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Can tree seedlings survive increased flood levels of rivers?

H. N. SIEBEL*, M. VAN WIJK† and C. W. P. M. BLOM†

**Institute for Forestry and Nature Research (IBN-DLO), PO Box 23, NL-6700 AA Wageningen, The Netherlands; and †Department of Ecology, University of Nijmegen, Toernooiveld 1, NL-6525 ED Nijmegen, The Netherlands*

SUMMARY

Flood tolerance and the avoidance of severe flood conditions in tree seedlings were examined experimentally to elucidate tree zonation along the Rhine and determine the effect of higher floods. In comparison with seedlings of *Acer campestre* from only incidentally flooded forest, seedlings of *Fraxinus excelsior*, *Quercus robur* and *Ulmus minor* from hardwood floodplain forest and *Alnus glutinosa* and *Populus nigra* from softwood floodplain forest showed a high tolerance to partial submergence. This partly correlated with morphogenetic adaptations, e.g. adventitious rooting and hypertrophy of stems and lenticels. Seedlings of all species were much more sensitive to total submergence than to partial submergence, especially when light transmission during flooding was strongly reduced. Seedlings of trees from softwood floodplain forest were able to endure longer periods of total submergence than those of hardwood floodplain forest. Because of their relative slow extension growth rates, seedlings of species from hardwood floodplain forest cannot avoid being totally submerged when flooded on low-lying sites. Therefore, the higher flood levels of the Rhine strongly reduce the likelihood of tree species from hardwood floodplain forests establishing on low-lying sites along this river.

Key-words: Alnus glutinosa, floodplain forest, *Fraxinus excelsior*, *Populus nigra*, *Quercus robur*, *Ulmus minor.*

INTRODUCTION

In the Rhine system, two main floodplain forest types are distinguished: frequently flooded pioneer softwood forest mainly occurring on low-lying sites, and hardwood floodplain forest of later successional stages mostly on higher elevations (Dister 1984; Hügin & Henrichfreise 1992; Schnitzler 1995). The softwood forest consists of *Alnus* spp., *Populus* spp. and *Salix* spp. The hardwood forest is dominated by *Fraxinus excelsior*, *Quercus robur* and *Ulmus minor*. Most of the natural floodplain forests in Western Europe, particularly the hardwood ones, have been excluded from flooding or have long since been felled, and what little remains has mostly been greatly altered by forestry (Schnitzler 1994). Although plans have recently been made for the restoration of floodplain forests along the Rhine, little information is available about the establishment of tree species and forest development in relation to the present flooding dynamics. It is known that, in common with most rivers, the flooding dynamics of the

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Rhine have changed during the past 1000 years. Flood levels have risen as a result of the accelerated water discharge upstream and the construction of dikes which have drastically narrowed the floodplain (Blom *et al.* 1990).

Investigating flood tolerance and avoidance of severe flooding conditions in species and the underlying adaptive mechanisms helps explain plant zonation along rivers (Blom *et al.* 1996; Blom & Voesenek 1996). As tree species are most sensitive to flooding during their early life stages (Gill 1970; Kozlowski 1984; Siebel & Blom 1998), tree zonation depends largely on the flooding resistance of their seedlings. Therefore, to elucidate tree zonation and determine the effect of higher flood levels, we examined flood tolerance and avoidance of severe flooding conditions in tree seedlings of six species from West European floodplain forests.

The flood tolerance in tree seedlings depends on the level to which they are submerged. In general, totally submerged tree seedlings survive flooding for shorter periods than partially submerged ones (Gill 1970; Kozlowski 1984; Good *et al.* 1992). Several morphogenetic adaptations such as adventitious rooting, hypertrophic swelling of lenticels and stem hypertrophy are thought to prolong tree seedling survival during partial submergence by enhancing internal aeration (Kozlowski 1984; Armstrong *et al.* 1994). The mortality rates of totally submerged plants are much higher at low light intensity in the water than at high light intensity (Blom *et al.* 1994). Light levels decrease down the water column, which may also influence the ability of tree seedlings to survive total submergence. To determine the flood tolerance of tree seedlings and some of the underlying adaptive mechanisms, we also examined the morphological response, damage and survival of tree seedlings in relation to depth of submergence and light availability.

Tree seedlings can avoid the more severe conditions of total submergence by growing rapidly in height to above flood level before a flood period occurs. The extension growth of tree seedlings can be retarded by flooding (Frye & Grosse 1992). This increases the likelihood of the seedlings being totally submerged during the next flooding period, which is why the extent to which extension growth is affected by flooding is important. Thus, to determine if tree seedlings can avoid being totally submerged, we examined their extension growth and how this is affected by flooding.

The study included seedlings of *F. excelsior* L., *Q. robur* L., *U. minor* Miller, *P. nigra* L., and *A. glutinosa* (L.) Gaertn. For comparison *Acer campestre* L. from only incidentally flooded sites in floodplain forests was included in some of the experiments. Our hypothesis was that species from softwood floodplain forests which at present survive at low-lying elevations near the river are better able to avoid total submergence, because of rapid extension growth, and are more tolerant of total submergence and are therefore better adapted to higher flood levels than the other species.

MATERIALS AND METHODS

Plant material

Plant material was collected from individual populations in the river area in the Netherlands. *A. campestre* and *F. excelsior* were collected in early spring as young seedlings with only cotelydons present. The other species were grown from seed. Seeds of *U. minor* and *P. nigra* were sown immediately after collection at the end of spring. Seeds of *Q. robur* and *A. glutinosa* were collected in autumn, stored at 4°C and sown in early spring. A few weeks after germination the seedlings were transplanted into plastic containers (diameter 14 cm, content 2 l) filled with clay collected from the river foreland near Wageningen (The Netherlands). The seedlings were kept outdoors until the start of the experiment.

Total versus partial submergence

In the first experimental series the effect of partial and total submergence on survival, growth and morphological response was examined. The experiment was performed in a greenhouse (20°C) to approach severe summer flooding conditions and started on 10 May 1994. One-year-old seedlings of *A. campestre*, *A. glutinosa*, *F. excelsior* and *U. minor* and 2-year-old seedlings of *P. nigra* of about the same weight were used. The plants were randomly divided into three groups ($n=7$): freely draining but watered regularly, partially submerged to a depth of 5 cm or totally submerged in clear water 65 cm deep. After 10 weeks the dry weight of adventitious roots, primary roots, stems and leaves and the length growth and hypertrophy of stems and lenticels were determined. Stem hypertrophy was detected by a larger stem diameter increase in flooded plants compared to non-flooded plants and a deviating stem anatomy checked under the microscope. Hypertrophy of lenticels was observed from strongly increased lenticel diameter. The hypertrophied lenticels were counted. Dry weights of stem, leaves and roots were determined after removal of dead parts. Death of root parts was assessed on the basis of discolouration and disintegration of the outer root layers. A tree seedling was considered not to have survived if the underground root system had totally died or if the stem had died back to below the lowest lateral bud.

Effect of light and of depth of total submergence

The influence of duration and depth of total submergence and light availability on damage and survival of tree seedlings was examined in a completely randomized three-way block design. The experiment started on 6 May 1994 in an outdoor basin. It involved totally submerging 1-year-old seedlings of *A. glutinosa*, *F. excelsior*, *Q. robur* and *U. minor* in clear water with a water column above the soil of 30 or 70 cm for 3, 6, 9 or 15 weeks. Half the plants were placed in a part of the basin which was covered with polythene sheeting resulting in dark flooding conditions (1% daylight). In the clear water light levels differed very little between the two flooding depths. Five plants were sampled from each duration and treatment. Additional groups of non-flooded seedlings were sampled at the beginning and end of the experiment. Plant measurements included dry weight of leaves, stems and roots. The flooded seedlings were sampled 3 days after the end of the flooding period to account for additional effects such as the loss of leaves, which occurred within a few days after flooding. Treatment differences in dry weight of leaves, stems or roots were tested for each species by analysis of variance after logarithmic transformation in which initial stem diameter was used as a covariable. Treatment differences in mortality were analysed using multiple logit regression.

Extension growth

To find out whether tree seedlings can avoid total submergence by growing in height before a flood occurs, we measured the extension growth of seedlings in The Netherlands in the field and of first-year seedlings grown in containers filled with clay in an experimental garden. Yearly height increment of plants in the field was estimated on the basis of year growth scars on the stem, substantiated with tree ring counts. Only plants without visible stem damage were used. *F. excelsior*, *Q. robur* and *U. minor* seedlings were sampled in a non-flooded hardwood floodplain forest. Those of *A. glutinosa* and *P. nigra* were sampled on a river bank that was not flooded in the growing season of the preceding 3 years.

Effect of flooding on growth

The effect of flooding on damage and recovery, especially in relation to extension growth, was studied in detail in *F. excelsior* and *Q. robur* to determine to what extent this further reduces the likelihood that species with a slow extension growth will grow above normal flood level. The damage and growth of first-year seedlings during flooding and their subsequent recovery were examined in relation to duration of flooding, flood depth and light availability in a completely randomized three-way block design. Seedlings were either partially submerged with a water column above the soil of 5 cm or totally submerged with a water column above the soil of 50 cm. They were submerged for 2, 4, 7 or 12 weeks. Half the plants were subjected to a reduced light treatment of approximately 15% full daylight. Flooding took place in an outdoor basin of 8 × 2·5 m in the experimental garden of the University of Nijmegen (The Netherlands) and started on 10 May 1993. Eight *Q. robur* and 10 *F. excelsior* seedlings were used for each treatment. Four plants from each group were sampled after the end of a flooding treatment. To determine recovery, the other plants were sampled the following year on 1 September. Additional groups of non-flooded seedlings were sampled at 0, 4 and 12 weeks and the following year. Measurements included stem length, stem diameter at 3 cm above soil surface and dry weight of roots, stems and leaves. When stems died back during flooding, stem length was measured to where the stem was observed to be brown or black. Stem length and stem diameter of each plant were also measured at the beginning of the experiment. Treatment differences in dry weight of leaves, stems or roots between flooding durations were tested per species and flood level by analysis of variance after logarithmic transformation in which stem diameter at the start of the experiment was used as a covariable to correct for variation in initial plant weight.

RESULTS

Partial versus total submergence

Only six seedlings of *P. nigra* and two of *A. glutinosa* and *U. minor* of an initial seven plants survived 10 weeks of total submergence. All other species were totally killed. Totally submerged seedlings did not show adventitious rooting or hypertrophy of stems and lenticels.

After 10 weeks of partial submergence all seedlings of *A. campestre* and one of *F. excelsior* and *U. minor* died. All species except *A. glutinosa* showed considerable damage of their original root system and the root dry weight was significantly lower (*t*-test, $P<0{\cdot}05$) than that of the plants in freely draining soil (Fig. 1). In *A. glutinosa*, the loss of roots was largely compensated by the formation of adventitious roots on the submerged parts of the stem. In none of the species significant differences in length growth and total plant weight were found between plants in freely draining soil and partially submerged plants that survived. When partially submerged, all plants produced adventitious roots and hypertrophied lenticels, although to different degrees (Table 1).

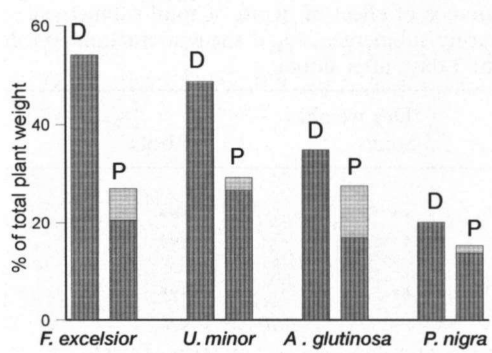

Fig. 1. Dry weight of roots of the tree seedlings after 10 weeks of partial submergence (P) or freely draining conditions (D) as percentage of total plant weight. ▩, Adv. roots; ■, roots.

Table 1. Morphological adaptation of tree seedlings to partial submergence

Species	Stem hypertrophy	Adventitious rooting	Hypertrophied lenticels
Acer campestre	−	+	+
Fraxinus excelsior	+	++	++
Quercus robur	+	++	++
Ulmus minor	−	+	++
Alnus glutinosa	+	++	++
Populus nigra	−	+	+

− = not detected, + = present, ++ = present and more than 5% of plant dry weight allocated to adventitious roots or more than 10 hypertrophied lenticels present. Data on *Quercus robur* are from the experiment on the effect of flooding on extension growth.

Only three species showed stem hypertrophy. Under the microscope a distinct boundary was often observed in the xylem of these species between the smaller cells formed before flooding and larger cells formed during flooding. No significant increase of bark thickness was found compared to non-flooded plants.

Effect of light and depth of total submergence

Depth of flooding had no significant effect on plant weight during total submergence (Table 2). There was, however, a negative effect of shading during total submergence in all species (Fig. 2). The size of the response to shading during total submergence varied among the species. In both *A. glutinosa* and *F. excelsior* the light availability during total submergence had a clear effect on weight of stem and roots, but this effect was much less evident in *Q. robur* and *U. minor*. All species shed their leaves within a month of being flooded. Seedlings of *A. glutinosa* and *F. excelsior* died significantly sooner ($P<0{\cdot}05$) during total submergence in the dark, but this was not found in the other two species (Fig. 3).

Table 2. Analysis of variance of effect of depth of total submergence, duration (3, 6, 9 weeks) and light availability during submergence and their interactions on dry weight of stems, roots and total seedling weight 3 days after flooding

Source of variation	Dry weight stems	Roots	Total
Alnus glutinosa			
Duration (Du)	**	***	***
Light (Li)	*	***	***
Depth (De)	—	—	—
Du × Li	**	***	***
Du × De	—	—	—
Li × De	—	—	—
Du × Li × De	—	—	—
Quercus robur			
Duration	—	***	**
Light	—	**	*
Depth	—	—	—
Du × Li	—	—	—
Du × De	—	—	—
Li × De	—	—	—
Du × Li × De	—	—	—
Ulmus minor			
Duration	—	***	***
Light	**	—	—
Depth	—	—	—
Du × Li	*	—	—
Du × De	—	—	—
Li × De	—	—	—
Du × Li × De	—	—	

— = non-significant, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$. (because of high mortality *Fraxinus excelsior* could not be analysed).

Extension growth

The extension growth of seedlings of the species from hardwood floodplain forests was only about 10–20 cm per year (Table 3). These plants often needed at least 4 years to attain a height of 50 cm. Although *F. excelsior* and *Q. robur* were taller than the other species at the beginning of summer in their first growing season, the other species had caught up or even surpassed them the end of their first growing season. Seedlings of *A. glutinosa* and *P. nigra* were only found as pioneers in well-illuminated sites. They mostly attained a height of 50 cm or more in 2 years. Average extension growth in the experimental garden was similar to that found in the field except for *A. glutinosa*, which grew less in height in the field population.

Effect of flooding on growth

No significant effect of light availability was found on the growth response to partial and total submergence of *F. excelsior* and *Q. robur*. Therefore, shaded and unshaded plants were pooled when investigating the effect of partial and total submergence (Fig. 4). Partially submerged *F. excelsior* continued to grow. In *Q. robur* a significant decrease in root weight was counterbalanced by an increase in weight of stem and leaves. After

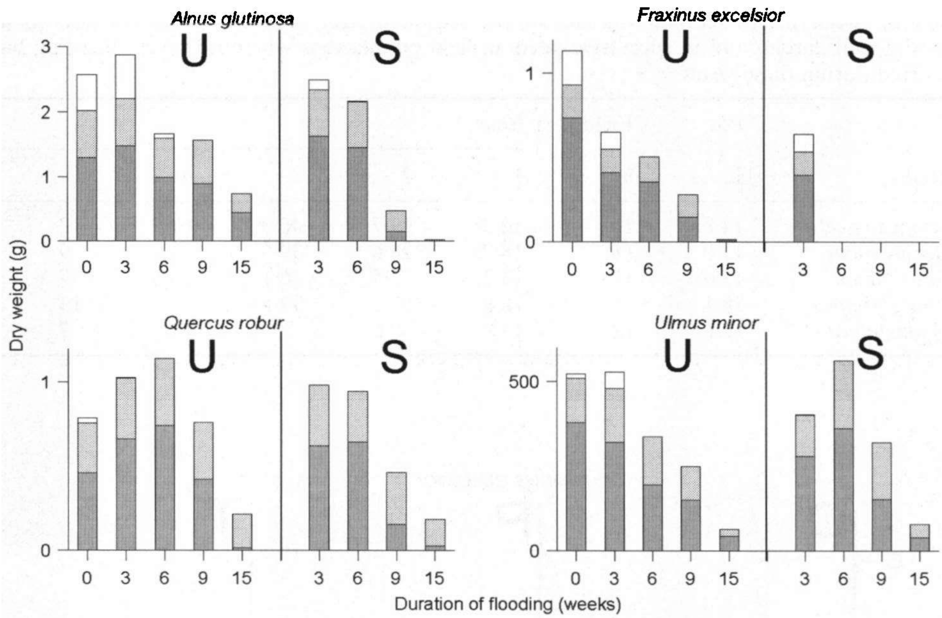

Fig. 2. Cumulative mean dry weight of roots, stems and leaves of tree seedlings 3 days after total submergence in relation to duration of total submergence and light availability during total submergence. U = unshaded, S = strongly shaded (1% full daylight). □, Leaves; ▩, stems; ■, roots.

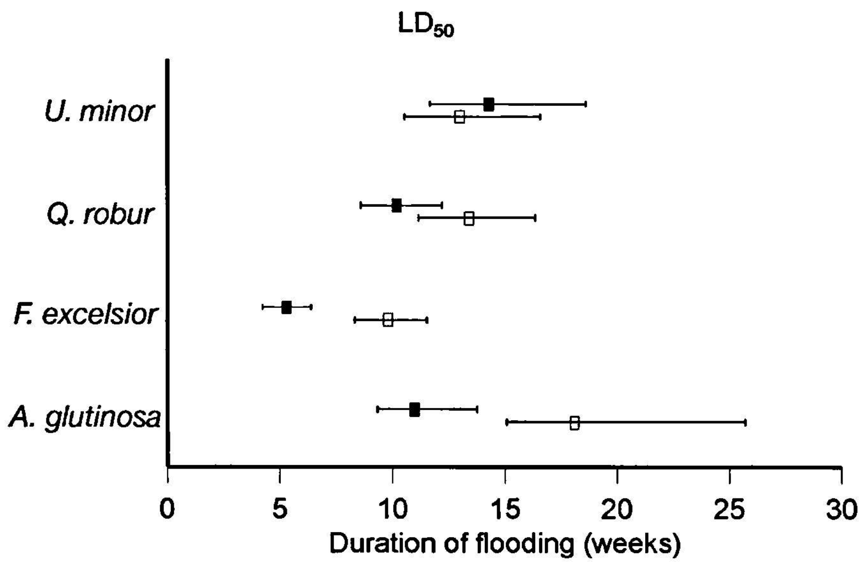

Fig. 3. Duration of total submergence which resulted in 50% of the tree seedlings dying (LD_{50}) in unshaded or shaded (= 1% full daylight) conditions. Bars indicate the 95% confidence interval. ■, shaded; □, unshaded.

Table 3. Mean height (cm) at the end of the season of tree seedlings grown in pots in an experimental garden and in successive years in field populations where no severe flooding had occurred during these years

	Pot	Field	Year				
Species	1	*n*	1	2	3	4	*n*
Fraxinus excelsior	14·8	10	12·3	29·7	46·3	61·9	12
Quercus robur	17·0	8	18·2	28·6	39·5		9
Ulmus minor	13·9	11	13·2	32·5	46·1	65·8	7
Alnus glutinosa	38·1	11	16·8	57·7	94·5		13
Populus nigra	16·6	12	13·9	50·6			7

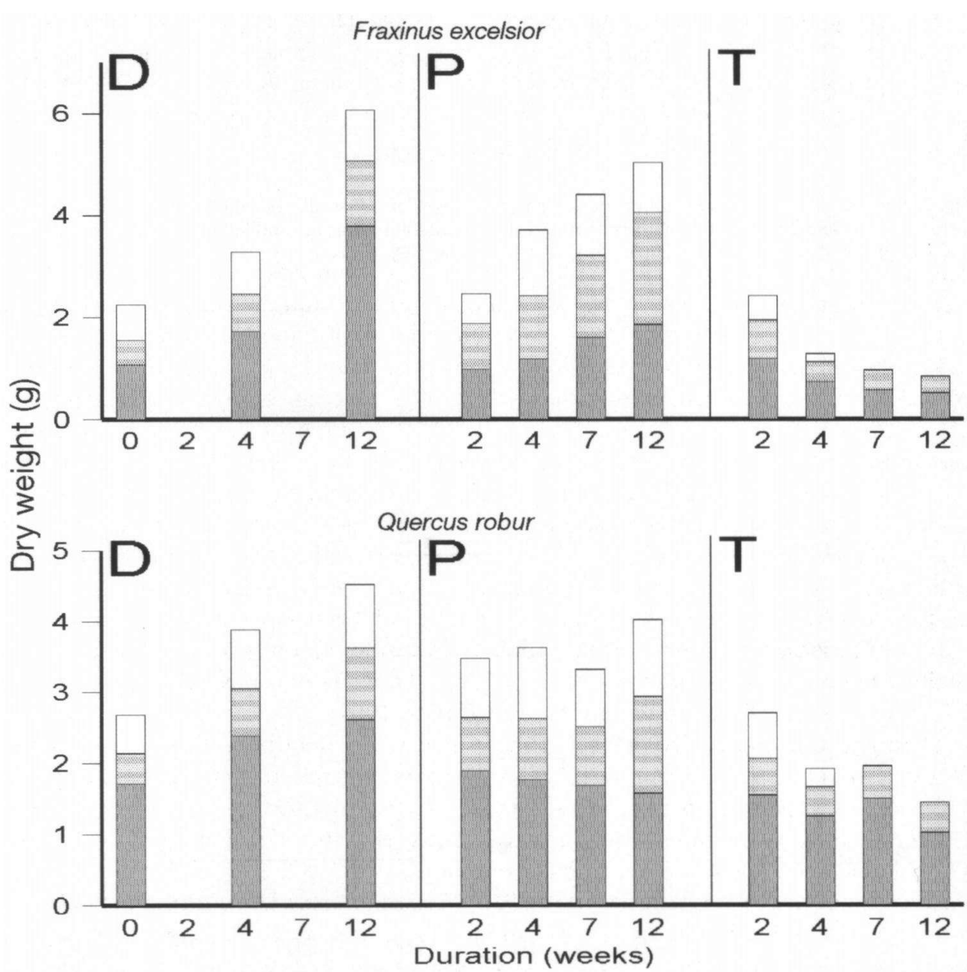

Fig. 4. Cumulative mean dry weight of roots, stems and leaves of tree seedlings 3 days after treatment in relation to the duration of this treatment. D = freely draining conditions, P = partial submergence, T = total submergence. □, Leaves; ▧, stems; ■, roots.

12 weeks of partial submergence both species showed significantly (*t*-test, $P<0.05$) less root biomass but more stem biomass than seedlings grown under drained conditions. Root mortality and stem dieback during total submergence caused a significant decrease in weight of roots and stems of *F. excelsior* seedlings. After 12 weeks 45% of the seedlings had died. *Q. robur* seedlings showed less root mortality and stem dieback during total submergence, which did not result in a significant decrease in weight of roots and stems. Only one *Q. robur* plant died after 12 weeks of total submergence.

One year later, a significant ($P<0.001$) decrease in weight of roots, stems and leaves at increasing duration of total submergence was still present in both species. Seedlings which were totally submerged for 12 weeks the previous year had reached about a quarter of the total plant weight of unflooded seedlings in both species. However, 1 year later no significant differences in stem, leaf and root weight of both species were present between partially submerged seedlings and seedlings on freely draining soil a year later.

The stem dieback during total submergence resulted in a significant decrease in height, which was still present 1 year later (Fig. 5). Partially submerged seedlings showed a significantly larger increase in stem length than unflooded plants. However, these differences were small compared to average stem length, which was about 18 cm at the start of the experiment in both species.

DISCUSSION

The tolerance of partial submergence we found in our experiments is in agreement with tree zonation and correlates partly with morphogenetic adaptations. The seedlings of *A. campestre*, a species which only grows on incidentally flooded sites, were sensitive to partial submergence and showed only a few hypertrophied lenticels and adventitious roots. No increased stem diameter growth as an indication of stem hypertrophy was observed in *A. campestre*. Frye & Grosse (1992) also found this lack of response in *A. campestre* and in other tree species which occur only on incidentally flooded sites and are sensitive to partial submergence. Seedlings of the main species from hardwood floodplain forests we examined showed a high tolerance to partial submergence. The 1-year-old seedlings of *Q. robur* and *F. excelsior* survived at least 3 months of partial submergence (including part of the summer) without much damage, as was also found by Frye & Grosse (1992). The same was found for *U. minor* partially submerged for a period of at least 4 months (Siebel, unpublished results). However, this only applies to shallow flooding, as mature trees of *F. excelsior* die when partially submerged in 1·5 m of standing water for 2 months in summer (Späth 1988).

The main tree species from the European hardwood floodplain forest we examined (*F. excelsior, Q. robur* and *U. minor*) showed a strong morphological response to partial submergence. This has also been found in species from hardwood floodplain forests in temperate regions on other continents (Hook & Brown 1973; Pereira & Kozlowski 1977; Sena Gomes & Kozlowski 1980; Newsome *et al.* 1982; Tang & Kozlowski 1982; Tang & Kozlowski 1984; Angeles *et al.* 1986; Yamamoto *et al.* 1995). Of the two species of the softwood floodplain forest we examined, *A. glutinosa* showed a particularly high tolerance of partial submergence. It has been found that seedlings of *A. glutinosa* survive being partially submerged for almost the entire growing season (Gill 1975). In our experiment, seedlings of *P. nigra* also showed a high tolerance of partial submergence, but little morphological response. However, physiological responses such as anaerobic

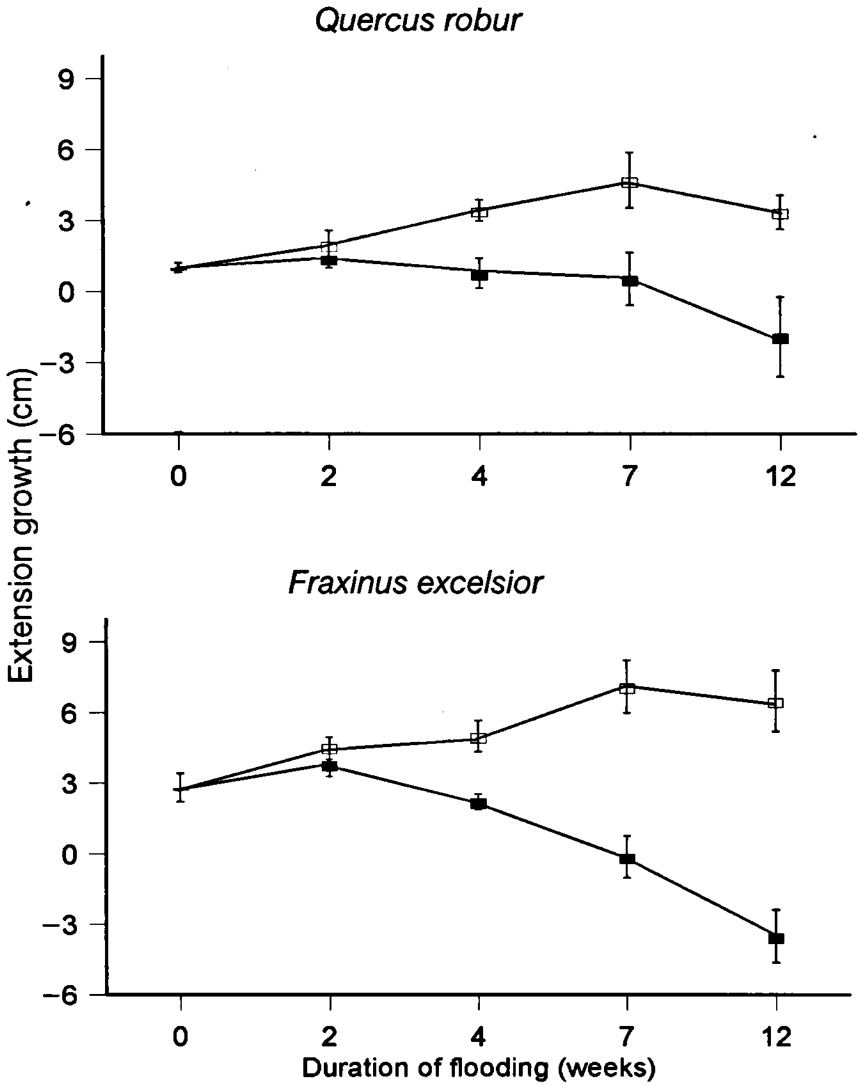

Fig. 5. Change in stem height (mean ± SD) 1 year after flooding compared to stem height at the start of the flooding period in relation to its duration. Solid symbols indicate total submergence, open symbols indicate partial submergence.

metabolism and dormancy are also important to survive flooding (Joly 1991), so perhaps the survival of *P. nigra* depends more on such physiological or metabolic adaptations.

Our results also show that tolerance of total submergence in clear water correlates with tree zonation. Seedlings of tree species from hardwood floodplain forest were less tolerant than seedlings of species from softwood floodplain forest. When seedlings were totally submerged, the depth of water had no effect on their survival. Light availability only had an effect on flooding tolerance when it was strongly reduced, and at a level of 15% of full daylight no effect was found. However, light levels are strongly reduced in turbid river water (Banga *et al.* 1995). Moreover, seedlings of *F. excelsior* emerge mainly at sites with less than 10% of full daylight. From this we infer that a further decrease in light caused by flooding with turbid water in the growing season leads easily to increased mortality of *F. excelsior* seedlings during flooding. The more severe effect of total submergence at low light intensities is attributable to a strong reduction of photosynthesis. Underwater photosynthesis can be important for the survival of plants (Laan & Blom 1990; Schlüter *et al.* 1993). Although leaves are already shed after only a few weeks of total submergence, young stems, especially those of *A. glutinosa* and *F. excelsior*, also have green photosynthetically active tissue.

Seedlings of species from hardwood floodplain forests showed only little extension growth compared with species from softwood floodplain forests. They are therefore less able to avoid total submergence. When floods are 0·5 m deep, the slowly growing *F. excelsior*, *Q. robur* and *U. minor* seedlings cannot avoid being totally submerged during their first 3 years.

A period of 4 weeks of total submergence in spring was enough to damage tree seedlings and reduce extension growth. The shorter plants are less likely to avoid total submergence during the next flood and therefore have less chance of surviving. In contrast, partial submergence for up to 3 months had little or no effect on the extension growth of seedlings of main tree species from floodplain forests. Indeed, a small increase was found in *F. excelsior* and *Q. robur*, although this is of little importance in situations where floods are deep. A small negative effect of prolonged partial submergence on the extension growth of these two species had previously been reported by Frye & Grosse (1992).

The flood tolerance of species we examined depends clearly on flood depth. Their seedlings have a much greater ability to endure flooding when only partly submerged than when totally submerged. The decrease in light availability with increasing water depth in turbid water may further reduce their tolerance of total submergence. Rhine water is often turbid, and the current hydrological management of the Rhine and its tributaries results in higher flood levels often more than a metre in the Dutch river forelands. This greatly reduces the possibilities for trees to establish along this river.

Given the present depths of flooding, the zonation of tree species will largely depend on species tolerance of total submergence. Although seedlings of the main tree species from hardwood floodplain forests in Western Europe exhibit large adaptations to partial submergence and can survive such submergence for long periods in the growing season, they are sensitive to total submergence, especially at low light availabilities. They are unable to avoid total submergence by rapid extension growth. This strongly limits the feasibility of restoring of hardwood floodplain forests on low-lying sites along the Rhine.

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