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Effects of irregular flooding on the establishment of tree species

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SUMMARY

The ability of tree seedlings to build up and maintain a high tolerance of total submergence in their first few years before severe flooding was examined, to elucidate tree zonation along the Rhine and to ascertain the impact of irregular high floods. Tolerance of total submergence was examined experimentally in relation to seedling age, time of the year and a previous period of total submergence. Seedlings of species characteristic of low-lying sites, such as *Alnus glutinosa* and *Populus nigra*, increased their tolerance of total submergence with age more and had a higher tolerance in their second or third year than species from higher sites, e.g. *Fraxinus excelsior*, *Quercus robur* and *Ulmus minor.* Degree of tolerance of total submergence was much less in summer than in spring. Species from high-lying sites had low tolerance in summer. Tolerance of total submergence was only slightly dependent on a previous period of total submergence earlier in the year. The results indicate that irregular high floods in late spring and summer such as those that occur in the Rhine system strongly reduce the probability of tree seedlings establishing, especially those of species from hardwood floodplain forest.

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

INTRODUCTION

Next to shading and root competition, flooding is an important factor limiting the growth and survival of tree seedlings in floodplain forests (Jones *et al.* 1989, Streng *et al.* 1989). Variation in flooding brings about spatial and temporal variation in species composition of the seedling layer (Streng *et al.* 1989). Flood tolerance increases with age in tree species (Gill 1970; Kozlowski 1984). When severity of flooding varies between years, as in the Rhine system, the lower limit in the zonation of tree species will depend especially on establishment in periods without severe flooding in which tree seedlings become sufficiently tolerant to survive a subsequent more severe flood. Growing taller than the mean flood level is important for this, because totally submerged tree seedlings survive flooding for much shorter durations than partially submerged ones (Gill 1970; Kozlowski 1984; Siebel *et al.* 1998). However, in the Rhine system accelerated water discharge upstream and narrowing of the floodplain by endiking have brought about high water levels during flooding downstream (Blom *et al.* 1990). Flooding occurs mostly in late winter and spring, but nowadays periods with excessive precipitation at other periods of the year cause flooding sooner and time and duration of floods vary greatly between years. As a consequence, seedlings are unlikely to avoid being totally submerged in their first years on low-lying sites. Therefore, building up and maintaining a high tolerance of total submergence in their first years is important if tree seedlings are to be able to establish on such sites.

Heavy-seeded species produce larger seedlings which are relatively resistant to the effects of environmental stress such as flooding (Streng *et al.* 1989). Early-germinating species have a disadvantage when flooding mostly occurs in early spring because they suffer from flooding just after germination, whereas late-germinating species avoid such floods in their first season (Streng *et al.* 1989). However, little is known about the changes in the sensitivity of tree seedlings to total submergence during their first years. Their tolerance to total submergence is likely to depend on their age, as found in herbs (Voesenek *et al.* 1993). The sensitivity of trees to flooding also varies with time of flooding within the year, being less in winter (Minore 1968; Gill 1970). The zonation of a tree species has been found to differ greatly between rivers differing in the time at which the floods occur (Metzler & Damman 1985). Tolerance of total submergence may also depend on the occurrence of earlier non-lethal flood periods. Although seedlings of trees from floodplain forests usually survive a few weeks of total submergence, they are often damaged and recover only slowly (Hosner 1958; 1960; Siebel *et al.* 1998). This may also increase their sensitivity to total submergence during a subsequent flood period shortly after.

To explain tree zonation along the Rhine and to determine the effect of irregular flooding, we examined the tolerance to total submergence of seedlings of several tree species in relation to their age, time of flooding in the year and the occurrence of an earlier flood period. Species included in the study were *Fraxinus excelsior* L., *Quercus robur* L. and *Ulmus minor* Miller, the main tree species of western European hardwood floodplain forest at high-lying sites, and *Alnus glutinosa* (L.) Gaertner and *Populus nigra* L. from softwood floodplain forest at low-lying sites. Our hypothesis was that tree species characteristic of low-lying sites build up a high tolerance to total submergence more quickly and maintain this better than species from high elevations.

MATERIALS AND METHODS

Plant material

Seedlings of *A. glutinosa*, *F. excelsior*, *P. nigra*, *Q. robur* and *U. minor* were grown from seeds, collected from individual populations in the river area in The Netherlands. Seed weight and timing of germination differ significantly between these species. Mean seed weight varies between 3·5 g for acorns of *Q. robur*, 29 mg for *F. excelsior*, 3 mg for *U. minor*, 1 mg for *A. glutinosa* and less than 0·1 mg for *P. nigra*. Seeds of *P. nigra* and *U. minor*, normally germinating in late spring, were sown at the end of spring immediately after collection. Seeds of the other species, which normally germinate in early spring, were collected at the end of the growing season, stored at 4°C in moist sand and sown at the beginning of spring. Seeds were sown on a sand/compost mixture and shortly 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 grown outdoors until the start of the flooding experiments, which were performed in outdoor basins of 8 × 2·5 m in the experimental garden of the University of Nijmegen, The Netherlands.

Seedling age

The influence of seedling age on tolerance to total submergence in spring was examined in 1994 with first-, second- and third-year seedlings of *A. glutinosa, F. excelsior* and *Q. robur* and with second- and third-year seedlings of *P. nigra.* The plants were totally submerged for 0, 3, 6, 9, 12 and 15 weeks from 13 May 1994 onwards with a water column above the soil of 70 cm. After each flooding period a group of seven plants per species was sampled.

Repeated flooding

The effect of an early flooding period on damage and survival of seedlings during a later flooding period in their first season and the effect of time of this later flooding period were examined in a completely randomized full factorial design. First-year seedlings of *A. glutinosa, F. excelsior* and *Q. robur* were used. The seedlings were totally submerged during flooding with a water column above soil of 50 cm. Half the seedlings of each species were subjected to an early flooding period of 2 weeks starting on 10 June 1993. The second flooding period started 1 (I), 3 (II) or 5 (III) weeks after the first, respectively, on 1, 15 or 29 July. This resulted in a total of six flooding treatments. At each flooding treatment seedlings were sampled at 0, 2, 4 and 8 weeks after the start of the second flooding period (five replicates each). An additional group of five seedlings was sampled directly after the early flooding period to ascertain if root damage had occurred.

Time of flooding

The effect of time of the flooding period in the growing season on damage and survival during flooding was examined in 1994 with 1-year-old seedlings of *A. glutinosa, F. excelsior* and *U. minor* and 2-year-old seedlings of *P. nigra.* The seedlings were totally submerged in clear standing water with a water column above the soil of 65 cm beginning in spring or in summer. The spring flooding started on 6 May (*A. glutinosa, F. excelsior*) or 13 May (*P. nigra, U. minor*). Seedlings were sampled after 0, 3, 6, 9 and 15 weeks. Those of *P. nigra* were also sampled after 12 weeks. The summer flooding period started on 20 June and seedlings were sampled after 0, 3, 6 and 9 weeks (six replicates each).

Plant measurements

Sampling took place 3 days after the end of a flooding period to include additional damage such as the loss of leaves which occurred within a few days after flooding. The measurements included root mortality, stem dieback and dry weight of leaves, stems and roots. Root mortality was determined by estimating the amount of dead primary and secondary roots as a fraction of total root length. Death of root parts was assessed on the basis of discolouration and disintegration of the outer root layers. When stem dieback occurred, stem length was measured up to where the stem was observed to be brown or black. Stem dieback was calculated relative to stem length at the start of the flooding period. Dry weights of stem, leaves and roots were determined by oven drying at 70°C for 2 days after dead parts were removed. A seedling was considered not to survive if the root system had completely died or if stem dieback extended to below the lowest lateral bud.

Statistical analysis

Treatment differences in dry weight of stem, roots or total plant were tested by analysis of variance after logarithmic transformation. Flooding durations which caused more than 25% mortality were omitted in the analysis. The effect of treatment differences on the occurrence of severe root mortality (>50% of root length damaged), stem dieback (>10% of stem length damaged) and mortality in relation to flooding duration was analysed using multiple logit regression in which duration of flooding was logarithmically transformed.

RESULTS

Seedling age

The species and age classes largely differed in biomass but all showed substantial damage to leaves, stems and roots within the experimental period (Fig. 1). The relative decrease in biomass caused by flood damage was slower in old seedlings than in young ones. Logistic regression on plant mortality and the occurrence of severe root mortality in relation to duration of submergence showed a significant effect of age in all species ($P<0{\cdot}05$). Older seedlings survived total submergence longer than young seedlings (Fig. 2). This increase in tolerance depended on species. *A. glutinosa* seedlings were small when flooded in spring in their first season and had a low tolerance of flooding. They grew fast, however, and older seedlings were more tolerant than *F. excelsior.* In their second year *P. nigra* seedlings already had the highest tolerance of total submergence.

Repeated flooding

The early flooding period of 2 weeks caused seedlings of *A. glutinosa* and *Q. robur* to shed leaves. In all species some seedlings showed root damage. The delay in growth due to the early flooding period and differences in time between the flooding periods caused large differences in biomass at the start of the second flooding period (Fig. 3). However, analysis of variance revealed no significant effect of the early flooding period on loss of weight of roots, stem or total plant during the second flooding period.

The effects of the previous flooding period and the time of flooding on severe root damage, stem dieback and seedling mortality were most pronounced in *F. excelsior* (Table 1). In this species severe root damage, stem dieback and seedling mortality depended significantly on the time of the flooding period in summer. The early flooding period led to a significant decrease of severe root damage ($P<0{\cdot}001$) and stem dieback ($P<0{\cdot}05$) in *F. excelsior* during a second flooding period. In *A. glutinosa* severe root damage and stem dieback during the second flooding period also differed significantly ($P<0{\cdot}05$) between the flooding periods. However, neither severe root damage nor stem dieback depended significantly on the earlier flooding period. Few *Q. robur* seedlings showed stem dieback. In this species severe root damage did not significantly differ between the three flooding periods but the early flooding period led to a significant ($P<0{\cdot}001$) increase of severe root damage during the second flooding period.

Time of flooding

In all species loss of root biomass and total seedling biomass occurred significantly ($P<0{\cdot}05$) faster during summer flooding than during spring flooding, although the

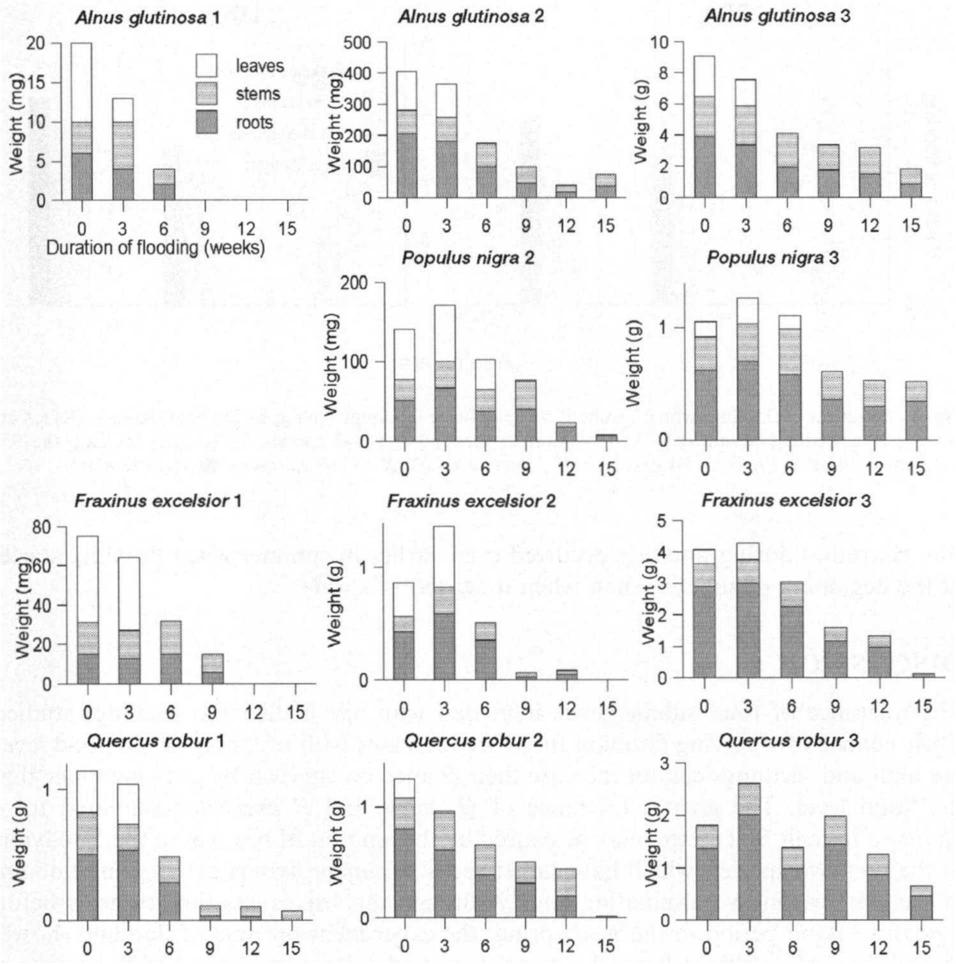

Fig. 1. Cumulative mean dry weight of roots, stems and leaves of tree seedlings ($n = 6$) in relation to duration of flooding and seedling age; 1 = first-year seedlings, 2 = second-year seedlings, 3 = third-year seedlings. □, Leaves; ▨, stems; ■, roots

seedlings had more biomass at the start of the summer flood period than at the start of the spring flood period (Fig. 4). The same was found for stem biomass in *F. excelsior.*

Severe root mortality and death of seedlings occurred faster during summer flooding than during spring flooding (Fig. 5). Time and duration of flooding and species all contributed significantly to the logit regression models on seedling mortality, the occurrence of severe root mortality and the occurrence of stem dieback. The effect of time of flooding on all three regression models depended significantly on species.

Seedling mortality during total submergence, which started in spring, only occurred when this submergence continued into summer. In *P. nigra* and *F. excelsior* death of seedlings already submerged from spring occurred about the same moment in summer as seedlings submerged from the beginning of summer. However, this was not seen in *U. minor* seedlings. *A. glutinosa* showed little seedling mortality. In this species, severe

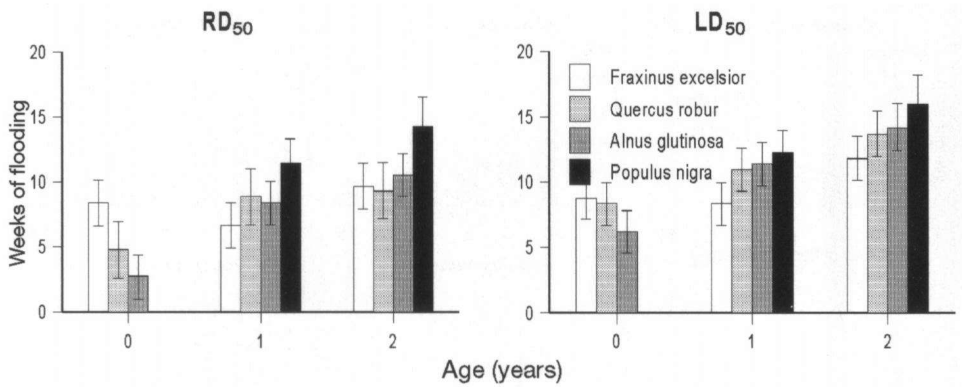

Fig. 2. Duration of flooding which resulted in 50% of tree seedlings having severe root damage (RD$_{50}$) and 50% of tree seedlings dying (LD$_{50}$) in relation to seedling age and species. Error bars indicate the 95% confidence interval. □, *Fraxinus excelsior*; ▨, *Quercus robur*; ▪, *Alnus glutinosa*; ■ *Populus nigra*.

root mortality during flooding occurred even earlier in summer when flooding started at the beginning of summer than when it started in spring.

DISCUSSION

The tolerance of total submergence increased with age in the tree seedlings studied. Their chance of surviving flooding therefore increases with age, even when flood levels are high and seedlings cannot increase their chance on survival by growing taller than the flood level. The greater tolerance of *Q. robur* and *F. excelsior* compared to *A. glutinosa* in their first spring may be caused by the amount of reserves in the cotedylons of the first two species, which have larger seeds. *U. minor* avoids early spring flooding in the first season by germinating later. Although this leaves less time to grow before a possible flood period in the next spring, the experiment on time of flooding showed that 1-year-old seedlings have the same degree of tolerance of total submergence in spring as *F. excelsior.* The two species from softwood floodplain forest, *A. glutinosa* and the late-germinating *P. nigra* acquire a higher tolerance of total submergence than the species from hardwood floodplain forest within 1 year. Small seedlings of *P. nigra* are sensitive to low soil moisture in summer (van Splunder *et al.* 1995), but under favourable growth conditions *P. nigra* seedlings acquire about the same degree of flood tolerance as *Q. robur* 6 weeks after germination (P. Veruren, personal communication). The stronger increase in flood tolerance with age enables the species from softwood floodplain forest to benefit more from periods without severe floods to establish on low-lying sites.

The duration of flooding that tree seedlings can endure depends greatly on the time of the year. They do not maintain a high tolerance throughout the year. Seedlings of all species examined survive total submergence in clear water for most of spring, but they show large differences in survival when flooding starts at the beginning of summer or starts at the beginning of spring and continues into summer. Therefore, total submergence of seedlings in late spring and summer has an especially important effect on tree zonation in floodplain forest along the Rhine. The degree to which seedling tolerance of total submergence decreased during the course of the growing season was

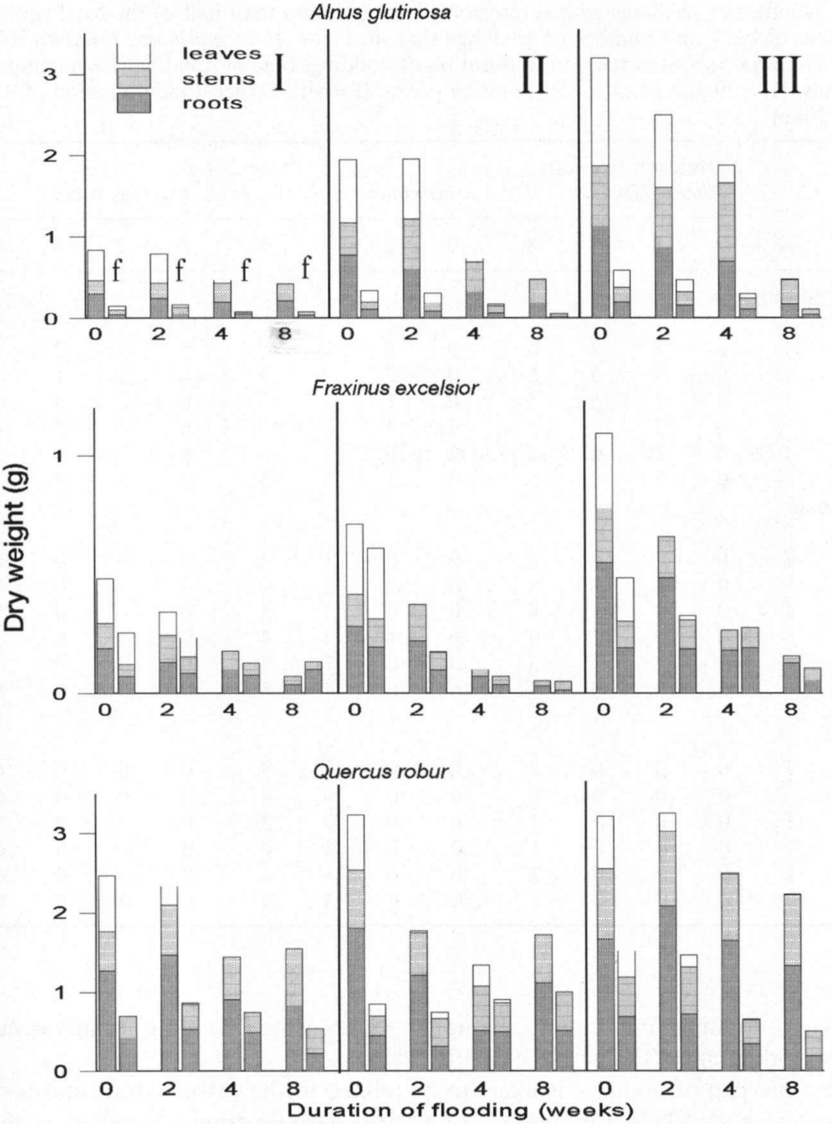

Fig. 3. Cumulative mean dry weight of roots, stems and leaves of tree seedlings ($n = 5$) in relation to time and duration of flooding and occurrence of an earlier flooding period. (I = total submergence starting 1 July, II = 15 July and III = 29 July; second bars (f) = with an earlier flooding period of 2 weeks from 10 June). □, Leaves; ▦, stems; ■, roots.

not generally larger in the species from hardwood floodplain forest than in the species from softwood forest. The increased sensitivity to summer flooding was especially present in *F. excelsior*, which had already died after a few weeks. In contrast, 1-year-old seedlings suffered very little damage in 8 weeks of total submergence in March and April (Siebel, unpublished results). The low tolerance of summer flooding in *F. excelsior* compared to *Q. robur* and *U. minor* found in this study is in agreement with its higher

Table 1. Number of seedlings with severe root damage (more than half of the total root length dead), stem dieback and number of seedlings that died, for *Alnus glutinosa*, *Fraxinus excelsior* and *Quercus robur* ($n=5$) in relation to duration of flooding, time of flooding (I = starting 1 July, II = 15 July, III = 29 July) and earlier flooding period (f = with earlier flooding period of 2 weeks from 10 June)

		Duration (weeks) *Alnus glutinosa*				*Fraxinus excelsior*				*Quercus robur*			
		0	2	4	8	0	2	4	8	0	2	4	8
Severe root damage													
Period													
I	f	0	1	2	5	0	0	0	0	0	1	2	5
		0	1	3	5	0	2	2	5	0	0	1	4
II	f	0	1	5	5	0	1	4	5	0	2	3	5
		0	3	5	5	0	4	5	5	0	1	2	4
III	f	0	1	3	5	0	0	1	4	0	3	4	5
		0	3	5	5	0	1	5	5	0	0	2	3
Stem dieback													
Period													
I	f	0	0	4	4	0	0	1	4	0	0	0	0
		0	0	2	4	0	0	2	4	0	0	0	0
II	f	0	0	1	4	0	0	3	5	0	0	0	0
		0	0	2	4	0	1	5	4	0	0	0	1
III	f	0	0	1	3	0	0	1	4	0	0	0	1
		0	0	0	3	0	0	4	5	0	0	0	0
Mortality													
Period													
I	f	0	0	0	2	0	0	0	3	0	0	0	0
		0	0	0	0	0	0	0	4	0	0	0	0
II	f	0	0	0	3	0	0	3	3	0	0	0	0
		0	0	0	1	0	0	5	4	0	0	0	0
III	f	0	0	0	2	0	0	1	4	0	0	0	2
		0	0	0	1	0	0	3	4	0	0	0	0

sensitivity to flooding found along the upper Rhine, where flooding usually occurs in late spring or summer (Dister 1983; Späth 1988).

Because survival of flooding is likely to be related to the carbohydrate status of the plant (Setter *et al.* 1987), the amount of reserve carbohydrates stored in roots and stems of tree seedlings, which usually decreases from the beginning of spring to summer (Kozlowski 1992), and also higher temperatures in summer which accelerate respiration may explain the greater sensitivity of tree seedlings to total submergence in summer.

A short period of total submergence in spring was sufficient to cause a large decrease in plant growth, but did not greatly reduce tolerance of total submergence later in the growing season. *Q. robur* was the only species in which an earlier flooding period led to a slight increase in root mortality during flooding later in the growing season. The decrease in root mortality during total submergence attributable to the early flooding period in *F. excelsior* even suggests that this species has a flood-induced tolerance mechanism, but the nature of this mechanism is unclear. We conclude that short flooding periods in spring have little influence on flooding tolerance in later months.

The experiments show that the sensitivity of tree seedlings to total submergence

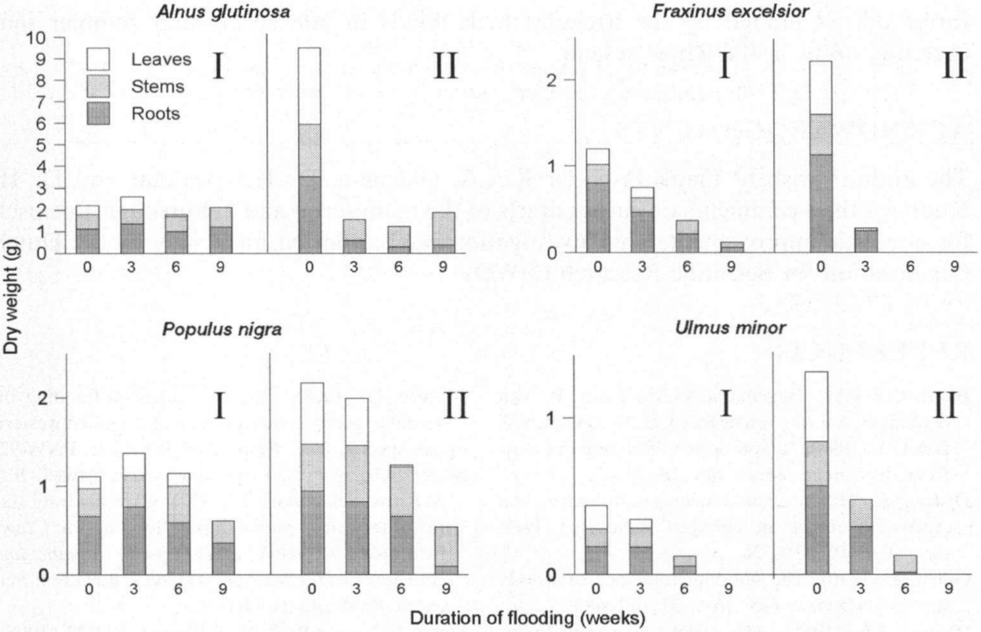

Fig. 4. Cumulative mean dry weight of roots, stems and leaves of tree seedlings ($n = 6$) in relation to duration of flooding starting in spring at the beginning of May (I) or in summer at the end of June (II). □, Leaves; ▨, stems; ■, roots

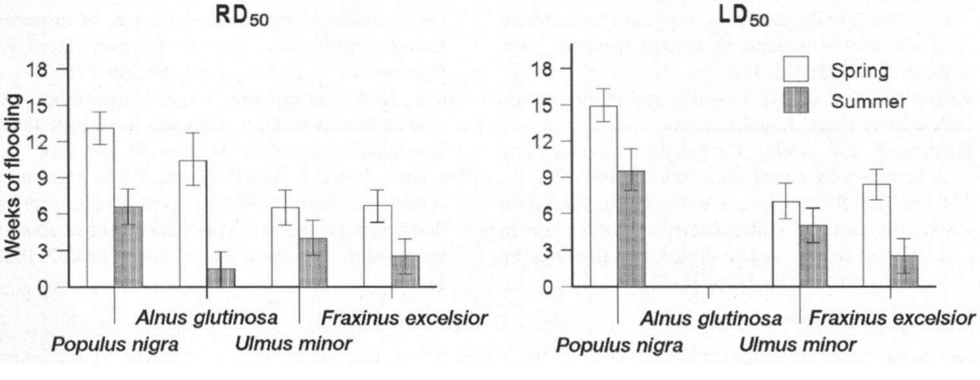

Fig. 5. Durations of flooding which resulted in 50% of tree seedlings having severe root damage (RD_{50}) and 50% of tree seedlings dying (LD_{50}) in relation to time of flooding. Bars indicate the 95% confidence interval. □, Spring; ▨, Summer

decreases with age but also depends strongly on when the flooding occurs in the year. Therefore, the zonation of tree species not only depends on duration of flooding but also on the time and frequency of flooding. The hardwood floodplain tree species are more adapted to regular but moderate levels of stress induced by total submergence. The softwood tree species are more adapted to irregular and severe floods. Therefore, it is especially the establishment of seedlings of tree species from hardwood floodplain forest that is limited by the irregular high floods in late spring and summer that currently occur in the Rhine system.

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