Summary
Introduction

Herbaceous riparian plant communities along lakes, rivers, channels and ditches such as reed beds, helophyte stands and mudflats with annuals and biennials, have high value for nature conservation. However, due to intensified land use during the past century, length of banks covered by riparian plant communities has decreased strongly. European legislation, notably the Water Framework Directive and Natura 2000, has been developed in order to demand that member states restore and maintain riparian plant communities. In the Netherlands, waterboards started the restoration of 4000-8000 km of riparian communities, involving methods such as water-level management and drawdowns, the construction of gently sloped banks, (re)creation of floodplain flats, and removal of vegetation and topsoil. These restoration measures have not always been successful, because riparian communities did not become established under every set of conditions. The cause of this failure often has remained unknown. Therefore, a better understanding is needed of how to optimize restoration measures, especially drawdown date and the design of gently sloped banks. This knowledge is also needed to anticipate climate change by adaptation or mitigation-oriented water management.

In this thesis I present a series of experiments that cover the establishment of riparian communities from the soil seed bank to the second year after a drawdown. As a case study I have used the artificial drawdown in the Oostvaardersplassen during 1987-1988. During this drawdown the expected large-scale establishment of a *Typha latifolia*-dominated community did not happen. Instead, several mudflat communities, dominated by *Chenopodium rubrum* and *Rumex maritimus*, or by *Senecio congestus*, covered large areas during the first year of drawdown. *Phragmites australis* established in 1987 and 1988, but its abundance remained low. There were indications that establishment of the various communities has been induced by different weather conditions, resulting in strongly different moisture and temperature conditions in the soil. Therefore, the experiments in this thesis simulated the moisture and temperature conditions during the drawdown in the Oostvaardersplassen.

First, I tested which species were present in the soil seed bank in the Oostvaardersplassen. This required a preliminary study to find a method that would reliably detect the occurring species and their numbers. Second, I tested seedling emergence and survival, growth and competition under various environmental conditions, on clay soil from the Oostvaardersplassen. I performed a similar series of experiments on two other, common used, soil types; clay from former agricultural fields and pleistocene sand from quarries. Using the results of these experiments, I simulated the establishment of riparian communities in the Oostvaardersplassen and compared those with the observed communities during the Oostvaardersplassen drawdown. Finally, I used the results of these studies to determine the effect of drawdown date on the probability that various riparian communities will establish under present climate and after climate change.
An improved method to determine the composition of a soil seed bank

Two categories of methods to determine the composition of the soil seed bank are available. Seed separation methods use sieving, washing, flotation, or hand sorting to separate seeds from the soil. Such methods have the disadvantage that small seeds are easily missed and that they are very laborious and only suitable to process small amounts of soil. This might result in an underestimation of the number of species and individuals. Using seedling emergence methods, soil is spread in a greenhouse and emerging seedlings are counted. Large volumes of soil can be processed and therefore, I used a seedling emergence method. However, seeds that are buried deeper in the soil may not germinate and emerge. Moreover, greenhouse conditions are not always suitable for the emergence of all species. To avoid an underestimation of the seed bank composition, I had to improve the seedling emergence method to assure high percentage germination. The most important improvement was that I washed the soil samples with water on a fine sieve, removing all fine material (chapter 2). The remaining concentrate was spread in pots in a layer of 3–5 mm and kept wet by placing the pots in containers with water to 4 cm below soil level. Temperatures fluctuated between 15°C at night and 25°C during day. To test the effectiveness of this method, a series of subsamples was not concentrated and parts of all samples were hand-sorted afterwards. After concentrating, 0 – 9% of the seeds remained ungerminated in the samples, but without concentrating 12 – 67% of the seeds was lost. After concentrating, 95% of the seedlings emerged within six weeks. This method was successful in determining seed banks in clay, peaty and sandy soils. Low percentage emergence in unconcentrated samples in a 3–5 mm layer indicated that most seeds buried deeper than 4 mm did not germinate.

In another series of experiments I tested the effect of water supply on the results of the improved method (chapter 3). This preliminary study was used to find the best method for a large-scale seed bank study in a dune slack, where soil-moisture conditions varied from waterlogged in spring to much drier in summer. Therefore I compared seedling emergence from a waterlogged soil (water level to 2 cm below soil level) and from a moist soil (watered every day from above). Some species emerged best under waterlogged conditions and others under moist conditions. I chose an intermediate treatment for the large-scale study; a greenhouse with a low evaporation and watering very frequent; two or three times every day. This maximized the number of species found.

These experiments show that a “standard” method is not always the most suitable for seed bank studies. Before large-scale and costly seed bank studies are planned, a preliminary study is needed. When only seeds in the top layer are able to germinate, deeper soil samples may not necessary be collected in order to enhance estimate accuracy.
Potential for the development of riparian communities from the seed bank after a drawdown

In chapter 4 I made a first attempt to understand and predict which communities could establish from the soil seed bank in the Oostvaardersplassen, starting with a seed bank study. Two different areas in the Oostvaardersplassen were sampled separately; a shallow one with many islands covered by riparian vegetation (mixed area) and a deeper one without islands (lake area). The most abundant species in the soil seed banks of both areas were *Typha latifolia*, *Senecio congestus*, *Chenopodium rubrum*, and *Rumex maritimus*. Among the species present, *Phragmites australis* was rare. Composition of the communities that could establish from these seed banks after a drawdown was simulated by the number of seedlings emerging from a 4 mm soil layer and the estimated plant size at the end of the growing season. The simulation in the mixed area predicted a community dominated by *Typha latifolia* with *Senecio congestus* as codominant and 100% cover. However, observations showed that two communities established in this area. One dominated by *Typha latifolia*, and a second one dominated by *Senecio congestus*. In the lake area, *Typha latifolia* was predicted to become dominant with 100% cover. However, a community dominated by *Senecio congestus*, and another by *Chenopodium rubrum* and *Rumex maritimus* established instead. In the last three communities, total cover was considerably less than 100%, indicating that not all seeds germinated, seedlings died, or that the plants did not grow as large as expected. The differences between the predicted and observed communities show that the predictions had to be improved. Events during the Oostvaardersplassen drawdown indicate that environmental conditions during the drawdown thereby should be taken into account. Establishment of each community took place under different weather conditions. The *Typha latifolia*-dominated community established during a very wet period, when mean evaporation surplus (or precipitation deficit) was 0 mm/day and the intervals between rainy periods were 2–3 days. The community that was dominated by *Chenopodium rubrum* and *Rumex maritimus* established during a very dry period, when mean evaporation surplus was 1.70 mm/day and the intervals between rainy periods were up to two weeks. *Senecio congestus* became dominant when, after a very dry period, the weather became very wet again. Together with the low percentage cover, this implies that differential emergence, survival and growth of the species under different moisture conditions could be the reason for the development of different communities.

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

In chapter 5 I present a series of experiments on emergence and mortality of riparian species under various moisture and temperature conditions. I used conditions that were
comparable with those during the drawdown in the Oostvaardersplassen. First I performed two experiments in Petri dishes to germinate and emerge seeds from a layer of soil under different temperature conditions. Moisture conditions were the same for all treatments: very wet. These experiments revealed that species responded in a species-specific way to various temperatures. Typha latifolia preferred warm conditions, Senecio congestus cooler conditions, and the other species showed less clear responses. Second, I grew species for a month using soil in 12 liter mesocosms, now testing the combined effects of moisture and temperature. Again, under cold & wet conditions, Senecio congestus was the best-performing species. Under very dry & hot conditions Typha latifolia emerged in lowest numbers and most seedlings died. Chenopodium rubrum, on the other hand, emerged better than all other species under very dry & hot conditions, and a lower proportion of its seedlings died. Some species showed an optimum under wet & cool conditions, others under dry & warm conditions. Phragmites australis was more drought tolerant than Typha latifolia. From sandy soil fewer seedlings emerged and survived than from clay soil, especially under very dry conditions when hardly any seedlings emerged and survived.

The previous experiment suggested that not all seeds germinated during the first month, and could remain viable in the soil. I tested if a second cohort of seedling would emerge under optimal -wet & warm- conditions during the following month. Indeed, a second cohort of seedlings appeared. The composition of this cohort, in relation to the amount of seeds that might have been left, depended on the previous treatments. After very wet & cold or wet & cool conditions, seedling emergence of Typha latifolia was highest and of Chenopodium rubrum lowest. After dry & warm or very dry & hot conditions, hardly any seedlings of Typha latifolia, Senecio congestus and Rumex maritimus emerged, while Chenopodium rubrum emerged in high numbers. From sandy soils a larger proportion of the remaining seeds emerged than from clay soils. Low percentage emergence of remaining seeds during these experiments indicated that part of the seeds may have become dormant.

The effect of moisture conditions and soil type on growth and competition of riparian plant species

The effect of various moisture conditions on growth and competition was tested in a series of experiments in mesocosms with 290 liter of clay from Oostvaardersplassen (Box 1). Seedlings were planted in April and grew during 11 weeks under four different moisture conditions; very wet, wet, dry and very dry. In August the soil was rewetted, as occurred during the Oostvaardersplassen drawdown. Plants were harvested in September. The yield of the different species in monoculture depended largely on moisture conditions, and this effect differed strongly among species. After very wet conditions yield of Typha latifolia was highest, yield of Chenopodium rubrum was lowest, while the
other species yielded in between. After dry or very dry conditions, yield of *Chenopodium rubrum* was highest and yield of *Senecio congestus* and *Rumex maritimus* lowest. I also grew species pairwise together to test the effect of competition. The same effects of moisture conditions were recorded. In mixed cultures, the species that was larger in monoculture grew even larger and suppressed the smaller species. As moisture conditions determined plant size, it also determined the outcome of competition.

The effect of soil type in combination with moisture conditions was tested by growing *Typha latifolia* and *Phragmites australis* on both clay from a former agricultural field and pleistocene sand from a quarry. In monoculture both species responded negatively to decreasing moisture condition, but *Phragmites australis* did not do so when the two species grew together, both on clay and sand. The yield on sand was substantially lower than on clay. On both soil types *Phragmites australis* was the strongest competitor under dry and very dry conditions.

**Simulations of the Oostvaardersplassen drawdown and drawdowns under current and future climate scenarios**

The experiments in this thesis showed that differences in soil moisture, temperature and soil type during a drawdown can result in a strong shift of species abundance. Based on these results, I defined a series of community assembly rules that determine the establishment of riparian communities (**chapter 6**):

1. Dispersal, including the soil seed bank, in riparian zones generally is not a limiting factor for the establishment of riparian communities (**chapter 4**).
2. Only seeds in the upper 4 mm of the soil will emerge and contribute to the riparian community (**chapter 2**).
3. When temperatures are between 3–10°C (night and day, respectively) seedling emergence rate is slow and species specific. Under higher temperatures species emerge fast and differences between species responses are small (**chapter 5**).
4. Seedling emergence and survival depends strongly on moisture conditions and soil type and this dependency is highly species specific (**chapter 5**).
5. Once the soil has dried out, seedling emergence of the soil when rewetted is highly species specific (**chapter 5**).
6. Adult growth depends strongly on moisture conditions and soil type, and this dependency is highly species specific (**Box 1**).
7. The effect of competition depends on the relative size of the competing species in monoculture, and therefore on species-specific response to moisture conditions and soil type (**Box 1**).
Species responses to moisture and temperature conditions as determined in chapter 4 and Box 1 are summarized as species preferences during seedling emergence (first month after drawdown) and adult growth (month 2–3.5) in Table 1.

**Table 1** Moisture and temperature preferences of the species studied during seedling emergence (first month after drawdown) and adult growth.

<table>
<thead>
<tr>
<th>Seedling emergence</th>
<th>Growth</th>
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<tbody>
<tr>
<td><em>Typha latifolia</em></td>
<td>wet &amp; cool</td>
</tr>
<tr>
<td><em>Senecio congestus</em></td>
<td>wet &amp; cool</td>
</tr>
<tr>
<td><em>Rumex maritimus</em></td>
<td>wet &amp; cool / dry &amp; warm</td>
</tr>
<tr>
<td><em>Phragmites australis</em></td>
<td>dry &amp; warm</td>
</tr>
<tr>
<td><em>Chenopodium rubrum</em></td>
<td>dry &amp; warm</td>
</tr>
</tbody>
</table>

Conditions, expressed as evaporation surplus and temperature: wet & cool: 0–0.86 mm/dag, 10–20°C; dry & warm: 0.86–1.43 mm/dag, 20–30°C; very wet: <0 mm/dag; wet: 0–0.96 mm/dag; dry: 0.86–1.43 mm/dag.

With these rules, together with the composition of the soil seed bank and the responses of the various species to environmental conditions, I simulated which communities might establish during the drawdown in the Oostvaardersplassen. The simulation predicted that various moisture and temperature conditions would result in the establishment of different communities. These predictions matched well with the communities that actually established during the Oostvaardersplassen drawdown; a *Typha latifolia*-dominated community during a very wet period, domination by *Senecio congestus* when a very dry period was followed by a very wet period and *Chenopodium rubrum* only establishing well during a very dry period. *Phragmites australis* was expected in low numbers in all four zones and found in three of them. Therefore, I conclude that these rules are sufficiently adequate for further use (chapter 6).

To simulate the results of drawdowns under current and future climate scenarios, I first calculated the probability that a range of moisture and temperature conditions would occur for each drawdown date. For this I used current KNMI-data and the KNMI W+ climate-change time-series. Second I simulated the effect of drawdown date on the probability that *Typha latifolia*, *Senecio congestus*, *Chenopodium rubrum*, *Rumex maritimus* en *Phragmites australis* will establish during the first growing season, starting with equal numbers of seeds. Simulations show that, under the current climate, the probability that a *Typha latifolia* dominated community will establish is more or less equal after a drawdown starting between March and July. However, the probability that a *Chenopodium rubrum* dominated community will establish is highest after a drawdown in March and decreases during later months. On the other hand, communities with *Phragmites australis*, *Senecio congestus* and *Rumex maritimus* will establish more likely during a late drawdown. After climate change, the risk increase that the soil remains bare after a summer draw-
down. The probability that a *Typha latifolia* dominated community will establish after a drawdown between March and July becomes smaller. The establishment of communities dominated by *Chenopodium rubrum* and communities with *Phragmites australis*, *Senecio congestus* and *Rumex maritimus* becomes more likely.

**Management implications**

This thesis research shows that various riparian plant species have strongly different moisture and temperature preferences. Information about the composition of the soil seed bank, preferred moisture conditions of species, together with knowledge of the local weather conditions, allow managers to optimize conditions for the establishment of riparian plant communities (chapter 6). “Very wet” preferring communities are likely after drawdowns during the whole growing season, “dry” communities after an early drawdown and “wet” communities after a late drawdown. Therefore, there is not a best drawdown date for riparian communities in general. In the Netherlands, I advise waterboards a natural water-level management with yearly lowering the water level slowly from March to August, with flooded conditions during winter. The alternation of dry and wet periods during these drawdowns will result in the establishment of a variety of riparian communities, dominated by emergents or annual/biannual mudflat pioneers. A semi-natural water-level management, starting in March and allowing the water level to drop naturally until the lowest allowable level is reached in April or May, is less suitable for species that prefer wet conditions. To promote helophyte communities, waterboards should decelerate the drawdown, especially during dry periods, or keep water level high until June and then lower the water level slowly. When climate warming proceeds, natural drawdowns between April and July might become unsuitable for the establishment of moisture dependent communities as this period generally will be too dry for most riparian species. To keep the soil wet, waterboards then might let in water to delay and slow down the drawdown. Moreover, waterboards could lower the water level artificially during wet periods in early spring or late summer.

Sand is a less suitable substrate for the construction of gently sloped banks as it dries out fast. When the plants do not establish well, the bank is vulnerable to erosion and needs to be protected. Therefore, I recommend covering sandy soils with a layer of clay, as is common practice to protect the shoreline against erosion when building a dike or embankment. Design of gently sloped bank should allow inundation during winter and drawdown during summer.