 1.41	0.09 ± 0.03 i	0.18 ± 0.03	19	18
Rhamnus cathartica	28.1	25.9	10.8 ± 1.61 D	6.5 ± 0.84	0.05 ± 0.01 N	0.05 ± 0.01	16	20
Salix purpurea	71.5	70.5	72.5 ± 3.01 D	33.5 ± 3.89	0.25 ± 0.02 N	0.25 ± 0.03	19	17
Sorbus aucuparia	58.2	55.4	35.3 ± 2.64 D	16.6 ± 1.77	0.16 ± 0.02 D	0.00 ± 0.01	20	17
Taxodium distichum	45.8	42.1	9.1 ± 0.83 I	15.2 ± 0.88	0.11 ± 0.02 I	0.24 ± 0.01	20	19
Tilia cordata	45.7	47.0	8.1 ± 1.00 D	2.2 ± 0.26	0.21 ± 0.02 N	0.15 ± 0.03	19	19
Ulmus glabra	40.0	35.0	11.4 ± 0.80 D	5.3 ± 0.57	0.11 ± 0.01 d	0.09 ± 0.01	20	19

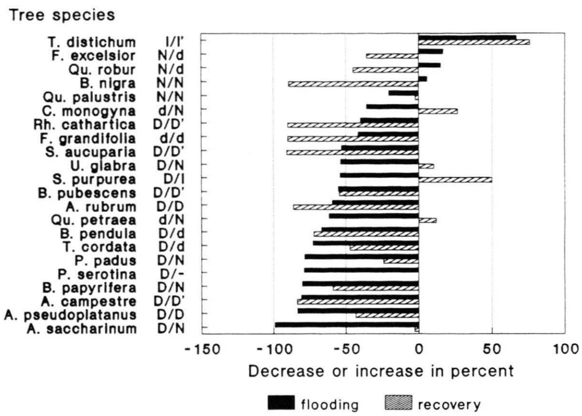

Fig. 1. Changes in height growth of seedlings of 22 tree species after 120 days of flooding in the growing season and recovery in the second year as compared in percent *vs.* the unflooded controls. According to t-tests, D′, D, and d = significantly decreased growth under flooded relative to control conditions at a level of $\alpha = 0.001$, $\alpha = 0.01$, and $\alpha = 0.05$, respectively. I′, I, and i = significantly increased growth at a level of $\alpha = 0.001$, $\alpha = 0.01$, and $\alpha = 0.05$, respectively, N = no significant difference.

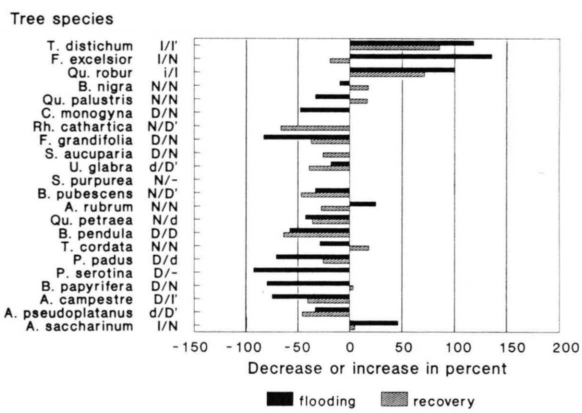

Fig. 2. Changes in stem diameter growth of seedlings of 22 tree species after 120 days of flooding in the growing season and recovery in the second year as compared in percent *vs.* the unflooded controls. Codes for level of significance are as in Fig. 1.

A. pseudoplatanus, and *A. saccharinum,* finally (Fig. 1). *A. saccharinum,* which had a negligible growth rate, and *A. rubrum* showed an increased diameter growth in the flooded *versus* control groups (Fig. 2).

When the young trees were assessed a second time in the following year after explanting into well drained trenches, the species exhibited a quite different recovery. Except for *T. distichum* with a significantly stimulated height (Fig. 1) and diameter growth (Fig. 2) through 160 days from March to August, 1991, and *S. purpurea* with an increased height growth, all other trees had equal or significantly reduced height and diameter growth, but the reduction of height growth was greater than during the period of flooding in *Rh. cathartica, F. grandifolia, S. aucuparia,* and *A. rubrum.*

Survival

Most of the flooded tree species had nearly equal survival (Table I; Fig. 3), but a significant decrease of survival in the two species *Qu. petraea* and *F. grandifolia.* A high mortality was observed in *P. serotina* with 2 surviving trees only, so that studies of recovery in a second growth period was inadequate with this species.

The rate of survival in the second growing season was very high with nearly all species except for *F. grandifolia* and *B. papyrifera* where about two thirds of all remaining young trees had died at the end of the experiments (Fig. 3). It may be of interest that three tree species, *B. nigra, B. pendula,* and *Rh. cathartica,* appeared to become highly susceptible to frost injury during the period of recovery. An unusually low temperature in the night of June 5 to 6, with temperatures below the freezing point (surface skin temperature −1.6 °C) caused a die-

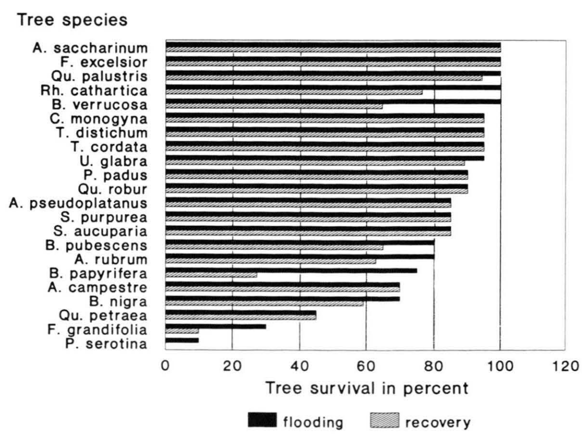

Fig. 3. Survival of seedlings of 22 tree species after 120 days of flooding in the growing season and after cultivation for recovery in the second year on well drained soil as compared in percent *vs.* the unflooded controls.

off of most of the shoot and a stem sprouting on 82%, 55%, and 31% of the specimens, respectively.

Tree height and biomass production

Taking the tree heights at the end of the experiments into consideration (Fig. 4) the three frost impaired tree species, *B. nigra, B. pendula,* and *Rh. cathartica,* exhibit nearly no height growth in the flooded provenances and are comparable with the high growth retarded species *A. campestre, A. rubrum,* and *F. grandifolia,* for example. On the other hand, tree species like *S. purpurea* and *A. saccharinum* had recovered from the flooding effects in the second growing season as shown by above ground biomass measurements (Fig. 5), while the species *B. papyrifera, F. excelsior, B. pubescens,* and *S. aucuparia,* with highly reduced height growth throughout both growing seasons, had a biomass production rates decreased 61%, 40%, 37%, and 34% of the control, respectively.

Even with the control there was a high variation of height increase among the species through the two growing seasons (Fig. 4). The specimens of the two *Quercus* species *Qu. palustris* and *Qu. petraea* did not differ significantly in their height at the beginning and the end of the experiments. Since other species, for example *A. campestre* and *B. pubescens* became 3 to 4 times taller at the same period, the retarded height growth of the *Quercus* species appeared not to be caused by nutrient deficiency, but by a vigorous branching frequency.

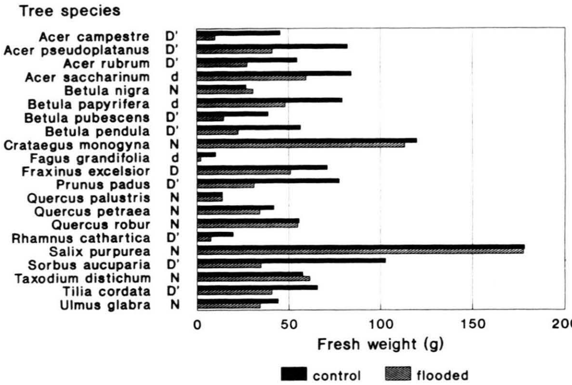

Fig. 5. Above ground biomass production of 22 tree species affected by 120 days of flooding in the growing season and cultivation for recovery in the second year on well drained soil as compared with unflooded controls. According to t-tests, D′, D, and d = significantly decreased fresh weight under flooded relative to control conditions at a level of $\alpha = 0.001$, $\alpha = 0.01$, and $\alpha = 0.05$, respectively, N = no significant difference.

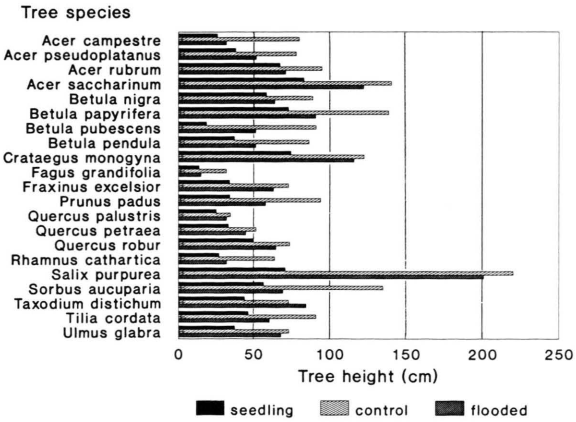

Fig. 4. Tree heights of 22 tree species affected by 120 days of flooding in the growing season and cultivation for recovery in the second year on well drained soil as compared with unflooded controls.

Discussion

We studied the net effect of all flood tolerance mechanisms on the survival and growth rates of 22 tree species representing 13 genera from 1 coniferous and 9 dicot families. The species were chosen on the basis of their commercial availability and natural occurrence in areas of intermittent or permanent flooding. Inundation with stagnant water is most stressful to plants [6] and was also relatively easy to implement at the scale of our study. It must be noted that juvenile and mature trees may respond differently to flooding stress, but our study was designed to examine its effects on seedlings.

Reports in the literature comparing responses of many tree species to flooding often summarize the results of studies quite differently designed. For example, the survival time under inundation of 23 flood-tolerant tree species as reported by Crawford [5] reviews observations from the Tennessee valley [23], river-bottoms [24], southern forests of the United States [25], margins of Illinois reservoirs [26], and flooding experiments [27]. Tree seedlings are much easier to cultivate under identical conditions than older trees and they are very important as well for afforestation and succession in natural forests. Therefore, tree seedlings appeared favourable for these studies to compare the responses of many species to inundation.

Taxodium distichum is exceptional among the species studied. Only a few species of gymnosperms are flood tolerant. The bald cypress is one, growing vigorously in standing water for many years [28]. Our observation confirms this result. Using height and diameter growth as indicators, *T. distichum* thrives under stagnant flooding conditions, more so, in fact, than under freely drained ones. No complete explanation of this phenomenon is currently available, although Grosse, Frye and Lattermann [18] have suggested the presence of an active gas transport mechanism in the bald cypress. Very noticeable is that this growth stimulation is continued in the following season even in well-drained soil.

Several of the other more flood-tolerant species tested, *F. excelsior, Qu. robur,* and *A. saccharinum* at least, exhibit enlarged stem bases in response to flooding. Since cambial growth depends on aeration for mitotic activity, which is adversely affected by the cessation of adenosine triphosphate (ATP) generation during periods of oxygen deficiency, the observed stem diameter increase is likely to be due to the formation of aerenchyma, which may be triggered by ethylene as shown for the air-space formation in adventitious roots of maize under reduced oxygen partial pressure [29] and *Pinus serotina* seedlings [30]. This may explain as well why *F. excelsior* and *Qu. robur* were able to maintain height growth under flooded conditions. *F. excelsior* has recently been shown to have an exceptionally high gas permeability in diffusion studies using ethane as a physiologically inert tracer [14, 18].

While seedlings of *Qu. robur* and *B. nigra* were indifferent to soil inundation, 120 days of flooding reduced height growth by the rest of the assessed species, with the rate of growth of unflooded trees two to five times that of flooded plants.

Although the flooding period exceeded the 40% margin of the total growing season, which has been emphasized by many investigators to be important for survival as reviewed by Kozlowski [31], except for *Qu. petraea, F. grandifolia,* and *P. serotina,* all of the studied species exhibited a high survival in the second growing season too. This may be due to the climatic situation in the temperate zone and the moderate soil temperature during summer and fall in the Rhine valley, Germany, but some species, *B. nigra, B. pendula,* and *Rh. cathartica,* appeared to be strongly handicapped by losing their natural resistance against frost after leafing out.

Considerable variation has been reported in flood tolerance of closely related species of the genus *Betula* [32]. Seedlings of *B. papyrifera* were more adversely affected by 5 weeks of flooding, and were slower to recover after the soil was drained, than seedlings of *B. nigra.* Height growth during flooding was negligible in *B. papyrifera* but substantial in *B. nigra.* Our observations corroborate these results on retarded growth during inundation, but we found a slow recovery with both species, which may result from the 3 times larger flooding period. The two additional species *B. pubescens* and *B. pendula,* which we have incorporated into our studies on growth responses and recovery rank in between.

Reduction of height growth is accompanied generally by a reduced above ground biomass production. It must be remembered, therefore, that long-term survival under natural conditions implies that the tree must be vigorous enough to compete successfully with its neighbours and able to propagate as well. This study did not directly assess fitness in that sense, but those species like *T. cordata, P. padus, P. serotina, A. pseudoplatanus,* and *A. saccharinum,* exhibiting an extremely high reduction of height grown, and species with a very poor recovery in concert with a highly reduced height growth during flooding like *Rh. cathartica, F. grandifolia, S. aucuparia, B. pubescens, B. pendula, B. papyrifera, A. rubrum,* and *A. campestre* will be at a competitive disadvantage to taller, faster growing neighbours and will be eliminated from the succession in the natural wetland forests. The high mortality of *Qu. petraea, F. grandifolia,* and *P. serotina,* or the high susceptibility against frost damage of *B. nigra, B. pendula,* and *Rh. cathartica,* we suggest, will make these species unable to occupy natural habitats, when these areas are more frequently flooded in the future as a result of heavier precipitation after the predicted climatic change.

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