Germination of acorns and development of oak seedlings (*Quercus robur* L.) following flooding

C. Kühne, N. Bartsch

Department I: Silviculture of Temperate Zones and Forest Ecology, Institute of Silviculture, Georg-August-University of Göttingen, Göttingen, Germany

ABSTRACT: Seeds and seedlings of *Quercus robur*, a characteristic tree species of the hardwood floodplain forests along the Rhine River, demonstrated high resistance to complete inundation under controlled conditions. In both experimental trials no significant difference between the different flooding periods (8, 10, and 12 weeks) could be established either for shoot emergence or for the measured morphological growth parameters. Flooding delayed the germination of submerged acorns till the end of inundation. However, seeds of the flooding treatments had significantly higher germination rates than the non-flooded acorns of the control. Likewise, dry weights of seedlings from the flooded seeds were significantly higher than those of seedlings from seeds not flooded. Aboveground growth in the 24-week growth period following flooding was reduced in favour of root development in either trial of the experiment. Restricted leaf development and reduced shoot elongation stalled the growth of young oaks in the seedling trial. The results confirm knowledge from earlier experiments about the flood tolerance of *Quercus robur* seed and seedlings. They also serve to explain why oak seedlings are widespread on the Rhine floodplain after mast years, but gradually disappear in successive years.

Keywords: inundation; experiment; mortality; morphology; recovery; pedunculate oak

Reconstruction of the Rhine River along the border between France and Germany in the last century has aggravated the flooding regime in the upper reaches of the stream (Pfarr 2002) and significantly reduced the predictability of floods (MU-RP 1993). At many recording points the frequency of peak flooding events (average return time) has been reduced by a half. Consequently, refuges of mature floodplain forests as well as intensively managed forests along the river have been affected by more frequent as well as more severe floods (Biegelmaier 2002; Späth 2002).

Quercus robur occurs naturally in hardwood floodplain forests along Central European rivers (Oberdorfer 1992; Schnitzler 1994). The broadleaf tree species is highly tolerant to flooding and exhibits optimal growth on floodplains (Röhrig, Bartsch 1992; Ellenberg 1996). Investigations by Späth (1988, 2002) after severe floods of the Rhine in 1987 and 1999 suggested that *Quercus robur* was one of the floodplain species best able to withstand the impact of flooding. On both occasions mature *Quercus robur* stands were flooded for more than 100 days on extreme sites. No withering or dying individuals were observed in the autumn thereafter (1987) and in the following year (2000), respectively. Depending upon the speed of the river, pole-sized regrowth stands withstood the floods for 41 to 55 days without damage.

Young *Quercus robur* plants were also found to be flood tolerant. In trials with waterlogged soil in the rooting zone, *Quercus robur* seedlings exhibited the least change in growth in comparison with other oak species (Colin-Belgrand et al. 1991; Dreyer 1994; Schmull, Thomas 2000). Levy et al. (1986) and Dreyer et al. (1991) demonstrated that the extent of the unsaturated soil layer above the water table influenced the sensitivity of waterlogged *Quercus robur* seedlings considerably. Biomass and plant height, as well as CO_2 assimilation rates and stomatal conductance decreased significantly with a rising water table. In a similar study with waterlogging in the entire rooting zone a considerable leaf loss in *Quercus robur* was only observed after 11 weeks and live plants were found even after 14 weeks (Roloff, Bonn 2002). Under the aforementioned conditions

Quercus robur revealed the least damage out of the six tested broadleaf tree species, demonstrating the best adaptation to flooding stress.

In spring 1999, the meeting of flood waters from the Rhine and many of its tributaries along the upper part of the stream resulted in the worst flood of the last century. The extreme rise in the water level was caused by unusually mild and wet weather in the northern Alps. In the course of this event Kühne et al. (2005) observed high mortality and growth inhibition of *Quercus robur* grown from direct seeding and nursery plants at study sites situated between Speyer and Karlsruhe (Germany). In the experiment presented in this paper flood conditions of 1999 were simulated when acorns and seedlings from *Quercus robur* were entirely submerged under controlled conditions in growth chambers and germination of seeds and regeneration capacity of seedlings following flooding were investigated. Based upon field observations the following hypotheses were tested in this work:

– Seeds begin to germinate only after flooding.
– Germination rate decreases as the duration of inundation increases.
– Inundation during the vegetation period results in leaf abscission and necrosis of the shoot.
– Mortality of seedlings increases as the duration of inundation increases.

MATERIAL AND METHODS

Seeds

Seeds were collected in a single-layered mature *Quercus robur* stand in southern Rhineland-Palatinate (Bellheim Forest District, Germany) in October 1999. The stand is subjected to annual floods from the Rhine River. Seeds were stored at 4°C until sowing. Prior to the commencement of the experiment, acorns with reduced germination capacity were removed by the floating test (Heiseke 1984) and the vigorous seeds were surface sterilised in an ethanol bath (60% solution). At the end of November 1999 the seeds were randomly divided between the experimental treatments.

Table 1. Substrate properties

pH (H_2O)	7.8
pH (KCl)	7.3
C/N	23.7
$Carbon_{organic}$ (%)	6.8
Nitrogen (%)	0.3
Phosphorus (%)	0.6
Cation exchange $capacity_{total}$ ($mmol_c$/kg)	285.9
Exchangeable Ca ($mmol_c$/kg)	209.6
Exchangeable K ($mmol_c$/kg)	3.6
Exchangeable Mg ($mmol_c$/kg)	17.2
Exchangeable Na ($mmol_c$/kg)	1.3

Sowing

Acorns from all treatments were placed individually into GL-II plant pots (diameter 5 cm, pot volume 270 cm^3) and pushed gently into the soil. The GL-II plant pots were filled with a soil substrate typical of the Upper Rhine floodplain. The sandy loam silt was sterilised with steam. Soil properties are presented in Table 1.

Growth chamber conditions

All experimental treatments were carried out in growth chambers (Weiss system) at the Institute of Silviculture, Göttingen University. HQL 400 light sources (42,000 lm, 3,700 K) produced a constant photosynthetic photon flux density (PPFD) of 4.3 mole/m^2/day during the daily 14 h light period. This light intensity corresponds to a relative light intensity of about 15% of full sunlight. According to Lüpke (1998) this radiation level, found underneath the canopy of lightly thinned floodplain forests (Kühne et al. 2005), is the minimum required for the satisfactory growth of *Quercus robur*. Plant pots were regularly watered to replace the loss from evapotranspiration determined by weighing during the growth period of all treatments in both experimental trials.

Seed trial

400 GL-II plant pots each containing one sound acorn were randomly divided between four treatments:

– **C**: control without inundation, 24-week growth period.
– **S8**: 8-week inundation followed by a 24-week growth period.
– **S10**: 10-week inundation followed by a 24-week growth period.
– **S12**: 12-week inundation followed by a 24-week growth period.

Plant pots of the flooding treatments S8, S10 and S12 were completely submerged in rain water. To simulate averaged conditions of the spring flood in April 1999, air and water temperatures were set to 11°C. During the experiment pH-value and oxygen content of the water were continuously controlled. Due to the basic soil substrate used in the plant pots pH-values remained constantly between 7 and 8 while the oxygen content was kept within the river's natural range of 7 to 9 mg/l (Tittizer, Krebs 1996) by using an aeration pump. Like the seedlings of the non-flooded control C, plants of the flooding treatments were grown at a constant temperature of 19°C for 24 weeks after the end of the respective inundation period.

Seedling trial

Seedlings were grown under the conditions described above for the control C of the seed trial. 24 weeks after sowing vigorous seedlings were randomly divided between the following treatments:

- **P8**: 8-week inundation followed by a 24-week growth period; 25 seedlings.
- **P10**: 10-week inundation followed by a 24-week growth period; 25 seedlings.
- **P12**: 12-week inundation followed by a 24-week growth period; 24 seedlings.

During the inundation period seedlings of all treatments were entirely submerged in rain water. Oxygen content and pH-value of the water were consistent with the conditions in the seed trial. Since the seedling trial was supposed to simulate an early summer flood, air as well as water temperatures were kept at 19°C (average of June 1999) during all stages of that part of the experiment.

Data collection

Germination of the acorns (seed trial) and shoot development (seed and seedling trial) were recorded weekly during the 24-week growth period following flooding in both trials. At the end of the growth period shoot length, root collar diameter, number of leaves, number of epicormic shoots, and leaf area (LI 3100, LI-COR Inc.) of all living seedlings were measured. Dry weights of shoots, leaves, and roots were determined separately after complete drying at 105°C.

Statistical analysis

One-factor analyses of variance (one-way ANOVA, Median-Test) and multiple comparisons of means were used to search for statistical differences between the different experimental treatments of either trial. Normal distribution of data and homogeneity of variances as the underlying assumptions for the analysis of variance were tested using the Kolmogorov-Smirnov-Test (Lilliefors-modification), and the Levene-Test, respectively. Calculations were undertaken using Statistica 6.1 (StatSoft Inc.).

RESULTS

Seed trial

Compared to the non-flooded control the inundation of acorns postponed germination, increased germination rate, and influenced the growth and morphology of emerging seedlings. The greatest differences were established in root collar diameter and biomass dry weight of roots and shoots. However, differences in germination rate and morphological parameters between the different flooding treatments were not significant.

Acorns of the flooding treatments did not start germinating until the end of inundation. In comparison with S10 and S12, a slight delay in germination was evident in the S8 treatment (data not shown). 20% of the acorns flooded for 8 weeks still germinated 8 to 12 weeks after the drainage. In both other flooding treatments germination was finished within week eight after the end of flooding. Germination rates of all flooding treatments differed significantly from the control. While 48% of the non-flooded seeds (100 acorns not subjected to flooding) germinated, the germination rate of acorns flooded for 8, 10, and 12 weeks reached 77, 83, and 73%, respectively.

Differences in shoot length between the seedlings from non-flooded seeds and those of flooding treatments were not significant (Table 2). However, at the end of the 24-week growth period seedlings of the non-flooded control were up to 95 cm high. In the flooding treatments the largest seedlings were only a half of this height (Fig. 1). In contrast to the values of flooding treatments the shoot lengths of control seedlings were widely distributed with no obvious clustering of the values. The majority of shoot development and elongation occurred during epicotyl elongation in all four treatments. At the end of that period the mean shoot length of control seedlings (26 cm) was significantly greater than the average in S8, S10, and S12 (all 16 cm). Differences between the control and the flooding treatments were smaller and not significant in the second growth period, the formation of epicormic shoots. 73% of the control seedlings had at least one epicormic shoot with a mean length of 17 cm and 6.2 leaves on average. Around 60% of the seedlings of each flooding treatment formed at least one epicormic shoot. Again, morphological parameters differed only slightly and not significantly between the different flooding treat-

Table 2. Dimensions and biomass parameters of seedlings from non-flooded seeds (C) after 24 weeks of growth and seedlings from seeds flooded for 8, 10, and 12 weeks (S8, S10, S12) left to grow for 24 weeks after flooding

	Number of plants	Shoot length (mm)	Root collar diameter (mm)	Number of leaves	Total leaf area (cm^2)	Root weight (g)	Shoot weight (g)	Leaf weight (g)
C	48	389.4	3.08	9.9	162.7	0.77	0.49	0.55
S8	78	249.3	4.19	7.7	169.1	2.00	1.08	0.64
Significance	**	–	***	–	–	***	***	–
S10	83	247.9	4.53	7.8	170.6	2.04	1.19	0.66
Significance	***	–	***	*	–	***	***	–
S12	73	254.0	4.28	7.5	157.4	2.05	1.12	0.63
Significance	*	–	***	–	–	***	***	–
Variants	–	–	–	–	–	–	–	–

Significance of differences between control plants and plants of S8, S10 and S12 is indicated as follows: – no significance; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$
The last line shows the degree of significance between the flooded treatments

ments. In all treatments the mean cumulative length of epicormic shoots was 15 cm while the average number of leaves ranged from 4.1 to 4.5. Despite the smaller number of leaves the mean leaf area (104.5 cm^2) was not significantly smaller compared to the control seedlings (107.5 cm^2).

The mean values of seedling root collar diameter and total seedling dry weight of S8, S10, and S12 were significantly higher than the averages of the control plants after the 24-week growth period following flooding (Table 2). A biomass increase occurred in all plant components. But whereas the dry weight of leaves increased only slightly, root biomass increased nearly by a factor of 3 (see also Table 4). Hence, in all flooding treatments the ratio of dry weight of roots, shoot and leaves was 3:2:1 compared to the ratio of 1.5:1:1 in the control.

Seedling trial

The flooding of seedlings resulted in a loss of leaves and, in many seedlings, in the occurrence of dieback in the upper part of the shoot. Again, no significant differences in any of the morphological growth parameters could be observed between the different flooding treatments.

Resprouting varied considerably between the different treatments (Table 3). Although the seedlings that had been flooded for 8 weeks had the highest survival rate, no clear trend regarding the duration of inundation was evident. Emergence of new shoots occurred mainly in the first four weeks after drainage. However, the seedlings flooded for 12 weeks showed a slight delay in new shoot development compared to both other treatments (data not shown).

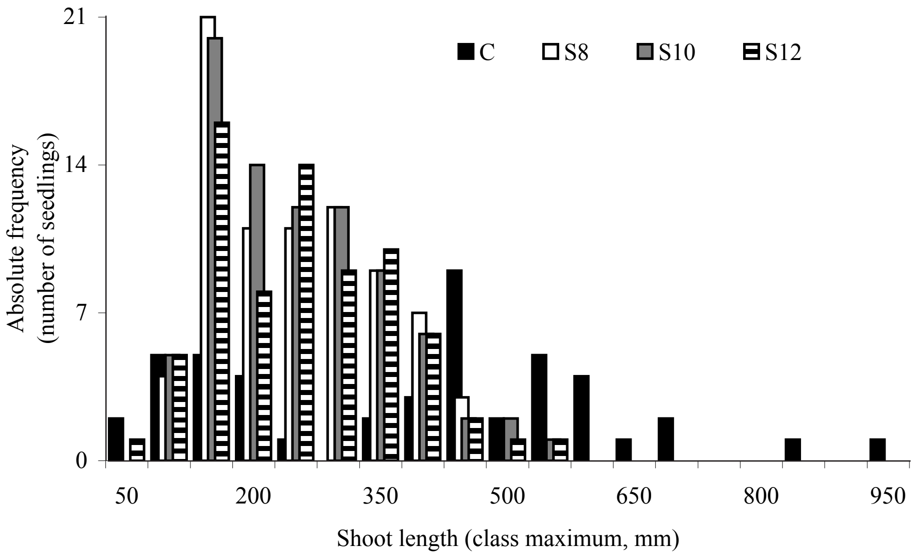

Fig. 1. Frequency of distribution of shoot lengths (classified in 50 mm steps) of seedlings from seeds without flooding (C) after 24 weeks of growth and seedlings from seeds flooded for 8, 10, and 12 weeks (S8, S10, S12), left to grow for 24 weeks after flooding

Table 3. Dimensions and biomass parameters of seedlings flooded for 8, 10, and 12 weeks (P8, P10, P12) after 24 weeks of recovery

	Number of plants	Shoot length (mm)	Root collar diameter (mm)	Number of leaves	Total leaf area (cm^2)	Root weight (g)	Shoot weight (g)	Leaf weight (g)
P8	20	252.0	4.94	7.9	101.5	2.78	1.21	0.48
P10	10	238.2	4.67	9.2	117.1	3.44	1.08	0.49
P12	15	239.5	4.63	7.5	100.2	2.70	1.14	0.42
Variants	*	–	–	–	–	–	–	–

Significance of differences between seedlings of P8, P10 and P12 is shown in the last line and indicated as follows: – no significance; * $P < 0.05$

In the P10 treatment, 80% of the plants that survived sprouted from the terminal bud compared to 47% in P12 and only 25% in P8. At least 80% of the resprouting seedlings in all treatments formed at least one epicormic shoot with an average length of 7.6 cm. The mean number of corresponding leaves ranged from 3.3 to 4.8 whereas the average leaf area varied between 70.6 cm^2 and 84.2 cm^2. Due to the occurrence of dieback in all treatments the average total shoot length increased only slightly compared to initial values measured at the beginning of the trial (data not shown). As observed in the seed trial, the dry weight ratio changed in favour of the root biomass (Table 4). At the end of the 24-week growth period following flooding the ratio of root, shoot and leaf dry weight of the seedlings was on average 6.5:2.5:1 in all treatments.

DISCUSSION

Seed trial

Studies of the germination of flooded seeds were primarily undertaken on tree species of American floodplain forests, where seed from *Taxodium distichum* and *Nyssa aquatica* showed high resistance to long-term flooding (Shunk 1939 in Briscoe 1961; Kozlowski, Pallardy 1997). Research on seeds from various American oak species provided considerably different results. A decline in the germination levels of *Quercus falcata* seeds occurred after 34 days flooding (Briscoe 1961). Acorns from *Quercus nuttallii* remained unaffected under the same conditions. Larsen (1963) observed a slight reduction in the germination rate of seeds from *Quercus falcata*, *Quercus phellos* and *Quercus lyrata* after flooding. The longest flood period of 8 weeks caused the highest losses in these three species. In contrast the number of acorn germinants from *Quercus laurifolia* increased significantly after 8 weeks of flooding. From the limited research it may be assumed that seeds from oaks at higher elevations and rarely flooded areas of North American riparian forests (upland oaks) have a higher sensitivity to flood than the oak species of the actual floodplains (bottomland oaks).

Table 4. Influence of flooding on root/shoot-dry mass ratio (RSR), leaf weight ratio (LWR), and leaf area ratio (LAR) in *Quercus robur* seedlings of both experimental trials

	RSR (g/g)	LWR[a] (g/g)	LAR[b] (cm^2/g)
C	0.7	0.30	90
S8	1.2	0.17	46
S10	1.1	0.17	44
S12	1.2	0.17	41
P8	1.7	0.11	23
P10	2.2	0.10	23
P12	1.7	0.10	24

[a]Leaf dry mass/total dry mass, [b]leaf area/total dry mass

The flooding of *Quercus robur* seeds in this study significantly influenced the germination rate of acorns. In all three flooding treatments (S8, S10, S12) the number of germinated acorns increased significantly compared to the non-flooded control. In contrast to this study, Jones (1958) found no increase in the germination capacity of flooded acorns over a non-flooded control. However, as Schmidt (in Briscoe 1961) had already found, *Quercus robur* seed was considerably less sensitive than acorns of *Quercus petraea*. *Quercus robur*, a species typically present in the hardwood floodplain forests where rare but periodic floods occur, responds similarly to the American bottomland oaks.

Research to date suggests that winter and spring floods affect the germination rate of acorns differently by virtue of their different water temperatures. Guo et al. (1998) found that a spring flood with higher water temperature affected seed from species with a lower flood tolerance to a greater extent than a winter flood. In contrast flood tolerant seed demonstrated the highest germination rates after floods during January and February. Varied explanations for the observed differences are offered in the literature. One assumption is that seed dormancy, influenced partially by temperature, is disturbed at higher water temperatures (Martin et al. 1991; Lyr et al. 1992). On the other hand, the oxygen content of natural waters is dependent upon water temperature (Baskin, Baskin 2001). It is thought that oxygen deficiency in warm water can lead to damage of the embryonic tissue in seeds (Guo et al. 1998). Hence, the conditions of the seed trial in this experiment (cool water temperature, constant air supply) probably enhanced the germination capacity of the seed and thereby averted significant differences between the flooding treatments.

In addition to higher germination rates in the experimental treatments S8, S10, and S12 other essential differences from the control were also apparent. The 24-week-old seedlings from the flooded seeds showed altered growth patterns in response to flooding. Significant increases occurred in root, shoot axes, and total dry weight as well as in root collar diameter. Shoot length clearly decreased compared to the control in all three experimental flooding treatments. Thus germinants from the flooded acorns reacted similarly to young seedlings from flood tolerant tree species subjected to flooding in the root zone (Kozlowski, Pallardy 1997; Siebel et al. 1998). Whether the flooding of seeds is actually responsible for the growth changes in germinants cannot be determined from this study. However, the observations corroborate previous findings.

Seedling trial

The resilience and tolerance of seedlings after being completely flooded have been less extensively analysed. Most studies of water stress arising from soil saturation have employed flooding in the belowground part of young plants and have observed the effect of oxygen deficiency for a brief period only. Lyr (1993) found a reduction in net photosynthesis and reduced stomatal conductivity in *Quercus robur* and *Fagus sylvatica* after anaerobic root conditions for 1 to 4 weeks. Two weeks after removing root anaerobic conditions photosynthesis and stomatal conductivity recovered both in *Quercus* and in *Fagus*. The ability of *Tilia cordata* seedlings to recover was clearly lower. In a similar study, seedlings from *Quercus robur*, *Quercus petraea* and *Quercus rubra* demonstrated no significant recovery 12 days after the completion of a two-week period of anaerobic conditions in the root space (Dreyer et al. 1991).

Parolin (1997) observed that the response of seedlings from tree species in the Central Amazon to complete flooding differed considerably. Despite losing all their leaves after being completely flooded for 18 weeks, the height increment of species such as *Crateva benthami* and *Tabebuia barbata* increased rapidly within 3 weeks of the flood subsiding. In contrast *Cecropia latiloba* and *Vitex cymosa* recovered more slowly, whereas *Senna reticulata* had no new shoots nine weeks after drainage.

In this study a high percentage of *Quercus robur* seedlings survived 12 weeks of complete inundation. For the selected flooding periods there was no relationship between the duration of the flood and the mortality rate of young oaks. Seedlings in treatment P8 demonstrated the highest survival rate, but the proportion of new shoot growth in treatment P12 was substantially higher than in P10. Siebel et al. (1998) were also able to show the high flood tolerance of *Quercus robur*. After 12 weeks of complete inundation only 1 out of the 16 one-year-old seedlings died, compared to 9 out of 20 plants of *Fraxinus excelsior*. The flood tolerance of young *Quercus robur* has also been observed in the field. After the Rhine flood in 1987 Späth (1988) documented new leaf emergence in oak seedlings that had been flooded for more than 50 days.

The ability of young plants to survive floods appears to be dependent upon their state of development and age (Siebel, Blom 1998) as well as the season in which the flood occurs (Glenz et al. 2006). Späth (1988) noted much damage in an oak plantation established shortly before the 1987 Rhine flood, resulting in the loss of half the stand. In contrast, an oak sapling plantation established in 1985 suffered no damage as a result of the flood. Siebel and Blom (1998) found that seedlings from the tree species *Alnus glutinosa*, *Fraxinus excelsior*, *Populus nigra* and *Ulmus minor* were more sensitive to summer floods than to spring floods. Kozlowski and Pallardy (1997) indicated that, in addition to age and species, the timing of the flood also influences flood tolerance. Seedlings are more tolerant to water stress either at the beginning or at the end of an undisturbed growth period. The late timing of the flood in this study, which corresponded to the end of the active growth period, possibly affected the regeneration of *Quercus robur* seedlings favourably.

In contrast to findings of Frye and Grosse (1992), who found great regeneration capacity and negligible effects on plant growth after 12 weeks of anaerobic root conditions, the complete inundation of seedlings from *Quercus robur* produced different results (Siebel et al. 1998). The shoot length of plants submerged for 12 weeks was significantly reduced after the next growing season. Flooded seedlings also had only one quarter of the biomass of non-flooded control plants. Results of the present experiment confirm these observations. The flooded oak seedlings demonstrated a strong reduction in growth increment in comparison with similar aged, non-flooded seedlings grown under slightly better light conditions and similar nutrition. In all treatments the measurements of total and shoot dry weight, leaf number and leaf area after the 24-week recovery period following flooding were about 80 to 90% below the values of plants grown in the absence of flood but under otherwise similar conditions (Ziegenhagen, Kausch 1995). Root growth was less strongly affected and decreased by about 60%. The different allocation of biomass to plant parts was particularly reflected in the parameter leaf weight ratio (LWR). While the formation of photosynthetically active tissue in treatments P8, P10 and P12 constituted only 10% of total plant weight, Welander and Ottosson (1998) reported the mean values of 20% for two-year-old *Quercus robur* seedlings that had not been flooded.

The inhibition of aboveground growth also affected the development of shoot axes, already disturbed through the dieback of upper parts caused by complete submergence. The average shoot length of seedlings in this study was reduced by two thirds in comparison with young oaks that were not flooded (Ziegenhagen, Kausch 1995). Under field conditions reduced height growth increases the period in which young oaks run the danger of complete submergence. At the same time the young plants are exposed to shade from competing vegetation for longer periods. This knowledge could, in addition to the lower light availability and severe browsing, provide an additional explanation as to why *Quercus robur* rarely regenerates naturally despite adequate seed production in the hardwood floodplain forest along the Upper Rhine River.

CONCLUSIONS

The results of this experiment are in agreement with observations of Kühne et al. (2005) at study sites with direct seeding and planting in hardwood floodplain forests along the Rhine, mostly verifying the hypotheses proposed in the introduction. However, in contrast to the respective hypothesis, the germination rate of flooded acorns was increased by inundation and apparently not affected by the duration of submergence. As acorns do not drift during Rhine floods (Kühne et al. 2005), seeding before the start of the flood season in spring can increase the density of regeneration. On the other hand, the planting of seedlings is likely to result in high mortality and poor stem development if exposed to a prolonged flooding event.

Acknowledgements

This research was a part of a project financed by the German Science Foundation (DFG). The authors are indebted to André Brückner for the installation of the experiment and data collection. We also thank Anke Nannen, Karl-Heinz Obal and Ulrike Westphal for technical support and Helen Desmond as well as Oda Godbold for improving the English.

References

BASKIN C.C., BASKIN J.M., 2001. Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination. San Diego, Academic Press.

BIEGELMAIER K.H., 2002. Auswirkungen des Hochwassers im Rheinauenwald. AFZ/Der Wald, *57*: 801–803.

BRISCOE C.B., 1961. Germination of cherrybark and nuttal oak acorns following flooding. Ecology, *42*: 430–431.

COLIN-BELGRAND M., DREYER E., BIRON P., 1991. Sensitivity of seedlings from different oak species to waterlogging: effects on root growth and mineral nutrition. Annals of Forest Science, *48*: 193–204.

DREYER E., 1994. Compared sensitivity of seedlings from 3 woody species (*Quercus robur* L., *Quercus rubra* L. and *Fagus sylvatica* L.) to water logging and associated root hypoxia: effects on water relations and photosynthesis. Annals of Forest Science, *51*: 417–429.

DREYER E., COLIN-BELGRAND M., BIRON P., 1991. Photosynthesis and shoot water status of seedlings from different oak species submitted to waterlogging. Annals of Forest Science, *48*: 205–214.

ELLENBERG H., 1996. Vegetation Mitteleuropas mit den Alpen. Stuttgart, Ulmer Verlag.

FRYE J., GROSSE W., 1992. Growth responses to flooding and recovery of deciduous trees. Zeitung für Naturforschung, Section C, *47*: 683–689.

GLENZ C., SCHLAEPFER R., IORGULESCU I., KIENAST F., 2006. Flooding tolerance of Central European tree and shrub species. Forest Ecology and Management, *235*: 1–13.

GUO Y., SHELTON M.G., LOCKHART B.R., 1998. Effects of flood duration and season on germination of black, cherrybark, northern red and water oak acorns. New Forests, *15*: 69–76.

HEISEKE D., 1984. Untersuchungen über Eichelmasten und Pflanzenausbeute in der Ghörde von 1979–1981. Forst- und Holzwirtschaft, *39*: 107–113.

JONES E.W., 1958. The storage of acorns in water. Forestry, *31*: 163–166.

KOZLOWSKI T.T., PALLARDY S.G., 1997. Growth Control in Woody Plants. San Diego, Academic Press.

KÜHNE C., BARTSCH N., RÖHRIG E., 2005. Waldbauliche Behandlung der Auenwälder am Oberrhein unter besonderer Berücksichtigung der Stieleiche (*Quercus robur* L.). Schriften aus der Forstlichen Fakultät der Universität Göttingen und der Niedersächsischen Forstlichen Versuchsanstalt, *140*.

LARSEN H.S., 1963. Effects of soaking in water on acorn germination of four southern oaks. Forest Science, *9*: 236–241.

LEVY G., BECKER M., GARREAU B., 1986. Comportement expérimental de semis de chêne pedonculé, chêne sessile et hêtre en présence d'une nappe d'eau dans le sol. Annales des sciences forestières, *43*: 131–146.

LÜPKE B.V., 1998. Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. Forest Ecology and Management, *106*: 19–26.

LYR H., 1993. Vergleichende Untersuchungen zu physiologischen Reaktionen auf Wurzelanaerobiose bei *Fagus sylvatica*, *Quercus robur* und *Tilia cordata.* Beiträge zur Forstwirtschaft und Landschaftsökologie, *27*: 18–23.

LYR H., FIEDLER H.J., TRANQUILLINI W. (eds.), 1992. Physiologie und Ökologie der Gehölze. Jena, Gustav Fischer Verlag.

MARTIN B.A., CERWICK S.F., REDING L.D., 1991. Physiological basis for inhibition of maize seed germination by flooding. Crop Science, *31*: 1052–1057.

MU-RP (Ministerium für Umwelt Rheinland-Pfalz, ed.), 1993. Der Einfluss des Oberrheinausbaus und der am Oberrhein vorgesehenen Retentionsmaßnahmen auf die Hochwasser am Mittelrhein von Kaub bis Köln. Mainz.

OBERDORFER E., 1992. Süddeutsche Pflanzengesellschaften Teil IV: Wälder und Gebüsche, Textband. Jena, Gustav Fischer Verlag.

PAROLIN P., 1997. Auswirkungen periodischer Vernässung und Überflutung auf Phänologie, Photosynthese und Blattphysiologie von Baumarten unterschiedlicher Wachstumsstrategie in zentralamazonischen Überschwemmungsgebieten. München, Herbert Utz Verlag.

PFARR U., 2002. Hochwasserschutz und Waldbau. AFZ/Der Wald, *57*: 797–800.

RÖHRIG E., BARTSCH N., 1992. Waldbau auf ökologischer Grundlage. Band 1. Hamburg, Parey Verlag.

ROLOFF A., BONN S., 2002. Konkurrenzdynamik und Ökophysiologie der wichtigsten Baumarten in Hartholzauenwäldern an der Mittleren Elbe. In: ROLOFF A., BONN S. (eds.), Ergebnisse ökologischer Forschung zur nachhaltigen Bewirtschaftung von Auenwäldern an der Mittleren Elbe. Stuttgart, Ulmer Verlag: 7–59.

SCHMULL M., THOMAS F.M., 2000. Morphological and physiological reactions of young deciduous trees (*Quercus robur* L., *Q. petraea* [Matt.] Liebl., *Fagus sylvatica* L.) to waterlogging. Plant and Soil, *225*: 227–242.

SCHNITZLER A., 1994. Conservation of biodiversity in alluvial hardwood forests of the temperate zone. The example of the Rhine valley. Forest Ecology and Management, *68*: 385–398.

SIEBEL H.N., BLOM C.W.P.M., 1998. Effects of irregular flooding on the establishment of tree species. Acta Botanica Neerlandica, *47*: 231–240.

SIEBEL H.N., VAN WIJK M., BLOM C.W.P.M., 1998. Can tree seedlings survive increased flood levels of rivers? Acta Botanica Neerlandica, *47*: 219–230.

SPÄTH V., 1988. Zur Hochwassertoleranz von Auenwaldbäumen. Natur und Landschaft, *63*: 312–315.

SPÄTH V., 2002. Hochwassertoleranz von Waldbäumen in der Rheinaue. AFZ/Der Wald, *57*: 807–810.

TITTIZER T., KREBS F. (eds.), 1996. Ökosystemforschung: Der Rhein und seine Auen – eine Bilanz. Berlin, Springer Verlag.

WELANDER N.T., OTTOSSON B., 1998. The influence of shading on growth and morphology in seedlings of *Quercus robur* L. and *Fagus sylvatica* L. Forest Ecology and Management, *107*: 117–126.

ZIEGENHAGEN B., KAUSCH W., 1995. Productivity of young shaded oaks (*Quercus robur* L.) as corresponding to shoot morphology and leaf anatomy. Forest Ecology and Management, *72*: 97–108.

Received for publication February 13, 2007
Accepted after corrections May 29, 2007

Klíčení osiva a vývin semenáčků *Quercus robur* L. po zaplavení

ABSTRAKT: Osivo i semenáčky *Quercus robur* – dřeviny charakteristické pro lužní lesy podél Rýna – prokázaly vysokou odolnost vůči celkovému zaplavení v řízených podmínkách. V obou experimentálních zkouškách nebyly zjištěny žádné významné rozdíly ve vzcházení ani v morfologických parametrech růstu mezi různě dlouhými obdobími zaplavení (8, 10 a 12 týdnů). Zaplavení pozdrželo klíčení zatopených žaludů až do konce záplavy. Osivo vystavené zaplavení však mělo významně vyšší klíčivost než kontrolní nezatopené žaludy. Podobně byly i hodnoty sušiny semenáčků ze zatopeného osiva statisticky významně vyšší než z nezatopených žaludů. V růstovém období 24 týdnů následujícím po zaplavení se u obou pokusů snížil růst nadzemní části rostlin ve prospěch vývinu kořenů. Omezený vývin listů a snížené prodlužování nadzemní části rostlin způsobily stagnaci růstu mladých rostlin dubu ve fázi semenáčku. Tyto výsledky potvrzují domněnky z dříve provedených experimentů, týkající se tolerance osiva a semenáčků *Quercus robur* vůči zaplavení. Slouží rovněž pro vysvětlení následného rozšíření dubových semenáčků v lužních lesích kolem Rýna po semenných letech a jejich postupného vymizení v letech následujících.

Klíčová slova: zaplavení; experiment; mortalita; morfologie; obnova; dub letní

Corresponding author:

Dr. Christian Kühne, Georg-August-University of Göttingen, Institute of Silviculture, Department I: Silviculture of Temperate Zones and Forest Ecology, Büsgenweg 1, 37077 Göttingen, Germany
tel.: + 49 551 391 2298, fax: + 49 551 393 670, e-mail: ckuehne@gwdg.de