

Effects of temperature, moisture and soil type on seedling emergence and mortality of riparian plant species

Aquatic Botany

ter Heerdt, Gerard N.J.; Veen, Ciska G.F.; van der Putten, Wim H.; Bakker, Jan P.

<https://doi.org/10.1016/j.aquabot.2016.09.008>

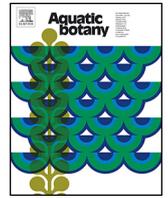
This publication is made publicly available in the institutional repository of Wageningen University and Research, under the terms of article 25fa of the Dutch Copyright Act, also known as the Amendment Taverne.

Article 25fa states that the author of a short scientific work funded either wholly or partially by Dutch public funds is entitled to make that work publicly available for no consideration following a reasonable period of time after the work was first published, provided that clear reference is made to the source of the first publication of the work.

This publication is distributed using the principles as determined in the Association of Universities in the Netherlands (VSNU) 'Article 25fa implementation' project. According to these principles research outputs of researchers employed by Dutch Universities that comply with the legal requirements of Article 25fa of the Dutch Copyright Act are distributed online and free of cost or other barriers in institutional repositories. Research outputs are distributed six months after their first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and / or copyright owner(s) of this work. Any use of the publication or parts of it other than authorised under article 25fa of the Dutch Copyright act is prohibited. Wageningen University & Research and the author(s) of this publication shall not be held responsible or liable for any damages resulting from your (re)use of this publication.

For questions regarding the public availability of this publication please contact openaccess.library@wur.nl



Effects of temperature, moisture and soil type on seedling emergence and mortality of riparian plant species

Gerard N.J. Ter Heerdt^{a,*}, Ciska G.F. Veen^b, Wim H. Van der Putten^{b,c}, Jan P. Bakker^a

^a Conservation Ecology, Groningen Institute of Evolutionary Life Sciences GELIFES, University of Groningen, P.O. Box 11103, 9700CC Groningen, The Netherlands

^b Department of Terrestrial Ecology, Netherlands Institute of Ecology, P.O. Box 50, 6700 AB Wageningen, The Netherlands

^c Laboratory of Nematology, Wageningen University and Research Centre, P.O. Box 8123, 6700 ES Wageningen, The Netherlands

ARTICLE INFO

Article history:

Received 22 October 2015

Received in revised form

19 September 2016

Accepted 21 September 2016

Available online 22 September 2016

Keywords:

Germination

Seedling emergence

Mortality

Temperature

Moisture

Soil type

Drawdown

Riparian plant species

Functional groups

Typha latifolia

Phragmites australis

Senecio congestus

Rumex maritimus

Chenopodium rubrum

ABSTRACT

Restoration of riparian plant communities on bare soil requires germination of seeds and establishment of seedlings. However, species that are present in the soil seed bank do not always establish in the vegetation. Temperature, moisture conditions and soil type could play a major role in the establishment of riparian plant communities, through impacting seedling emergence.

We studied the effects of temperature, combinations of temperature and moisture conditions, and soil type on seedling emergence and mortality of perennial reeds (*Typha latifolia* and *Phragmites australis*) and annual or biannual pioneer species (*Senecio congestus*, *Rumex maritimus* and *Chenopodium rubrum*). The responses to the environmental conditions were species-specific and resulted in context-dependent differences in proportions of species emerging from the soil seed bank. *Typha latifolia* and *S. congestus* preferred wet or very wet conditions, *C. rubrum* and *R. maritimus* preferred dry to very dry conditions. *Phragmites australis* was able to establish under all conditions. Both cold and very dry conditions resulted in low emergence and survival, which was not fully compensated for when conditions became favorable again. *Senecio congestus*, *R. maritimus* and *C. rubrum* benefitted from secondary seedling emergence when, after a very dry period, the weather became very wet again, while *T. latifolia* and *P. australis* remained absent.

When the conditions remained wet, more seedlings emerged from sand than from clay. However, when the soil was drying out, fewer seedlings emerged from sand than from clay.

We propose that using information on plant species-specific responses to abiotic environmental conditions during germination, emergence and establishment can help to restore different target riparian plant communities.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Natural well-developed banks and shorelines are characterized by a variety of riparian plant communities. The zone around the waterline is dominated by perennial reed species such as *Phragmites australis* and *Typha latifolia*. In areas where the water level drops in spring and summer, for example in non-regulated lakes and rivers, mudflats emerge with annual or biannual mudflat and pioneer species such as *Senecio congestus*, *Chenopodium rubrum* and *Rumex maritimus*. The reed zones are important as a breeding habitat for fauna and the pioneer communities as a food source for

waterfowl (Clevering and Van Gulik, 1997; Lenssen et al., 1999; Coops et al., 1999; Nijhof, 2002). However, many water systems have strongly changed due to water regulation, often involving loss of riparian plant communities. Restoration of riparian plant communities is a major issue; both in North America (Van der Valk and Pederson, 1989; Van der Valk, 2005) and Western Europe (Coops et al., 2004; Abrahams, 2006). In the Netherlands, the Water Framework Directive stimulates large-scale restoration measures, such as (re)construction of gently sloped banks (Clevering and Van Gulik, 1997; Boedeltje et al., 2003a; Everaert et al., 2013), increased fluctuations in water level and drawdowns (Vulink and Van Eerden, 1998; Coops and Hosper, 2002; Sarneel et al., 2014), creating flood-plain flats (Nijhof, 2002) and removal of the topsoil or vegetation (Lenssen et al., 1999). These methods all result in bare soil, where the establishment of riparian plant communities is supposed to start from seeds (Ter Heerdt and Drost, 1994; Van der Valk et al.,

* Corresponding author. Present address: Waternet, P.O. Box 94370, 1090 GJ Amsterdam, The Netherlands.

E-mail address: gerard.ter.heerdt@waternet.nl (G.N.J. Ter Heerdt).

1992; Boedeltje et al., 2003a). Dispersal is often not considered a major constraint for establishment of riparian plant species, as they generally disperse well by water, wind, birds or mammals (Boedeltje et al., 2003b; Soons, 2006; Vogt et al., 2007; Van Leeuwen et al., 2012; Stroh et al., 2012) and their seeds remain viable in the soil seed bank for several years (Ter Heerdt and Drost, 1994; Boedeltje et al., 2003a; Jensen, 2004).

However, there is still insufficient knowledge to precisely predict which communities may become restored. Some riparian species, though abundant in the soil seed bank, do not establish after restoration measures, while others do (Welling et al., 1988; Leck and Simpson, 1995; Brown, 1998; Hopfensperger, 2007). Such differences between species establishment could be caused by differences in environmental conditions and differential seed germination and seedling mortality of the species present in the soil seed bank (Galinato and Van der Valk, 1986; Weiher and Keddy, 1995; Keddy, 1999). Temperature and moisture content of the soil largely determine the germination of seeds (Baskin and Baskin, 2001), so that knowledge of the response of the species in the seed bank to these environmental factors should enable us to predict which communities may be able to establish after restoration measures. These responses are not known, but can be tested experimentally. The fate of the seeds that do not emerge when conditions are unfavorable is also unknown. Baskin and Baskin (1988) and Baskin et al. (1989) suggested that seeds that did not germinate due to unfavorable conditions such as drought, may become physiologically dormant. Therefore, not all seeds will germinate when environmental conditions become favorable again (secondary seedling emergence). This might also be species specific, and can be tested experimentally.

The present study is based on the experiences during a large-scale drawdown from 1987 to 1988 in the Oostvaardersplassen in the Netherlands (52°26'N, 5°19'E). The Oostvaardersplassen are shallow, non-tidal freshwater lakes, without strong water-level fluctuations. The bottom consists of clay. Due to a high grazing pressure by Greylag geese (*Anser anser*) most of the helophyte communities with *P. australis* and *T. latifolia* disappeared, including their rhizomes. As the water level hardly fluctuated, mudflats with annual and biennial species became scarce and helophytes did not re-establish (Wigbels, 1990; Vulink and Van Eerden, 1998; Beemster et al., 2010). The main goal of this drawdown was the re-establishment of *T. latifolia* and *P. australis* stands (Vulink and Van Eerden, 1998). However, during the first year of drawdown several other riparian plant communities established. This variation was not caused by variation in the composition of the soil seed bank, as all species were present in sufficient numbers to become abundant or dominant, except *P. australis* (Ter Heerdt and Drost, 1994). The vegetation development appeared to depend on different weather conditions during the early establishment of each community. A community dominated by *T. latifolia* established during a very wet period. *Chenopodium rubrum* and *R. maritimum* were the most abundant species after a very dry period. *Senecio congestus* became dominant when, after a very dry period, the weather became very wet again. *Phragmites australis* was present in low densities, apparently independent of the weather.

Earlier studies do not provide sufficient detailed information about the preferences of these species to understand how different communities could arise (Ter Heerdt and Drost, 1994). In the present study we will test, with a series of experiments, if differential species responses to various moisture conditions and temperatures could explain the establishment of different communities from the same soil seed bank after a drawdown. As the moisture content of the soil depends largely on evaporation and, therefore, on temperature, we tested effects of temperature and several combinations of temperature and moisture conditions. As germination characteristics may depend on the history of the seeds

(Baskin and Baskin, 1988) we used seeds collected from a natural soil seed bank in the Oostvaardersplassen.

In the Netherlands, there are plans to restore riparian vegetation on clay soils or on pleistocene sandy soils. When moisture conditions determine germination and mortality, this may vary between soil types, as clay soils can hold more water than sandy soils. This we tested in an additional second series of experiments, focusing on the two major target species for the restoration of riparian vegetation: *P. australis* and *T. latifolia*. These species disperse seeds in early spring, when the weather is warm and the water level drops; therefore we used freshly harvested seeds for the experiments.

If it is known how temperature, the combination of temperature and moisture conditions and soil type affect the germination of the various species in the soil seed bank, it is understood how this should lead to the establishment of different communities and it should be possible to predict more precisely which plant communities may establish. Therefore, the aim of the present study is to determine if *T. latifolia*, *P. australis*, *S. congestus*, *R. maritimum* and *C. rubrum* respond differentially to temperature, combinations of temperature and moisture conditions, and soil type. The responses tested are seedling emergence and mortality, as germination cannot be determined in buried seeds. We hypothesize that (1) seedling emergence and mortality in response to temperature, the combination of temperature and moisture and soil type differ between plant species. Based on the Oostvaardersplassen case study, we expected that *T. latifolia* and *S. congestus* prefer very wet conditions, *C. rubrum* and *R. maritimum* prefer dry conditions and *P. australis* is able to establish under all conditions (2) that after a period with unfavorable conditions for seedling emergence and survival, some species will emerge when conditions become favorable (secondary seedling emergence), while others will not. We expected that *S. congestus* should benefit from secondary seedling emergence when, after a very dry period, the weather becomes very wet again.

2. Methods

2.1. Experimental setup

We set up a series of experiments where we measured the emergence and mortality of seedlings of five riparian plant species under different environmental conditions. The experimental combinations of temperature and moisture were considered as treatments and were based on the weather conditions during the large-scale drawdown in the Oostvaardersplassen from 1987 to 1988. During a very wet period mean evaporation surplus (or precipitation deficit) was zero mm/day and the intervals between rainy periods were 2–3 days. During a very dry period mean evaporation surplus was 1.70 mm/day and the intervals between rainy periods were up to two weeks. Therefore we used moisture treatments ranging from very wet (evaporation surplus = 0.00 mm/day) to very dry (evaporation surplus = 1.70 mm/day) and two treatments in between (Table 1).

The drawdown in the Oostvaardersplassen took place between March/April and October. Air temperature in this period varied between near 0 °C and over 30 °C. During clouded and rainy periods, the temperature of the upper few mm of the soil would be close to the air temperature. During summer, temperature at three cm soil depth in the Netherlands could become 30–34 °C during midday. Due to radiation the upper five mm may have been several degrees warmer during hot and dry periods (Ten Berge, 1990). Therefore we tested temperatures between 3 °C and 30–40 °C (Table 1). This study focuses on the first 30 to 40 days of seedling emergence, when plant coverage is still small and competition for water, light and nutrients is supposed to play only a minor role. The species used to

Table 1
Environmental conditions tested in the six experiments. In the first two experiments seedling emergence under five temperature treatments was tested. In the second two experiments seedling emergence under several moisture treatments was tested. In the last two experiments the mesocosms from the former experiment were kept wet and warm afterwards for 30 days to detect remaining viable, non-dormant seeds. Species tested: *Typha latifolia* (Tl), *Phragmites australis* (Pa), *Chenopodium rubrum* (Cr), *Rumex maritimus* (Rm) and *Senecio congestus* (Sc).

Effect of temperature on seedling emergence and T ₅₀ by species; five species on clay						
Soil: clay	treatment	1	2	3	4	5
Species: Tl, Pa, Sc, Cr, Rm	temperature (°C, night-day)	3–10	5–15	10–20	15–25	20–30
Petri-dishes	evaporation	low	low	low	low	low
Replicates: 5	evaporation surplus (mm/day)	0.0	0.0	0.0	0.0	0.0
Effect of temperature on seedling emergence and T ₅₀ by soil and species; two species on clay or sand						
Soil: clay & sand	treatment	1	2	3	4	5
Species: Tl, Pa	temperature (°C, night-day)	3–10	5–15	10–20	15–25	20–30
Petri-dishes	evaporation	low	low	low	low	low
Replicates: 5	evaporation surplus (mm/day)	0.0	0.0	0.0	0.0	0.0
Effect of temperature and drought on seedling emergence, T ₅₀ , E _{max} and % survival by species; five species on clay						
Soil: clay	treatment	very wet & cold	wet & cool	dry & warm	very dry & hot	
Species: Tl, Pa, Sc, Cr, Rm	temperature (°C, night-day)	3–10	10–20	20–30	30–40	
Mesocosms	evaporation (mm/day)	0.7	1.1	3.3	4.5	
Replicates: 6	evaporation surplus (mm/day)	0.00	0.57	1.14	1.70	
Effect of temperature and drought on seedling emergence, T ₅₀ , E _{max} and % survival by soil and species; two species on clay or sand						
Soil: clay & sand	treatment	wet & cool	intermediate		very dry & warm	
Species: Tl, Pa	temperature (°C, night-day)	10–20	15–25		20–30	
Mesocosms	evaporation (mm/day)	1.4	2.7		4.0	
Replicates: 5	evaporation surplus (mm/day)	0.57	1.14		1.70	
Effect of previous treatment on secondary seedling emergence by species; five species on clay						
Soil: clay	previous treatment (exp. 3)	very wet & cold	wet & cool	dry & warm	very dry & hot	
Species: Tl, Pa, Sc, Cr, Rm	temperature (°C, night-day)	20–30	20–30	20–30	20–30	
Mesocosms	evaporation (mm/day)	4.0	4.0	4.0	4.0	
Replicates: 6	evaporation surplus (mm/day)	0.0	0.0	0.0	0.0	
Effect of previous treatment on secondary seedling emergence by soil and species; two species on clay or sand						
Soil: clay & sand	previous treatment (exp. 4)	wet & cool	intermediate		very dry & warm	
Species: Tl, Pa	temperature (°C, night-day)	20–30	20–30		20–30	
Mesocosms	evaporation (mm/day)	4.0	4.0		4.0	
Replicates: 5	evaporation surplus (mm/day)	0.0	0.0		0.0	

test our hypotheses were the five most abundant ones during the drawdown from 1987 to 1988 (*T. latifolia*, *C. rubrum*, *R. maritimus* and *S. congestus*) or the following years (*P. australis*).

Saturated, unripened clay that never dried out before and that has not been subject to soil formation, obtained from the Oostvaardersplassen reserve, was used for a first series of experiments, where we tested the performance of five species on clay: *T. latifolia*, *P. australis*, *C. rubrum*, *R. maritimus* and *S. congestus*, under different temperature and moisture regimes. Additionally, in a second series of experiments with two species, the performance of *T. latifolia* and *P. australis* was tested on ripened clay obtained from a former agricultural field and fine grained pleistocene sand obtained from a quarry.

2.2. Seed sources and treatment

2.2.1. Experiments with five species on clay

Seeds of *T. latifolia*, *P. australis*, *C. rubrum*, *R. maritimus* and *S. congestus* used in the first series of experiments were collected from the soil seed bank in the Oostvaardersplassen in March 1992. Soil samples were washed on a 0.212 mm mesh to remove all clay (Ter Heerdt et al., 1996). The remaining mixture of detritus and seeds was kept wet, dark and cool (4 °C) for six to eight months until they were used end 1992. This material contained viable and non-dormant seeds of the five species that we wanted to test (Ter Heerdt et al., 1996). Special care was taken to supply each replicate with the same amount of seeds. In the five-species experiments on clay with five temperature treatments, five batches of detritus-seed mixture were split in five equal parts, one for each treatment, resulting in five replicates per treatment. In the five-species experiment with four combinations of moisture and temperature, two batches of mixture were split in 12 parts each, three for each treat-

ment, resulting in six replicates for each treatment. After the end of each experiment, the replicates were stirred and kept wet for four weeks at 20–30 °C to test for remaining viable, non-dormant seeds (Ter Heerdt et al., 1996). The number of viable, non-dormant seeds sown was estimated by the maximum number of seeds that emerged during the experiments plus the number of seeds that emerged afterwards. These numbers of seeds were taken as 100% and are presented in Table 2.

2.2.2. Experiments with two species on sand and clay

Seeds of *T. latifolia* and *P. australis* used were harvested from plants in the Oostvaardersplassen in November 1998, stored dry, dark and cool (4 °C) for 3–4 months until they were used the beginning of 1999. Before sowing they were soaked in water for at least 24 h. In the temperature experiment, 50 seeds of each species were sown. In the experiment where we tested the effect of temperature and moisture combined, 100 seeds per species were sown. After the end of each experiment, the replicates were stirred and kept wet for four weeks at 20–30 °C to test for remaining viable, non-dormant seeds (Ter Heerdt et al., 1996). The number of viable non-dormant seeds sown was determined by the maximum number of seeds that emerged during the experiments plus the number of seeds that emerged afterwards, the same way as in the experiment with five species on clay (Table 2).

2.2.3. Experimental soil layer

Under natural conditions seeds are buried in the soil and, generally, only seeds in the upper few mms will germinate (Galinato and Van der Valk, 1986; Ter Heerdt et al., 1996; Gleason et al., 2003). Therefore, in all experiments the seeds were mixed with sand, or clay, and water to a soil-seed mixture and poured in a 3 mm thick layer on the substrate used. Burial, especially in clay,

Table 2

Number of viable non-dormant seeds detected during the experiments plus additional tests afterwards. These numbers were taken as the total number of seeds present (100%) when comparing the effects of the different treatments.

	Experiments with five species on clay					Experiments with two species on clay and sand					
	Effect of temperature					Effect of moisture and temperature		Effect of temperature		Effect of moisture and temperature	
	Batch 1	Batch 2	Batch 3	Batch 4	Batch 5	Batch 1	Batch 2	clay and sand	clay	sand	
<i>T. latifolia</i>	129	116	118	115	125	198	184	50	27	44	
<i>P. australis</i>	8	7	7	11	10	21	23	50	53	66	
<i>S. congestus</i>	30	24	29	27	25	135	139				
<i>R. maritimus</i>	9	10	13	10	9	146	128				
<i>C. rubrum</i>	70	48	62	58	55	197	221				

decreases germination (Ter Heerdt et al., 1996), which is why not all 100 seeds in the two-species experiment, where we tested the effect of moisture conditions on sand and clay, were able to emerge.

2.3. Description of the experiments

All experiments were performed in climate chambers designed for plant growth experiments. Environmental conditions tested in the six experiments are summarized in Table 1. Day length was 12 h. Temperature fluctuated diurnally by 10 °C differences between day and night, as wetland species generally germinate best under these conditions (Galinato and Van der Valk, 1986).

2.3.1. Effect of temperature and soil type on seedling emergence

In the five-species temperature experiment on clay we tested the emergence of all five plant species in response to five different temperature treatments (Table 1) on clay soil. All five species grew together. This experiment was performed end 1992. In the two-species temperature experiment we tested the emergence of *P. australis* and *T. latifolia*, in response to the same five different temperature treatments on clay and sandy soils. Seeds of each species were sown in separate Petri dishes. This experiment was performed beginning 1999.

The soil-seed mixture (see Section 2.2.3) was poured in a 3 mm layer on paper on water-saturated rock-wool in well-closed 10 cm Petri dishes. The maximum numbers of seeds detected, taken as 100%, are shown in Table 2. The soil-seed mixture was watered until saturation every 2–4 days. The experiment was finished after 35 days. Number of replicates was five. Seedlings were counted and removed after emergence, the first three weeks every 2–4 days and later weekly.

2.3.2. Effect of combinations of moisture and temperature, and soil type on seedling emergence and mortality

Here we tested differences between riparian species, regarding the effect of combinations of temperature and evaporation surplus, and soil type on seedling emergence and mortality. Buckets of twelve liters were used as mesocosms. In the five-species experiment all five species were compared on clay (Table 1). In each mesocosm all five species grew together. The mean initial soil water content of the saturated clay was 51% (w/w), the mesocosms contained approximately 7.6 l of water. Number of replicates was six. In the two-species experiment the effect of soil type (clay vs sand) was additionally tested, but only with *P. australis* and *T. latifolia* (Table 1). The mean initial soil water content of the saturated sand was 16.4% (w/w). Mesocosms with sand contained approximately 3.1 l of water. The surface of the mesocosms was divided in two equal parts. On one half 100 *T. latifolia* seeds were sown, on the other half 100 *P. australis* seeds. Due to the burial in the soil, not all those seeds emerged as seedlings. The max-

imum numbers of seeds detected, taken as 100%, are shown in Table 2.

Evaporation depended on four temperature regimes (Table 1) and was measured by weighing the mesocosms. The four treatments ranged from very wet & cold to very dry & hot (Table 1). Evaporation surplus was manipulated by replenishing the weight loss of the mesocosms with different amounts of water. The watering frequency during the five-species experiment on clay was four, two or one times per fortnight. Each combination of moisture level (four treatments) and watering frequency (three frequencies), thus four × three treatments, was replicated two times. During the two-species experiment on sand or clay the watering frequency was four times per fortnight (very wet & cold), twice per fortnight (intermediate) or once per fortnight (very dry & hot). Number of replicates in the two-species experiment on sand or clay was five. Emerged seedlings were counted and marked individually twice a week. Seedlings that had died were counted and removed. Both experiments lasted 30 days. The five-species experiment on clay was performed the end of 1992 and the two-species experiment on sand or clay the beginning of 1999.

2.3.3. Secondary seedling emergence

In the experiments where we studied secondary seedling emergence, we tested how unfavorable conditions with respect to the combination of evaporation surplus and temperature, followed by subsequent favorable conditions, affect seedling emergence in the second cohort. We used the mesocosms of the five- and two-species moisture experiments (see Section 2.3.2). At the end of these experiments, we removed all seedlings and kept all mesocosms under optimal conditions for wetland seedling emergence, i.e., saturated soils and a temperature of 20 °C at night and 30 °C at day (Ter Heerdt et al., 1996). This combination of high temperature and saturated soil is unlikely to occur for more than a few days under field conditions, but is commonly used to determine the composition of the soil seed bank. Seedlings in the second cohort were counted and removed, until no new seedlings emerged (after 30 days). Number of replicates was the same as in five- and two-species moisture experiments; 6 and 5 respectively.

2.4. Data analyses

The highest number of seedlings per species per experiment, including the check for viable seeds afterwards, was considered as the number of viable and not dormant seeds that was sown and taken as 100% (Table 2). Percentage seedling emergence was calculated for each sampling date. Maximum emergence capacity (E_{max}) in each mesocosm was calculated per species and treatment as percentage of the number of seeds sown. Mortality was expressed as percentage of the seedlings that emerged. Time to reach 50% seedling emergence (T_{50}) was calculated in each mesocosm as a proxy of emergence rate (Grime et al., 1981; Joosen et al., 2010). Cumulative emergence data were used to calculate T_{50} . Secondary

Table 3

Five species on clay. Overview of the effects of species identity and temperature regime on T_{50} and E_{max} . Bold values represent statistically significant differences.

	T_{50}			E_{max}		
	F	P	df	F	P	df
Species	117.48	<0.001	4/100	2.70	0.035	4/100
Temperature	652.35	<0.001	4/100	0.44	0.781	4/100
Spec × temp	28.76	<0.001	16/100	3.82	<0.001	16/100

seedling emergence was calculated as percentage of the potential number of viable seeds, left at the end of the previous moisture experiments.

The data were analyzed with general linear models using T_{50} , E_{max} and percentage mortality as response variables. Species identity, temperature, the combination of temperature and moisture regime, watering frequency and soil type were used as fixed factors, depending on the experiment. Residuals were tested for normality with a Shapiro test and for homogeneity of variances with a Levene's test. T_{50} data were log-transformed in all experiments to obtain a normal distribution of the residuals. The numbers of seeds were sufficient to detect significant effects of treatments. The only exceptions are the numbers of *P. australis* and *R. maritimus* in the five-species temperature experiment on clay, which were too low to detect an effect of temperature on E_{max} . All statistical analyses were carried out in R version 2.13.0 (R Development Core Team).

3. Results

3.1. Effect of temperature on seedling emergence

3.1.1. Five species on clay

For all five species, the emergence rate increased with increasing temperature, as T_{50} decreased (Table 3, Fig. 1A). The emergence rate also depended on the interaction between species identity and temperature regime, indicating that the tested species responded differently to changes in temperature regimes (Table 3). For example, *T. latifolia* had the lowest emergence rate of all species at low temperature, while it had the highest emergence rate of all species at high temperature (Fig. 1A). For this species, seedlings emerged 6.7 times as fast at high than at low temperature. Differences in T_{50} between temperatures could be nearly 20 days. Some other species did not have such strong variation in emergence rates across temperature. For example, *S. congestus* seedlings emerged just over 2 times faster at high than at low temperature and the difference in T_{50} between temperatures was only 5 days.

There was no general relationship between E_{max} and temperature across the different species (Table 3). For some species (e.g. *T. latifolia*) E_{max} increased at higher temperature, while for other species (e.g. *S. congestus*) E_{max} decreased at higher temperature (Fig. 1B). Some species (e.g. *P. australis*) did not show a clear relationship between E_{max} and temperature. The species × temperature interaction indicated a significant difference between the response of the various species (Table 3). The time series on which these results are based are shown in Appendix A.

3.1.2. Two species on clay and sand

Seedling emergence rate increased with increasing temperature (Table 4, Fig. 2A). The interaction between species identity and temperature regime indicated that the two species responded differently to changes in temperature regimes (Table 4), but the differences were very small (Fig. 2A). Soil type did not affect T_{50} of *P. australis*, but for *T. latifolia* T_{50} was lower in sand than in clay. Differences in T_{50} were relatively small, three days or less, but sta-

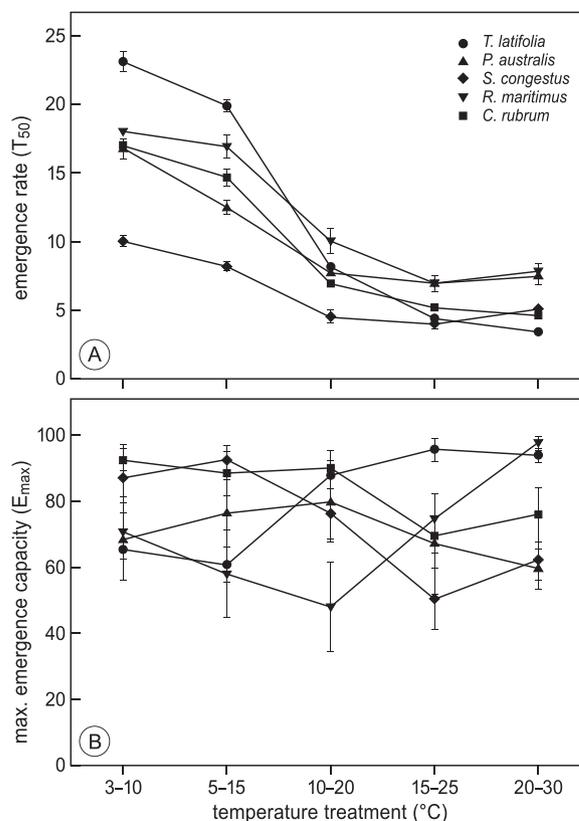


Fig. 1. Effect of temperature regimes on A: emergence rate (T_{50}) and B: maximum emergence capacity (E_{max}). Comparison between *Typha latifolia*, *Phragmites australis*, *Chenopodium rubrum*, *Rumex maritimus* and *Senecio congestus* on clay. Marks indicate means, error bars indicate ± S.E. of the mean (n=5). Temperature regime is temperature (°C) during night and day (Table 1).

Table 4

Two species on clay and sand. Overview of the effects of species identity, temperature regime and soil type on T_{50} and E_{max} . Bold values represent statistically significant differences.

	T_{50}			E_{max}		
	F	P	df	F	P	df
Species	43.21	<0.001	1/77	121.96	<0.001	1/77
Temperature	1632.62	<0.001	4/77	378.86	<0.001	4/77
Soil	4.08	0.047	1/77	417.73	<0.001	1/77
Spec × temp	15.11	<0.001	4/77	14.64	<0.001	4/77
Spec × soil	17.57	<0.001	1/77	298.69	<0.001	1/77
Temp × soil	3.16	0.019	4/77	10.79	<0.001	4/77
3-way	3.29	0.015	4/77	7.61	<0.001	4/77

tistically significant. Both T_{50} and E_{max} were affected by the 3-way interaction between species identity, temperature regime and soil type, by all 2-way interactions between these factors and by the main effects of these factors (Table 4).

Overall, E_{max} increased with temperature, was higher in sand than in clay and was on average higher for *P. australis* than for *T. latifolia* (Table 4, Fig. 2B). The interaction effects in E_{max} (Table 4) may be explained by the relatively low E_{max} of *T. latifolia* in clay, as compared to *T. latifolia* in sand and *P. australis* in both sand and clay. Moreover, *T. latifolia* in clay had the lowest E_{max} of all soil × species combinations, while *T. latifolia* in sand had the highest E_{max} . The time series where these results are based on are shown in Appendix B.

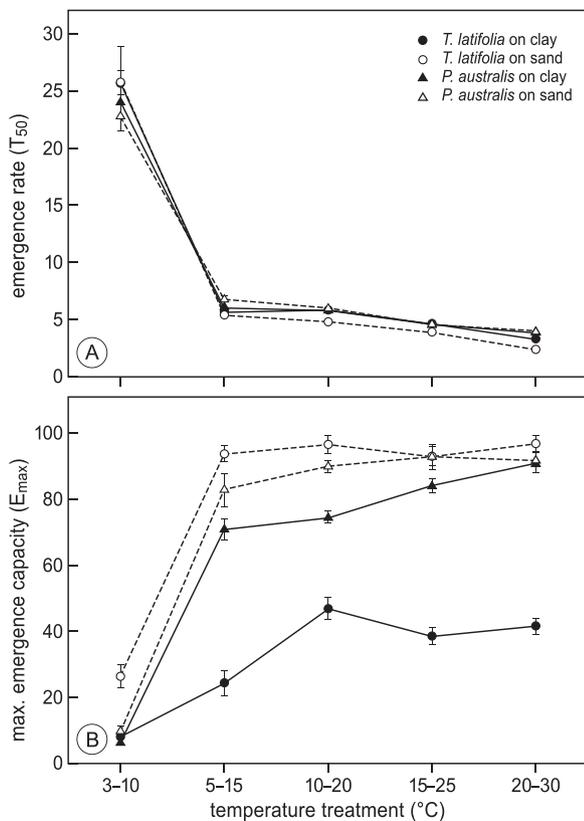


Fig. 2. Effect of temperature regime on A: emergence rate (T_{50}) and B: maximum emergence capacity (E_{max}). Comparison between *Typha latifolia* and *Phragmites australis* on clay and sand. Marks indicate means, error bars indicate \pm S.E. of the mean (n=5). Temperature regime is temperature (°C) during night and day (Table 1).

3.2. Effect of combined temperature and moisture conditions on seedling emergence and mortality

3.2.1. Five species on clay

All variables, i.e. T_{50} , E_{max} and percentage mortality, were affected by an interaction between species identity and combined temperature and moisture conditions, indicating that species responded differently to the droughts imposed by the evaporation moisture treatments (Table 5). For all species T_{50} decreased with increasing temperature and evaporation surplus, indicating that under drier and warmer conditions, species emerged faster (Fig. 3A). *Senecio congestus* emerged faster under very wet & cold and cool & wet conditions than the other four species (Fig. 3A). All species showed an optimum E_{max} at the two intermediate moisture treatments (Fig. 3B). *Senecio congestus* and *T. latifolia* had their optimum at wet & cool conditions. For the other three species, the optimum was at dry & warm conditions. Moreover, under very wet & cold conditions all species had an extremely low maximum emergence capacity, only *S. congestus* was performing relatively well. Mortality was affected by moisture conditions. No seedlings died at the two wetter treatments, but under very dry & hot conditions a large number of the seedlings died (Fig. 3C). The time series on which these results are based are shown in Appendix C.

Watering frequency had a significant effect on T_{50} . Emergence was slower when there were longer periods of drought. An interaction between watering frequency and moisture conditions influenced mortality (Table 5). This indicated that mortality of seedlings increased when watering frequency was reduced, but only in the dry & warm and very dry & hot treatments.

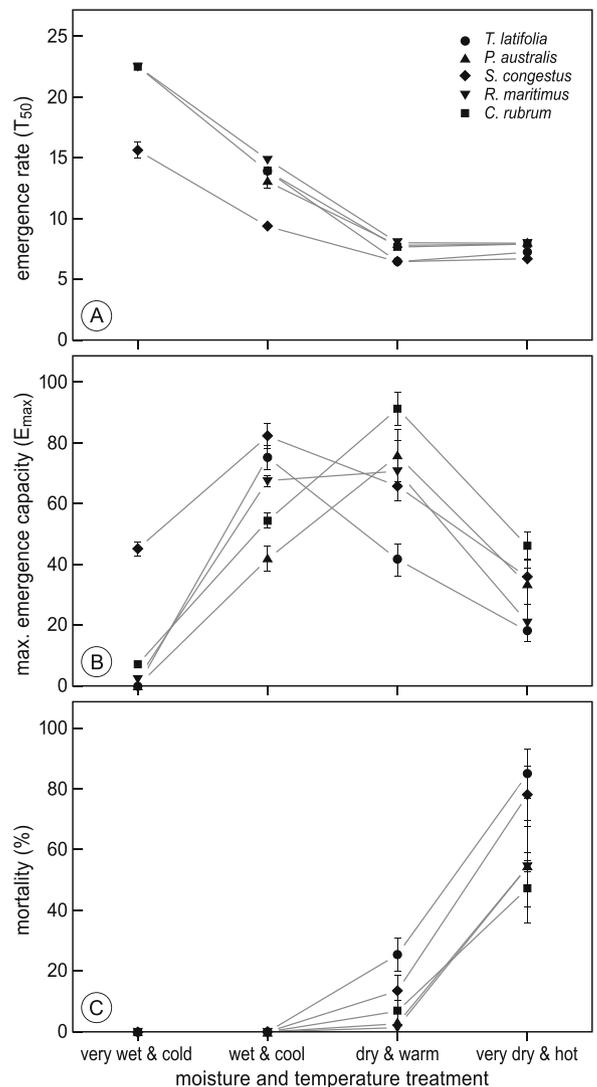


Fig. 3. Effect of moisture and temperature treatment on A: emergence rate (T_{50}), B: maximum emergence capacity (E_{max}), C: percentage mortality. Comparison between *Typha latifolia*, *Phragmites australis*, *Chenopodium rubrum*, *Rumex maritimus* and *Senecio congestus* on clay. Marks indicate means, error bars indicate \pm S.E. of the mean (n=6). Moisture and temperature treatments are described in Table 1.

3.2.2. Two species on sand and clay

Combined temperature and moisture regime affected T_{50} (Table 6). Soil type did not affect T_{50} and T_{50} did not differ significantly between the two species (Table 6). For *T. latifolia* and *P. australis*, both in sand and clay, emergence was faster under very dry & warm conditions than under wet & cool conditions (Fig. 4A). Moisture affected E_{max} of both species (Table 6) and E_{max} was optimal at the intermediate moisture regime (Fig. 4B). Various 2- and 3-way interactions between species identity, moisture regime and soil type affected E_{max} (Table 6). This indicated that the two species responded differently and that the effect of moisture treatment depended on soil type. Under wet & cool conditions, E_{max} of *T. latifolia* was higher than of *P. australis*. In contrast, at the two drier and warmer treatments *P. australis* had a higher E_{max} than *T. latifolia*. In sandy soil both *P. australis* and *T. latifolia* emerged less than in clay soil (Fig. 4B), thus E_{max} was affected strongly by soil type. Mortality was affected by moisture and soil type (Table 6), and was highest under very dry & warm conditions and on sandy soil (Fig. 4C). Mortality, however, was low as only a few seedlings died within 30 days. The time series on which these results are based are shown in Appendix D.

Table 5
Five species on clay. Overview of the effects of species identity, moisture conditions and watering frequency on T_{50} , E_{max} and percentage survival. Bold values represent statistically significant differences.

	T_{50}			E_{max}			Percentage mortality		
	F	P	df	F	P	df	F	P	df
Species	48.97	<0.001	4/53	10.79	<0.001	4/63	10.75	<0.001	4
Moisture	740.56	<0.001	3/53	37.46	<0.001	3/63	121.96	<0.001	3
Frequency	4.02	0.024	2/53	2.05	0.137	2/63	14.10	<0.001	2
Spec × moist	5.23	<0.001	10/53	3.00	0.003	11/63	6.46	<0.001	10
Spec × freq	1.92	0.076	8/53	0.20	0.991	8/63	3.98	0.001	8
Moist × freq	1.56	0.176	6/53	0.81	0.566	6/63	4.36	<0.001	6
3-way	0.72	0.783	20/53	0.13	0.999	22/63	3.13	<0.001	20

Table 6
Two species on clay and sand. Overview of the effects of species identity, moisture conditions and soil type on T_{50} , E_{max} and percentage survival. Bold values represent statistically significant differences.

	T_{50}			E_{max}			Percentage mortality		
	F	P	df	F	P	df	F	P	df
Species	0.02	0.887	1/30	4.38	0.042	1/48	2.34	0.132	1
Moisture	17.59	<0.001	2/30	35.67	<0.001	2/48	5.33	0.008	2
Soil	0.96	0.336	1/30	177.99	<0.001	1/48	14.14	<0.001	1
Spec × moist	0.45	0.640	2/30	20.00	<0.001	2/48	1.25	0.295	2
Spec × soil	0.04	0.838	1/30	1.54	0.220	1/48	0.48	0.494	1
Moist × soil	0.13	0.876	2/30	18.47	<0.001	2/48	4.34	0.018	2
3-way	NA	NA	NA	6.31	0.004	2/48	0.33	0.723	2

3.3. Effect of previous treatment on secondary seedling emergence

When the mesocosms with clay and sand were kept wet and warm after the end of the previous moisture experiments, in all cases less than 100% of the potential viable seeds had emerged (Fig. 5A and B). Secondary seedling emergence of *T. latifolia* and *P. australis* decreased with increasing temperature and drought during the previous treatment (Fig. 5A and B). *Senecio congestus* and *R. maritimus* had an optimum when the previous conditions were wet & cool (Fig. 5A). Secondary seedling emergence of *C. rubrum* increased as temperature and drought during the previous treatment increased (Fig. 5A). In both the five-species experiment on clay and the two-species experiment on sand or clay, the effect of the previous treatment was statistically significant (Table 7). In the five-species experiment on clay, the various species responded differently to the previous moisture treatment, as the interaction between species and treatment shows (Table 7A). In the two-species experiment on sand or clay the two species did not show such a difference (Table 7B). Secondary seedling emergence was lower from clay than from sand for both *T. latifolia* and *P. australis* (Fig. 5B and Table 7B).

4. Discussion

In this paper we determined the responses of a number of potentially dominant riparian plant species to temperature, combined temperature and moisture conditions, and soil type. For all experiments we found strong interactions between the response to environmental conditions (i.e., temperature, moisture regimes and soil type) and species identity. This indicates that responses of species to changes in these environmental conditions were highly species specific. In line with our first hypothesis, *T. latifolia* and *S. congestus* preferred wet or very wet conditions, *C. rubrum* and *R. maritimus* preferred dry to very dry conditions. *Phragmites australis* was able to establish under all conditions. In line with our second hypothesis, *S. congestus*, as well as *R. maritimus* and *C. rubrum* benefitted from secondary seedling emergence when, after a very dry

period, the weather became very wet again, while *T. latifolia* and *P. australis* remained absent. *Senecio congestus* emerged better under very wet & cold conditions than the other species. Under wet & cool conditions all species did well. Under the two driest conditions, *C. rubrum* emerged and survived better and *T. latifolia* worse than the other species.

These results show that the composition of riparian plant communities can be influenced by specific settings of the environmental conditions during the phase of seedling emergence and establishment and therefore also during the restoration process. This applies to the re-establishment of riparian vegetation on the large areas of bare soil during the drawdown of lakes, on river floodplains after winter flooding, or on new build gently sloped banks (Coops and Hesper, 2002; Nijhof, 2002; Boedeltje et al., 2003a). Our results also apply to established riparian stands, where species richness depends on the creation and recolonization of open soil in gaps (Lenssen et al., 1999; Vogt et al., 2007; Kotowski et al., 2010). Our results are in line with older (Weiher and Keddy, 1995) and more recent studies (Engels et al., 2011), where species-specific responses during early establishment explain variation in community composition.

4.1. Effect of temperature on seedling emergence

The effect of temperature on emergence rate (T_{50}) and maximum seedling emergence (E_{max}) differed per species. For example, when temperature was low *S. congestus* was the fastest and *T. latifolia* the slowest. However, rate differences between these two species were reversed at high temperature. Differences in T_{50} between species varied between several hours and 13 days. Small differences in emergence rate can affect the relative abundance of the species in the seedling community during the first few weeks after drawdown. An advantage of one week can enable one species to outcompete another (Grace, 1987). Temperature regime differences during germination are an important factor determining the final assemblage of restored wetland vegetation (Ross and Harper, 1972; Van der Valk and Welling, 1988; Stockey and Hunt, 1994). Under high temperature *C. rubrum*, *S. congestus* and *P. australis*

Table 7

Overview of the effects of species identity, moisture conditions, watering frequency and soil type on secondary seedling emergence. Bold values represent statistically significant differences.

A: five species on clay				B: two species on clay and sand			
	F	P	Df		F	P	Df
Species	1.24	0.305	4/56	Species	0.67	0.417	1/48
Moisture	20.20	<0.001	3/56	Moisture	14.12	<0.001	2/48
Frequency	0.37	0.693	2/56	Soil	46.43	<0.001	1/48
Spec × moist	7.91	<0.001	12/56	Spec × moist	0.53	0.592	2/48
Spec × freq	1.38	0.225	8/56	Spec × Soil	1.39	0.245	1/48
Mois × freq	0.94	0.472	6/56	Moist × Soil	1.26	0.294	2/48
3-way	2.20	0.008	24/56	3-way	2.41	0.101	2/48

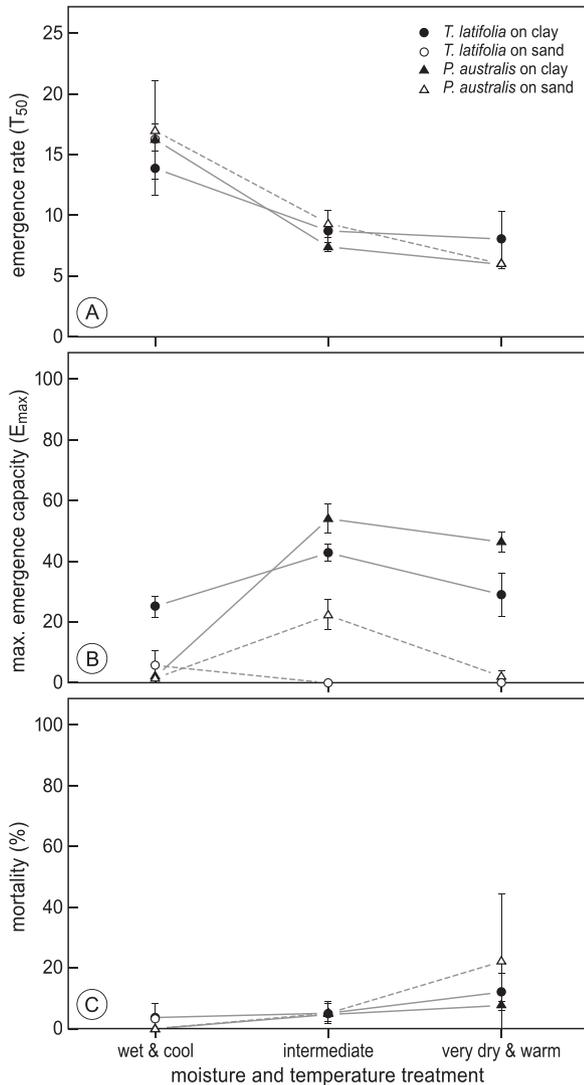


Fig. 4. Effect of moisture and temperature treatment and soil type on A: emergence rate (T_{50}), B: maximum emergence capacity (E_{max}), C: percentage mortality. Comparison between *Typha latifolia* and *Phragmites australis* on clay and sand. Marks indicate means, error bars indicate \pm S.E. of the mean ($n=5$). Missing values for T_{50} and mortality appear when no seedlings emerged. Moisture and temperature treatments are described in Table 1.

showed a lower E_{max} than under lower temperature, while *R. maritimus* and *T. latifolia* did not. High temperature may have induced secondary physiological dormancy in part of the seeds (Baskin and Baskin, 1988; Baskin et al., 1989) and apparently species differ in this regard.

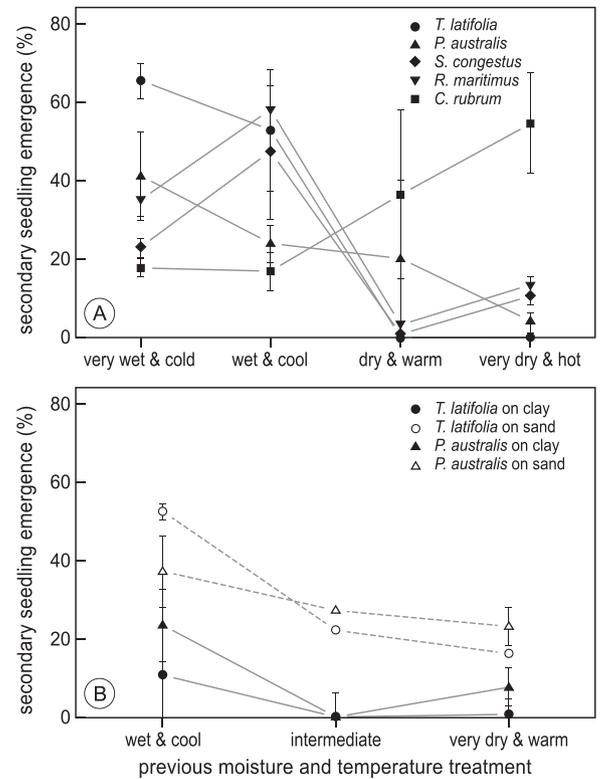


Fig. 5. Effect of previous moisture and temperature treatments on secondary seedling emergence (%). A: *Typha latifolia*, *Phragmites australis*, *Chenopodium rubrum*, *Rumex maritimus* and *Senecio congestus* on clay ($n=6$). B: *Typha latifolia* and *Phragmites australis* on clay and sand ($n=5$). Marks indicate means, error bars indicate \pm S.E. of the mean. Previous moisture and temperature treatments are described in Table 1.

4.2. Effect of combined moisture and temperature conditions on seedling emergence and mortality

The combination of temperature and moisture conditions affected T_{50} , E_{max} and mortality and this response differed per species. Very wet & cold conditions may be unfavorable for seedling emergence, due to the low emergence rate at low temperature (see Section 4.1) and the lack of gas exchange in waterlogged soil as shown by Baskin and Baskin (2001). Seeds might have germinated, but died before they emerged, though this is uncommon (Jensen, 2004). During a very wet & cold period seeds or seedlings could have died from fungus infections (Schafer and Kotanen, 2003). Very dry and hot conditions will be unfavorable when the soil dries out too fast, as most wetland species need wet or even waterlogged soils to germinate (Ter Heerdt et al., 1999).

After one month, the proportion between the numbers of species seedlings differed between treatments. We expect that

these differences will result in the establishment of different plant communities. For example, after a drawdown under very wet & cold or a wet & cool conditions *S. congestus* will be the dominant species. After a drawdown during a dry & warm or a very dry & hot period *C. rubrum* will be the most abundant species, while *T. latifolia* and *P. australis* perform best under intermediate conditions. Such differences are in line with the observations in the Oostvaardersplassen (Ter Heerdt and Drost, 1994) and in a North American marsh (Harris and Marshall, 1963). Other studies show that decreasing soil moisture resulted in an increase of the relative density of terrestrial annuals, such as *C. rubrum* and a decrease of reeds, such as *T. latifolia* (Welling et al., 1988; Van der Valk and Pederson, 1989; Evans and Etherington, 1990; Van der Valk et al., 1992).

4.3. Effect of soil type on seedling emergence and mortality

When the soil was allowed to dry, fewer seedlings emerged in sand than in clay. *Typha latifolia* hardly emerged at all in sand. Sandy soils in our experiments contained less water than clay soils and may, therefore, become too dry before watering events. When clay dries out, its porosity decreases irreversibly (Dent et al., 1976; Hazelden and Boorman, 2001). This decreases gaseous exchange and oxygen concentrations and increases soil water potential, which inhibits the germination of seeds (Baskin and Baskin, 2001). Under warm & wet conditions, increased microbial oxygen consumption might decrease oxygen even further. In the five-species experiments all species emerged well in clay, while that was not the case in the two-species experiments. An important difference between these two sets of experiments could be that in the five-species experiments a relatively large volume of coarse detritus substrate was present, and not in the two-species experiments. The presence of detritus might have increased gas exchange and lowered soil water potential, thus enhancing seedling emergence.

4.4. Secondary seedling emergence

Seeds that did not emerge as a result of unfavorable conditions might have become physiologically dormant but might also have lost their viability, as they did not emerge when condition become favorable later. For all species, secondary seedling emergence did not compensate for former low emergence rates as primary and secondary emergence together never reached 100%. Secondary seedling emergence was affected by the temperature and moisture conditions and soil type during the previous month and this response differed per species. As a result, the proportion between the species in a second cohort of seedlings depended on the previous weather conditions. Again, we expect that this might result in different riparian communities after drawdowns under different weather conditions. For example, after very dry or dry periods *C. rubrum* can emerge in higher numbers than the other four species, while after very wet or wet periods *T. latifolia* will be more abundant. Drought and warmth can have induced secondary physiological dormancy of the seeds of all species, except in *C. rubrum*, as a strategy of wetland species to avoid emergence in summer with a high risk of drying out. Cold stratification may be needed to break this dormancy again. Other studies also show that cool and wet periods do not induce physiological dormancy (Baskin and Baskin, 1988; Baskin et al., 1989; Jensen, 2004). Secondary seedling emergence under warm & wet conditions was considerably lower in clay than in sand, probably because of the irreversible decrease of porosity when clay dries out (see Section 4.3).

4.5. Management implications

The results of the present study show that moisture conditions, temperature and soil type can contribute to the assembly

of different plant communities. These environmental conditions do not result in presence/absence, as suggested by Van der Valk (1981) and Keddy (1992), but determine the proportion of the species during the early stages of the establishment of a community. To apply the results of our study, we suggest that the species in wetland soils belong to different functional groups which have different responses to temperature, moisture and soil type (Lavorel and Garnier, 2002). Boutin and Keddy (1993) classified wetland species in seven groups: ruderals (obligate or facultative annuals), interstitials (reed, perennial clonal and tussock species) and matrix species (perennial clonal dominants or stress-tolerators). *Chenopodium rubrum* is an obligate annual, *R. maritimus* and *S. congestus* are facultative annuals/biannuals and *T. latifolia* and *P. australis* are perennial reeds. The response to temperature and moisture conditions of representative species of each of these groups can be tested. These groups could be subdivided; using Ellenberg (Ellenberg and Leuschner, 1996) soil moisture values (F). For example; both *C. rubrum* as *R. maritimus* are ruderals, but have different soil moisture values (F=6 and F=9, respectively), which is in line with our study were *C. rubrum* is the more drought tolerant species.

When the establishment requirements regarding temperature and moisture of the functional groups present in the soil seed bank are known, weather conditions can be used to predict which community will establish where and when. During a very wet or wet period probably all species will emerge, but at the end of the growing season the reeds *T. latifolia* or *P. australis* will dominate, as the cover and height of its individuals are much larger compared to the other species (Ter Heerdt and Drost, 1994; Kleyer et al., 2008). During a dry or very dry period reeds will not emerge well, leaving space for drought tolerant annuals and biannuals. This will be especially the case on sandy soils. In the Netherlands both very wet and very dry months occur frequently from March to August/September. Therefore, one can expect a variety of riparian communities, annuals/biannuals as well as reeds, to establish during a drawdown in this period. In August and September summer showers will create more warm and wet conditions and the establishment of reeds is more likely than earlier in the season. A fast or short drawdown creates the risk that the moisture conditions will be unfavorable for the desired groups; too wet for annuals that prefer dry conditions or too dry for reeds and annuals that prefer wet conditions. Therefore we recommend a slow and gradual drawdown from March to September. Lowering the water table gradually also will keep the moisture conditions higher in the fresh exposed zone. This applies in particular in areas with sandy soils, which dry out faster, resulting in a lower seedling emergence.

Once the topsoil is dried out, re-wetting may not be sufficient to start the emergence of most wetland species again. Bringing up deeper layers, that remained moist with non-dormant seed banks, will then enhance the restoration process. Repeating the drawdown for several years, with flooded conditions during winter is another option. During winter, waves and currents will supply the area with fresh sediment and seeds.

When gently sloped banks are built, reeds are supposed to protect these banks against erosion. As shown in our study reeds establish hardly on sand under dry conditions, which leaves the bank unprotected. Therefore we suggest covering new created banks with a layer of clay, as common practice when dikes or embankments are built.

5. Contributors

GtH and JPB designed experiments, GtH carried out experiments, GtH and GFV analyzed the data and all contributed to writing of ms. All authors have approved the final article.

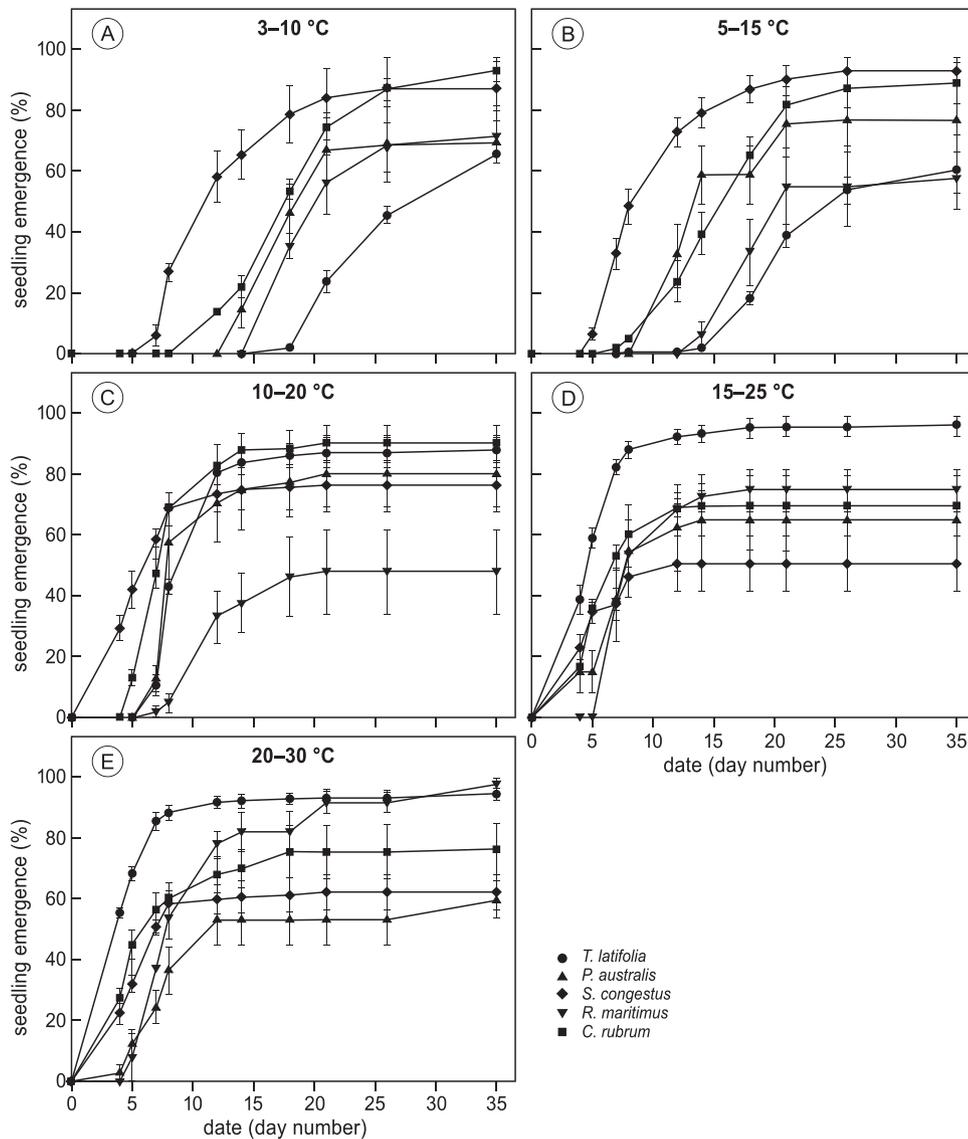
Acknowledgements

This project was commissioned by the former Ministry of Transport, Public Works and Water Management and funded by the Dr.ir. Cornelis Lely Foundation. We wish to thank H.J. Drost for initiating

this study and A. Schutter, S. Nijdam, J.J. Hogendorf, M. Zijlstra and G.L. Verweij for technical assistance.

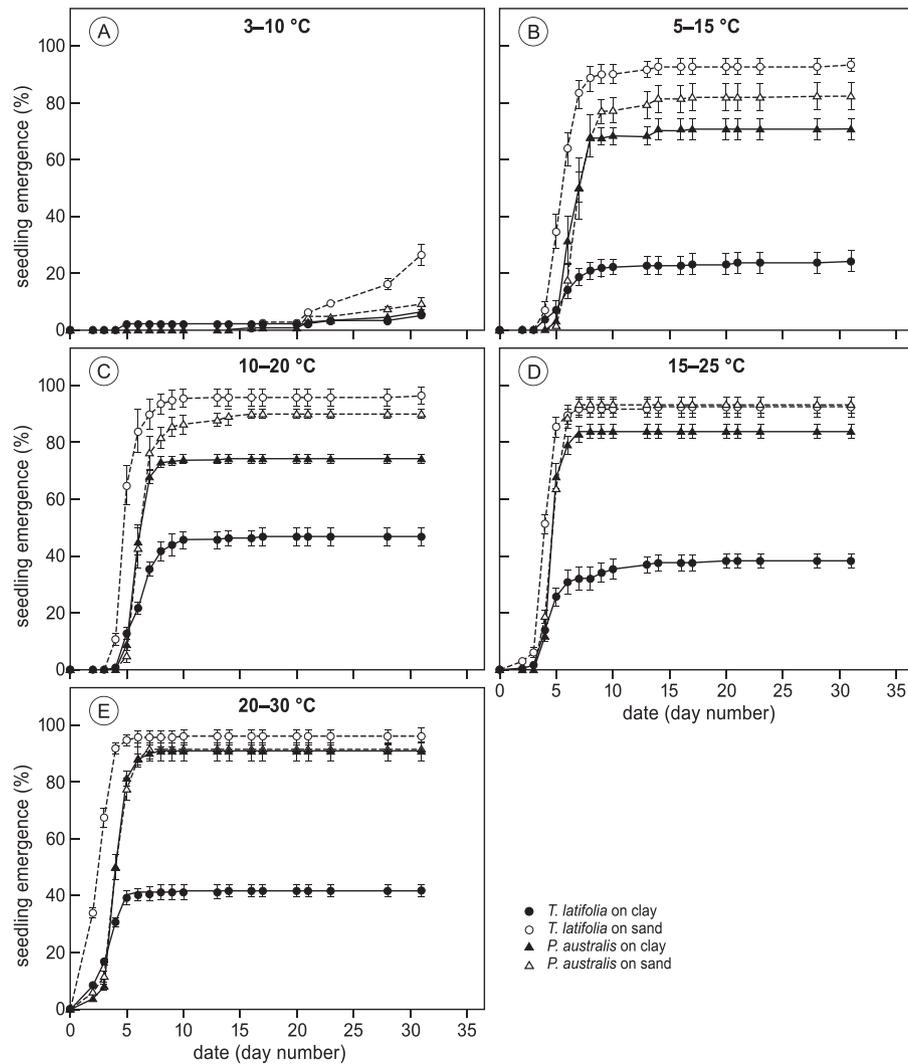
Appendix A.

Time series corresponding to Fig. 1. Effect of temperature regimes on seedling emergence. Night-day temperatures: A: 3–10, B: 5–15, C: 10–20, D: 15–25, E: 20–30 °C (Table 1). Comparison between *Typha latifolia*, *Phragmites australis*, *Chenopodium rubrum*, *Rumex maritimus* and *Senecio congestus* on clay. Marks indicate means, error bars indicate \pm S.E. of the mean ($n = 5$).



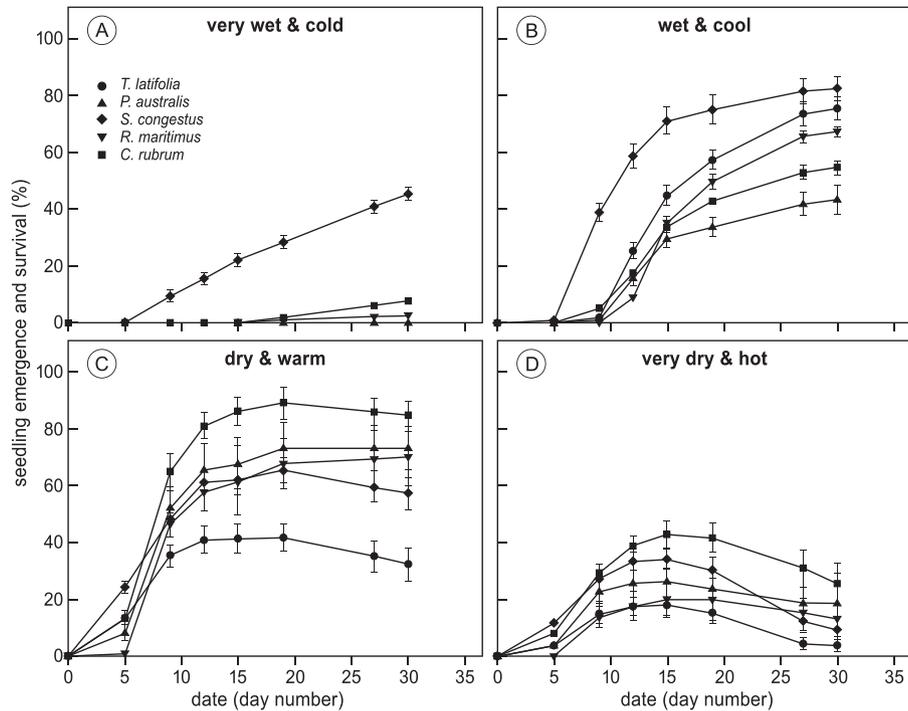
Appendix B.

Time series corresponding to Fig. 2. Effect of temperature regimes on seedling emergence. Night-day temperatures: A: 3–10, B: 5–15, C: 10–20, D: 15–25, E: 20–30 °C (Table 1). Comparison between *Typha latifolia* and *Phragmites australis* on clay and sand. Marks indicate means, error bars indicate \pm S.E. of the mean ($n = 5$).



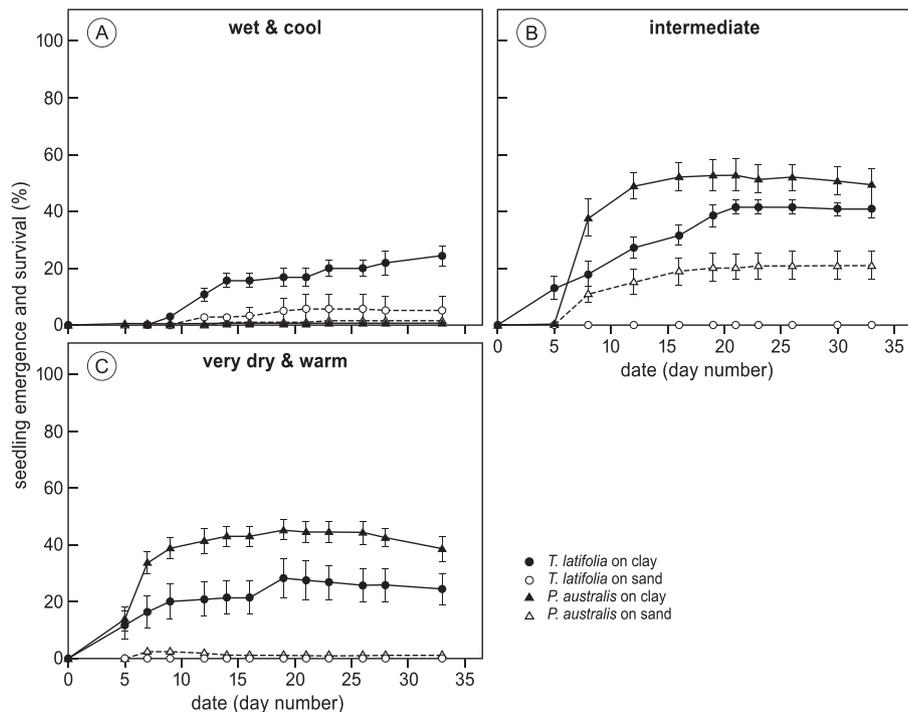
Appendix C.

Time series corresponding to Fig. 3. Effect of temperature and moisture treatment on seedling emergence and survival. Treatments: A: very wet & cold, B: wet & cool, C: dry & warm, D: very dry & hot. Comparison between *Typha latifolia*, *Phragmites australis*, *Chenopodium rubrum*, *Rumex maritimus* and *Senecio congestus* on clay. Marks indicate means, error bars indicate \pm S.E. of the mean ($n=5$). Moisture and temperature treatments are described in Table 1.



Appendix D.

Time series corresponding to Fig. 4. Effect of temperature and moisture treatment on seedling emergence and survival. Treatments: A: wet & cool, B: intermediate, C: very dry & warm. Comparison between *Typha latifolia* and *Phragmites australis*, on clay and sand. Marks indicate means, error bars indicate \pm S.E. of the mean ($n=5$). Moisture and temperature treatments are described in Table 1.



References

- Abrahams, C., 2006. Sustainable Shorelines: the management and revegetation of drawdown zones. *J. Pract. Ecol. Conserv.* 6, 37–51.
- Baskin, C.C., Baskin, J.M., 1988. Germination ecophysiology of herbaceous plant species in a temperate region. *Am. J. Bot.* 75, 286–305.
- Baskin, C.C., Baskin, J.M., 2001. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, London.
- Baskin, J.M., Baskin, C.C., Spooner, D.M., 1989. Role of temperature, light, and date seeds were exhumated from soil on germination of four wetland perennials. *Aquat. Bot.* 35, 387–394.
- Beemster, N., Troost, E., Platteeuw, M., 2010. Early Successional Stages of Reed *Phragmites Australis* Vegetations and Its Importance for the Bearded Reedling *Parus Biarmicus* in Oostvaardersplassen. 98. *Ardea*, The Netherlands, pp. 339–354.
- Boedeltje, G., Bakker, J.P., Ter Heerdt, G.N.J., 2003a. Potential role of propagule banks in the development of aquatic vegetation in backwaters along navigation canals. *Aquat. Bot.* 77, 53–69.
- Boedeltje, G., Bakker, J.P., Bekker, R., Van Groenendael, J.M., Soesbergen, M., 2003b. Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. *J. Ecol.* 91, 855–866.
- Boutin, C., Keddy, P.A., 1993. A functional classification of wetland plants. *J. Veg. Sci.* 4, 591–600.
- Brown, S.C., 1998. Remnant seed banks and vegetation as predictors of restored marsh vegetation. *Can. J. Bot.* 76, 620–629.
- Clevering, O.A., Van Gulik, W.M.G., 1997. Restoration of *Scirpus lacustris* and *Scirpus maritimus* stands in a former tidal area. *Aquat. Bot.* 55, 229–246.
- Coops, H., Hosper, S.H., 2002. Water-level management as a tool for the restoration of shallow lakes in the Netherlands. *Lake Reserv. Manage.* 18, 293–298.
- Coops, H., Geilen, N., Van der Velde, G., 1999. Helophyte zonation in two regulated estuarine areas in the Netherlands: vegetation analysis and relationships with hydrological factors. *Estuaries* 22, 657–668.
- Coops, H., Vulink, J.Th., Van Nes, E.H., 2004. Managed water levels and the expansion of emergent vegetation along a lakeshore. *Limnologia* 34, 57–64.
- Dent, D.L., Downing, E.J.B., Rogaar, H., 1976. Changes in the structure of marsh soils following drainage and arable cultivation. *J. Soil Sci.* 27, 250–265.
- Ellenberg, H., Leuschner, C., 1996. *Vegetation Mitteleuropas Met Den Alpen*. Ulmer, Stuttgart.
- Engels, J.G., Rink, F., Jensen, K., 2011. Stress tolerance and biotic interactions determine plant zonation patterns in estuarine marshes during seedling emergence and early establishment. *J. Ecol.* 99, 277–287.
- Evans, C.E., Etherington, J.R., 1990. The effect of soil water potential on seed germination of some British plants. *New Phytol.* 115, 539–548.
- Everaert, G., Pauwels, I.S., Boets, P., Verduin, E., De la Haye, M.A.A., Blom, C., Goethals, P.L.M., 2013. Model-based evaluation of ecological bank design and management in the scope of the European Water Framework Directive. *Ecol. Eng.* 53, 144–152.
- Galinato, M.I., Van der Valk, A.G., 1986. Seed germination traits of annuals and emergents recruited during drawdowns in the Delta Mars, Manitoba, Canada. *Aquat. Bot.* 26, 89–102.
- Gleason, R.A., Euliss, N.H., Hubbard, D.E., Duffy, W.G., 2003. Effects of sediment load on emergence of aquatic invertebrates and plants from wetland soil egg and seed banks. *Wetlands* 23, 26–34.
- Grace, J.B., 1987. The impact of preemption on the zonation of two *Typha* species along lakeshores. *Ecol. Monogr.* 47, 283–303.
- Grime, J.P., Mason, G., Curtis, A.V., Rodman, J., Band, D.R., Mowforth, M.A.G., Neal, A.M.S.S., 1981. A comparative study of germination characteristics in a local flora. *J. Ecol.* 69, 1017–1059.
- Harris, S.W., Marshall, W.H., 1963. Ecology of water-level manipulations on a northern marsh. *Ecology* 44, 331–343.
- Hazelden, J., Boorman, L.A., 2001. Soils and 'managed retreat' in South East England. *Soil Use Manage.* 17, 150–154.
- Hopfenperger, K.N., 2007. A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos* 116, 1438–1448.
- Jensen, K., 2004. Dormancy patterns, germination ecology, and seed-bank types of twenty temperate fen grassland species. *Wetlands* 24, 152–166.
- Joosen, R.V.L., Kodde, L., Willems, L.A.J., Ligterink, W., Van der Plas, L.H.W., Hilhorst, H.W.M., 2010. GERMINATOR: a software package for high-throughput scoring and curve fitting of *Arabidopsis* seed germination. *Plant J.* 62, 148–159.
- Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* 5, 157–164.
- Keddy, P.A., 1999. Wetland restoration: the potential for assembly rules in the service of conservation. *Wetlands* 19, 716–732.
- Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimes, L., Klimesova, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Gent, Beatrijs Bossuyt U., Dannemann, A., Endels, P., Goetzenberger, L., Hodgson, J.G., Jackel, A.-K., Kuehn, I., Kunzmann, D., Ozinga, W.A., Roemermaann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *J. Ecol.* 96, 1266–1274.
- Kotowski, W., Beauchard, O., Opdekamp, W., Meire, P., Van Diggelen, R., 2010. Waterlogging and canopy interact to control species recruitment in floodplains. *Funct. Ecol.* 24, 918–926.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556.
- Leck, M.A., Simpson, R.L., 1995. Ten-year seed bank and vegetation dynamics of a tidal freshwater marsh. *Am. J. Bot.* 82, 1547–1557.
- Lenssen, J., Menting, F., Van der Putten, W., Blom, K., 1999. Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. *Oikos* 86, 523–534.
- Nijhof, B.S.J., 2002. *Vegetation Succession in Floodplain Flats. Inventarisatie and Modelling of Measured Data and Expert Judgement*. Alterra, Green World Research, Wageningen.
- Ross, M.A., Harper, J.L., 1972. Occupation of biological space during seedling establishment. *J. Ecol.* 60, 77–88.
- Sarneel, J.M., Janssen, R.H., Rip, W.J., Bender, I.M.A., Bakker, E.S., 2014. Windows of opportunity for germination of riparian species after restoring water level fluctuations: a field experiment with controlled seed banks. *J. Appl. Ecol.* 51, 1006–1014.
- Schafer, M., Kotanen, P.M., 2003. The influence of soil moisture on losses of buried seeds to fungi. *Acta Oecol.* 24, 255–263.
- Soons, M., 2006. Wind dispersal in freshwater wetlands: knowledge for conservation and restoration. *J. Veg. Sci.* 9, 271–278.
- Stockey, A., Hunt, R., 1994. Predicting secondary succession in wetland mesocosms on the basis of autecological information on seeds and seedlings. *J. Appl. Ecol.* 31, 543–559.
- Stroh, P., Mountford, J.O., Hughes, F.M.R., 2012. The potential for endozoochorous dispersal of temperate fen plants species by free-roaming horses. *Appl. Veg. Sci.* 15, 359–368.
- Ten Berge, H.F.M., 1990. *Heath and Water Transfer in Bare Topsoil and the Lower Atmosphere*. PUDOC, Wageningen.
- Ter Heerdt, G.N.J., Drost, H.J., 1994. Potential for the development of marsh vegetation from the seed bank after a drawdown. *Biol. Conserv.* 67, 1–11.
- Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M., Bakker, J.P., 1996. An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. *Funct. Ecol.* 10, 144–151.
- Ter Heerdt, G.N.J., Schutter, A., Bakker, J.P., 1999. The effect of water supply on seed-bank analysis using the seedling-emergence method. *Funct. Ecol.* 13, 428–430.
- Van Leeuwen, C.H.A., Van der Velde, G., Van Groenendael, J.M., Klaassen, M., 2012. Gut travellers: internal dispersal of aquatic organisms by waterfowl. *J. Biogeogr.* 39, 2031–2040.
- Van der Valk, A.G., Pederson, R.L., 1989. Seed banks and the management and restoration of natural vegetation. In: Leck, M.A., Parler, V.T., Simpson, R.L. (Eds.), *Ecology of Soil Seed Banks*. Academic Press, San Diego, pp. 329–346.
- Van der Valk, A.G., Welling, C.H., 1988. The development of zonation in freshwater wetlands. An experimental approach. In: During, H.J., Werger, M.J.A., Willems, J.H. (Eds.), *Diversity and Pattern in Plant Communities*. SPB Academic Publishing, The Hague, The Netherlands, pp. 145–158.
- Van der Valk, A.G., Pederson, R.L., Davis, C.B., 1992. Restoration and creation of freshwater wetlands using seed banks. *Wetlands Ecol. Manage.* 1, 191–197.
- Van der Valk, A.G., 1981. Succession in wetlands: a Gleasonian approach. *Ecology* 62, 688–696.
- Van der Valk, A.G., 2005. Water-level fluctuations in North American prairie wetlands. *Hydrobiologia* 539, 171–188.
- Vogt, K., Rasran, L., Jensen, K., 2007. Seed deposition in drift lines: opportunity or hazard for species establishment? *Aquat. Bot.* 86, 385–392.
- Vulink, J.Th., Van Eerden, M., 1998. Hydrological conditions and herbivory as key operators for ecosystem development in Dutch artificial wetlands. In: Wallis de Vries, M.F., Bakker, J.P., Van Wieren, S.E. (Eds.), *Grazing and Conservation Management*. Kluwer Academic Publishers, Dordrecht, pp. 217–252.
- Wigbels, V.L., 1990. *Wetland Management in the Oostvaardersplassen*. Rijkswaterstaat Directie Flevoland, Lelystad.
- Weiber, E., Keddy, P.A., 1995. The assembly of experimental wetland plant communities. *Oikos* 73, 323–335.
- Welling, C.H., Pederson, R.L., Van der Valk, A.G., 1988. Temporal patterns in recruitment from the seed bank during drawdowns in a prairie wetland. *J. Appl. Ecol.* 25, 999–1007.