

Preference of wet dune species for waterlogged conditions can be explained by adaptations and specific recruitment requirements

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Abstract

The preference of wetland angiosperms for waterlogged soils has been explained by several hypotheses: (1) wetland species are adapted to waterlogging and sensitive to drought; (2) wetland species are tolerant to drought, but inferior competitors at drier conditions; (3) wetland species have narrow moisture optima for recruitment. We tested these hypotheses by the application of permanent and fluctuating water levels to experimental wet dune plant communities with four species that frequently occur in wet dune slacks (*Carex flacca*, *Molinia caerulea*, *Samolus valerandi* and *Schoenus nigricans*) and one competitive species of drier conditions (*Calamagrostis epigejos*). After 3 years, fluctuating water levels had led to lower total biomass production than permanent water levels, indicating that switching from aerated to anoxic soil conditions involved physiological costs. The collective biomass of wetland species was highest at permanently waterlogged conditions with interspecific variation in the biomass optima. At the nutrient-poor growth conditions of this long-term experiment, biomass of *Calamagrostis* was independent of water level treatment, thus the hypothesized competitive superiority of this species at drier conditions could not explain the biomass responses of the wetland species in this study. Instead, this is evidence for an ecological preference of adult wet dune plants for waterlogged to moist conditions. Recruitment of most wet dune slack species occurred in a narrower range of water levels than adult growth, indicating that recruitment requirements also pose a limitation to the distribution of these wet dune species. Incorporation of recruitment into nature management support models may improve their predictions.

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1. Introduction

Zonation of angiosperms along water level gradients is one of the earliest and best-studied phenomena in plant ecology (see, e.g., Godwin and Bharucha, 1932; Jones and Etherington, 1971; Wheeler, 1999). Seedling performance, growth and seed production of terrestrial species all depend on water level, with an optimal plant performance limited by water shortage at low water tables and oxygen shortage at water excess (Blom and Voesenek, 1996; Wheeler, 1999). The strongest differences in plant responses to water levels occur at the transition of aerated soil to waterlogged soil (Armstrong, 1982; Casanova and Brock, 2000; Moore and Keddy, 1988). While (temporarily) waterlogged conditions may be stressful to many terrestrial plant species, wetland angiosperms reach their highest abundance

under these conditions. Three partially complementary hypotheses – of which the individual feasibility is so far unknown – have been coined to explain the preferential occurrence of wetland angiosperms with a common set of traits at these conditions.

A first hypothesis emphasises the adaptations of wetland angiosperms to waterlogging by superficial rooting, the formation of aerenchyma, formation of thin leaves with thin cuticles and shoot elongation (Armstrong, 1982; Blom and Voesenek, 1996; Voesenek et al., 2004). These adaptations represent trade-offs, making them disadvantageous at low water tables, because such adaptations make species vulnerable for drought or mechanical damage (Engelaar et al., 1993; Končalová, 1990). Thus, species that have their highest abundance in waterlogged conditions may also have their optimal growth at these waterlogged conditions.

The second hypothesis postulates that adult wetland angiosperms are tolerant to lower water levels, but are inferior competitors under these dry conditions. This is supported by studies in which adult plants or plant parts were transplanted to drier conditions than where these species occurred naturally

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and where, in the absence of interspecific competition, no reduction of plant growth was found (Wilson and Keddy, 1986). Thus, wetland species would be displaced at moist to dry soils by superior competitors without adaptations to waterlogging (Budelsky and Galatowitsch, 2000; Grace and Wetzel, 1981; Lenssen et al., 1999). For brevity, such species will be referred to as “dry competitors” throughout this paper. This hypothesis is compatible with the CSR theory (Grime, 2001) that regards wetland species as stress (i.e., waterlogging) tolerators, which are outcompeted by highly competitive species in the absence of that particular stressor.

According to a third hypothesis, the restriction of wetland angiosperms to a narrower zone than tolerated by adult plants may be explained by a higher sensitivity of recruitment (i.e., seed production, germination and seedling performance) of wetland species to water shortage. Germination can be strongly limited by water shortage, as imbibition of seeds is often required to break dormancy (Baskin and Baskin, 1998) and seedlings may be more sensitive to drought due to the less developed root system (Reader et al., 1992). This may result in large differences in recruitment success over elevational gradients of only a few cm around the submergence/emergence threshold (Vivian-Smith, 1997).

Not only the occurrence of waterlogging *per se* is important for determining the occurrence of wetland species, but also the duration of waterlogging (Willis et al., 1959; Moreno-Casasola and Vázquez, 1999) and the timing of waterlogging are important, with waterlogging in winter having less pronounced effects than waterlogging late in the growing season (Toner and Keddy, 1997; Weiher and Keddy, 1995; Wheeler, 1999). Seasonal fluctuations in water levels, common in wetlands (Wheeler, 1999), require rapid physiological adaptations of plants (Blom and Voeselek, 1996) and a replacement of non-adapted roots and leaves (Armstrong, 1982; Robe and Griffiths, 1998). The physiological adaptations to a change in water tables may be costly in terms of energy and nutrients (Blom and Voeselek, 1996) compared to permanently high water tables. The cost of physiological plasticity in response to waterlogging may be higher for dry competitors, that have their phenotypic optimum elsewhere, than for wetland species (DeWitt et al., 1998). These higher costs upon fluctuating water levels may decrease growth and the competitiveness of dry competitors compared to wetland plants.

Vegetation of oligotrophic wet dune slacks is strongly structured by, often fluctuating, groundwater levels (Jones and Etherington, 1971; Grootjans et al., 1998). In dune slacks at the west coast of the Netherlands, this habitat has decreased over the last century as a result of desiccation and eutrophication (Grootjans et al., 1998) and the characteristic vegetation was replaced by highly productive stands, dominated by the grass *Calamagrostis epigejos* (Van Beckhoven, 1995; Runhaar et al., 2000). A set of oligotrophic wet dune slack species and *Calamagrostis* may therefore be used to test hypotheses on responses of wetland plants and dry competitors as a function of water levels. The following questions were addressed to investigate this relation:

1. Do oligotrophic wet dune slack angiosperms obtain their highest growth at (temporarily) waterlogged conditions, independently of the presence of dry competitors?
2. Does the ability of *C. epigejos* to invade a community of oligotrophic wet dune slack angiosperms depend on the water regime?
3. Does recruitment of new seedlings determine the preference of wet dune angiosperms for (temporarily) waterlogged conditions?
4. Do fluctuating water tables have different effects on plant growth and recruitment than constant water tables?

These questions were investigated by building artificial dune slack communities of species that frequently occur in wet dune slacks (*Carex flacca*, *Molinia caerulea*, *Samolus valerandi*, *Schoenus nigricans*) and one highly competitive species that occurs at drier conditions (*C. epigejos*). During 3 years, high, intermediate and low water levels were maintained in these communities as well as fluctuating water regimes that were waterlogged in winter and fell dry in the course of the growing season.

2. Methods

2.1. Experimental design

A 3-year growth experiment was performed in an outdoor experimental garden in Amsterdam, the Netherlands, with planted communities of wet dune slack species in mesocosms. Mesocosms were made in tubs, filled with calcareous dune sand up to 7 cm below the brim of the tub. Each tub had a height of 32 cm and contained 0.040 m³ of sand. The surface area of the sand was 0.21 m². The dune sand was poor in nutrients (4.5 µg inorganic P/g soil, extracted following Olsen et al. (1954) and 23 µg N/g soil, measured as inorganic nitrate and ammonia by a 1N KCl extraction for 2 h) and had a reducible iron content of 74 µg Fe/g soil measured following Lovley and Phillips (1986). The tubs were placed within larger tubs and could be lifted in three positions: dry, moist and wet, corresponding to a water level of 20 cm below the soil surface, 8 cm below the soil surface and 5 cm above the soil surface, respectively. The wet conditions represented waterlogging (to all species) and submergence (to seeds and to adult *S. valerandi* given its rosette growth form) with potential oxygen deficit, the moist conditions ample moisture supply, with aerated topsoil and the dry treatment represented potential drought stress. The outer tubs were kept completely water-filled throughout the experiment by supplying demineralised water. Excess water after a rain shower could freely flow over the brim of the outer tub. Exchange of water between the inner and outer tub was possible through holes at the bottom of the inner tubs. Outflow of sand was prevented by nylon mesh.

Three treatments had constant water tables at the dry (treatment 1), moist (treatment 2) and wet (treatment 3) position, respectively, throughout the 3-year experiment. The other five treatments had fluctuating water tables, starting with high water tables in winter. One series of tubs (treatment 4) was

elevated in March from the wet position to the moist position and then in April from the moist to the dry position. Four more series (treatments 5–8) went from wet to moist in April–July and from moist to dry in May–August, respectively. The fluctuation treatments thus mimicked different positions on elevation transects along shores of (temporary) lakes in dune slacks. Every treatment was replicated five times in a randomized block design to correct for potential spatial variability in conditions within the experimental garden.

In each mesocosm, the same combination of species was planted in autumn 2000, consisting of four species from oligotrophic wet dune slacks: *C. flacca* Schreb, *S. nigricans* L., *S. valerandi* L. and *M. caerulea* (L.) Moench. For reasons of brevity, these species will be indicated by their generic names only. Ten individuals of *Schoenus*, *Carex*, *Molinia* and *Samolus* were randomly assigned to each of the 40 mesocosms. The plants were arranged such that each individual plant had the other three species as the closest neighbour. *Schoenus* was planted as cuttings from tussocks, with an average of nine leaves. *Carex* was also vegetatively propagated and planted with a few cm of rhizome. *Molinia* cuttings were taken from larger tussocks and clumps of two or three shoots with root material were planted. *Samolus* was grown from seed and was planted as a small rosette with an average of five leaves. All tubs were kept at moist conditions till the first week of January 2001, when the experiment started.

2.2. Species measurements

All emerging seedlings of species other than *Carex*, *Schoenus*, *Samolus* and *Molinia* were hand weeded throughout the experiment. Because the soil in the mesocosms originated from dry dunes, none of the four wet dune species emerged spontaneously. This was checked in eight control trays that were kept at the moist position during the first year of the experiment.

To mimic invasion of a highly competitive species at drier conditions like those prevailing in the dry treatments, four individuals of *C. epigejos* (L.) Roth, of two or three shoots with roots and a few cm of rhizome, were randomly planted in each mesocosm in September 2002.

The diameter of *Schoenus* tussocks and the number of shoots of *Molinia* and *Carex* were measured each year in August. The number of leaves of *Samolus* rosettes was measured in June. The planted individuals could be recognized till the end of the experiment, except for the rhizomatous *Carex*. During the experiment, no germinating individuals reached the size of the mature plants and biomass data are presented for the planted individuals only. The number of flowering heads of *Samolus* and *Schoenus* and the number of flowering stalks of *Carex* and *Molinia* were counted in the autumn of 2002 and seed production per flowering head or stalk was estimated by counting the number of seeds in 10 heads or stalks per mesocosm. This seed production assay was performed in 2002 because seed production of some species took place till late autumn, and therefore seed production in 2003 was not complete at the time of harvest. *Calamagrostis* did not flower during the experiment.

Recruitment from seeds was measured at the end of the experiment, by hand sorting and counting seedlings for each mesocosm. Because recruitment is the result of seed rain, germination and seedling survival, additional germination and seedling assays were performed for *Schoenus*. Germination was measured by putting nylon mesh bags with 100 nuts into each mesocosm at 16 April 2003. The bags were harvested at July 3, 2003 and the number of germinated seeds was counted. Growth and survival of *Schoenus* seedlings was estimated for seedlings planted into the mesocosms at May 20, 2003. Seedlings had on average two leaves at the time of planting. After 11 weeks, seedlings were harvested and length of all leaves was measured.

The experiment was harvested in September 2003. Above-ground biomass of all species was clipped and sorted for each species separately and then dried for 48 h at 70 °C. Root biomass was measured for all species together, since roots could not be separated by species. The root mat was dense with many soil particles adhering. Therefore, it was washed, dried in a stove at 70 °C till no weight loss occurred (up to 5 days) and then ash free dry weight was measured by heating dried subsamples in ceramic cups at 800 °C for 12 h, weighing the residual ash and subtracting the ash weight from the total dry weight. Visual observations showed that almost all ash weight consisted of soil particles. Ash free dry weight is therefore assumed to equal root dry weight.

2.3. Statistics

All hypotheses were tested with repeated measures ANOVAs with water table treatment as fixed between-subjects factor and block as fixed within-subjects factor. No interactions between treatment and block could be tested, because each treatment × block combination occurred only once. Homogeneity and normality of the residuals assumptions were checked by visual inspection of the residuals in normal probability plots and residuals versus predicted values plots. Additionally, homogeneity of residuals was checked with Levene's test (Neter et al., 1996). Data on percent germination were arcsine-square root transformed and the number of seedlings of all species was log-transformed prior to testing to remediate non-homogeneity of residuals among treatments. Otherwise, all residuals were homogeneous and did not deviate from a normal distribution. When the treatment effect was significant, differences between individual treatments were tested with Tukey's post hoc test (Neter et al., 1996). All tests were performed with SPSS Version 9.0.

3. Results

3.1. Effects of water tables on biomass production

Total, i.e., root plus aboveground, biomass in the experimental wetland communities was strongly affected by block effects, indicating a strong spatial variability and by water regime ($F = 6.00$; d.f. = 7,28; $P < 0.001$). Highest biomass was measured in treatments that were permanently wet or moist, while the permanently dry treatment had a lower biomass

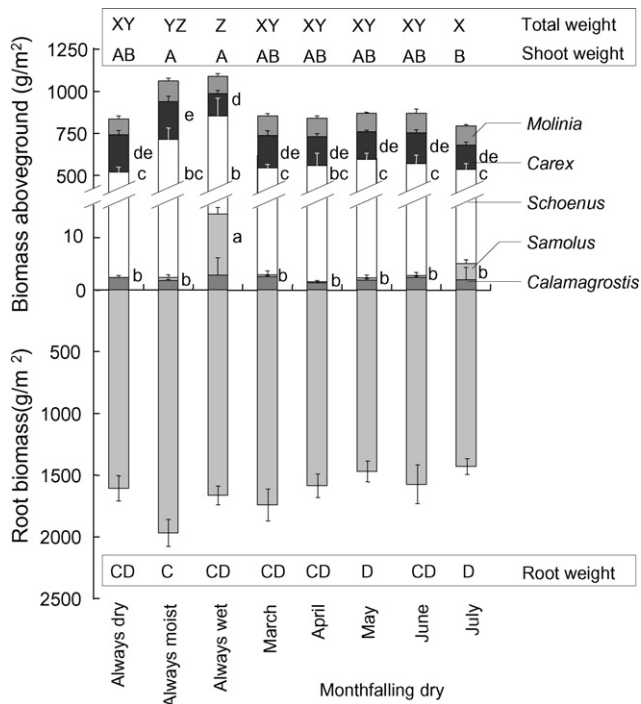


Fig. 1. Aboveground and belowground biomass of five species from experimental wetland communities that were exposed to different permanent or fluctuating water level treatments. Negative bars represent total root biomass. Uppercase letters indicate significant differences for biomass of all species aboveground (A–B), belowground (C–D) and total biomass (X–Z). Lowercase letters indicate significant differences of individual species, only for species that had a significant response to treatment. Error are S.E.

(Fig. 1). When root mass was analysed separately, again a treatment effect was found ($F = 2.94$; d.f. = 7,28; $P = 0.019$), with highest root mass in the permanently moist treatment (Fig. 1). Also in the aboveground biomass of all species together, a water treatment effect was found ($F = 6.12$, d.f. = 7,28; $P < 0.001$) with higher aboveground biomass in permanently wet and permanently moist treatments than in the permanently dry treatment (Fig. 1). Root biomass was between 1.5 and 2 times higher than shoot biomass.

Table 1
Biomass, seed production and seedling numbers of wetland plants in experimental communities that have been exposed to different water level treatments

Species	Effect	Biomass		Seed production		Seedling numbers	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
<i>Carex flacca</i>	Treatment	2.40	0.046	1.80	0.127	0.88	0.535
	Block	0.233	0.917	3.74	0.015	2.58	0.059
<i>Molinia caerulea</i>	Treatment	0.43	0.87	4.15	0.003	14.25	<0.001
	Block	2.98	0.036	2.85	0.043	12.111	<0.001
<i>Schoenus nigricans</i>	Treatment	5.95	<0.001	1.42	0.24	1.33	0.273
	Block	4.81	0.004	2.88	0.041	6.26	0.001
<i>Samolus valerandi</i>	Treatment	18.52	<0.001	1.81	0.125	5.77	<0.001
	Block	4.60	0.006	1.52	0.225	5.071	0.003
<i>Calamagrostis epigejos</i>	Treatment	0.65	0.71				
	Block	1.82	0.153				

F and *P* values for both treatment and block effects of a repeated measures ANOVA are given. In all tests $N = 40$, in treatment effects d.f. = 7,28 and in all block effects d.f. = 4,28. Significant treatment effects ($P < 0.05$) are shown in bold.

Total biomass in treatments that fell dry in the course of the growing season was not intermediate between the permanently wet treatment and the permanently dry treatment. Instead, the fluctuation treatments had a biomass that was equal to the dry treatment and significantly lower than the permanently wet and permanently moist treatment, with the lowest biomass in the treatment that fell dry in July (treatment 8) (Table 1, Fig. 1).

Biomass production of the dry competitor species *Calamagrostis* was low and did not differ between treatments (Table 1, Fig. 1). *Schoenus* was the dominant species, comprising more than 50% of aboveground biomass in all treatments, always followed by *Carex* and *Molinia* as second and third species in order of biomass. *Samolus* and *Calamagrostis* were the fourth and fifth species, the order depending on the treatment (Fig. 1). *Schoenus* had the highest aboveground biomass at the permanently wet treatment and lowest at the permanently dry treatment (Table 1, Fig. 1). Aboveground biomass of *Schoenus* in the fluctuation treatments was equal to the permanently dry treatment and thus lower than in the permanently wet treatment. *Samolus* was the only species that went extinct in some of the mesocosms. It had the highest biomass at the permanently wet treatment and a significantly lower biomass at the other treatments (Table 1, Fig. 1). *Carex* had a different pattern, with highest biomass at permanently moist treatments, lowest biomass at permanently wet treatments and an intermediate biomass at the permanently dry treatment. In the fluctuation treatments, *Carex* had a biomass that was intermediate compared to the dry and moist treatments. Biomass of *Molinia* did not differ among treatments.

While biomass at the end of the experiment provided an estimate of performance across the whole time period, non-destructive growth measurements on these plants (i.e., number of shoots and tussock or rosette diameter) showed a shift in treatment preference over time for *Samolus* (year \times treatment interaction, $F = 6.83$; d.f. = 14,92; $P < 0.001$). In the first year of the experiment, this species performed best in the permanently moist treatment and in treatments that fell dry early in the growing season. At the end of the experiment

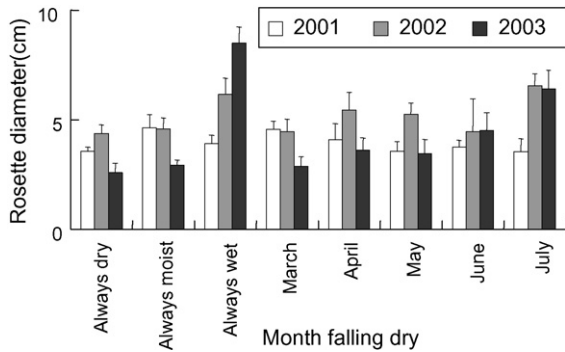


Fig. 2. Rosette diameter of *Samolus valerandi*, exposed to different permanent or fluctuating water level treatments in 3 consecutive years. Error bars are S.E.

however, the largest plants of this species were found in the permanently wet treatment, followed by the treatment that fell dry in July (Fig. 2). None of the other species had a significant time \times treatment interaction for growth. Regardless of the treatment, a large increase over time was recorded for the number of *Molinia* shoots ($F = 581.1$ d.f. = 2,14; $P < 0.001$) and *Schoenus* tussock diameter ($F = 114.0$; d.f. = 2,14; $P < 0.001$), while the number of *Carex* shoots decreased ($F = 20.9$; d.f. = 2,14; $P < 0.001$).

3.2. Seed production, germination and seedling performance

Seed production was in the order of 5000–50,000 seeds/m²/year for all species. Apart from a significant block effect for some species, indicating spatial variability (Table 1), seed production was independent of treatment for all species, except for *Molinia*. This species had highest seed production at the treatment that fell dry early in the year and in the permanently dry treatment and lowest in the permanently moist and wet treatments (Table 1, Fig. 3). There was also a large amount of variation in recruitment among the mesocosms, as shown by the highly significant block effects. *Molinia* had more seedlings

established at the dry treatment compared to the wet treatment (Table 1, Fig. 4). *Samolus* had a higher number of seedlings in the wet treatment compared to the dry treatment. No post hoc test was performed for this species since common transformations could not remediate the heteroscedastic variances. The number of seedlings of *Carex* and *Schoenus* did not differ between treatments.

The separate germination assay and seedling assay for *Schoenus* provided more detailed information on recruitment: germination almost exclusively occurred in treatments that were submerged during (part of) the germination trial (Fig. 5, $F = 2.96$; d.f. = 7,28; $P = 0.019$). Seedling performance of *Schoenus* showed the opposite pattern, with smallest seedling size in the permanently wet treatment and higher seedling growth in the moist and dry treatment (Fig. 5, $F = 3.74$; d.f. = 7,28; $P = 0.007$).

4. Discussion

4.1. Effects of water tables on biomass production

Wet dune slack angiosperms grew best at waterlogged conditions and were negatively affected by drought, as is evident from the significantly different total biomass. Their adaptations probably prevented stress induced by waterlogging. As a result, the permanently wet treatment had a predominantly positive effect mediated by high moisture availability, while the negative effect of drought prevailed in the dry treatment. This supports the hypothesis that the adaptations to waterlogging represented a trade-off (Blom and Voesenek, 1996; Končalová, 1990; Voesenek et al., 2004). Since the only species of drier conditions, *Calamagrostis*, was introduced in the last year and comprised less than 1% of total biomass, independent of treatment, the lower biomass production of the wetland species in the permanently dry treatment cannot be attributed to a competitive effect of this dry competitor. This response of oligotrophic plant species from dune slacks is in contrast to studies with meso- to

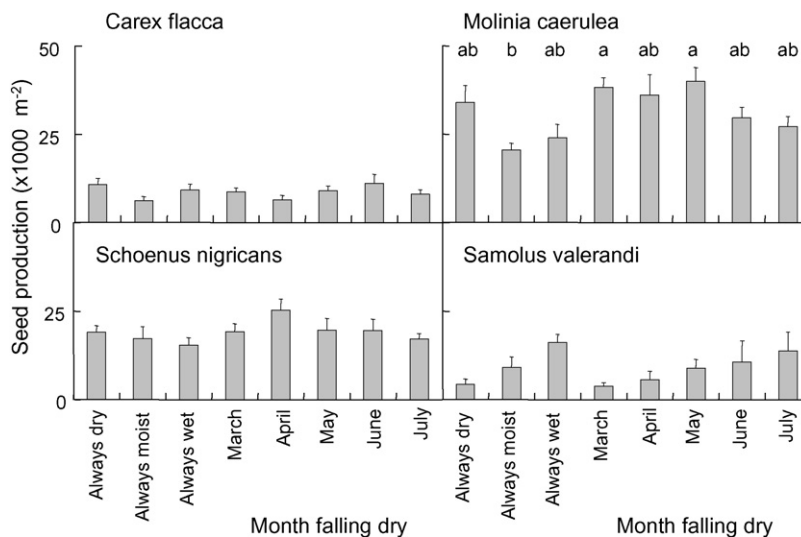


Fig. 3. Seed production of four wetland species in experimental wetland communities that were exposed to different permanent or fluctuating water level treatments. Letters indicate significant differences between treatments. Error bars are S.E.

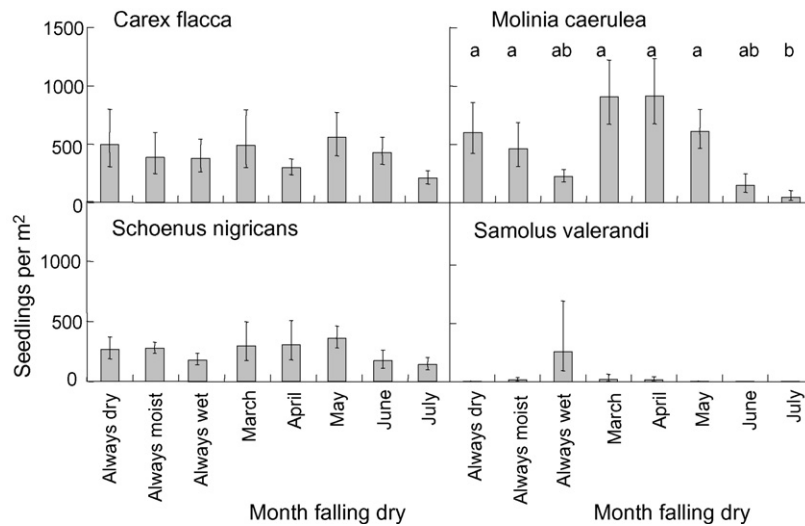


Fig. 4. Seedling recruitment of four wetland species in experimental wetland communities that were exposed to different permanent or fluctuating water level treatments. Letters indicate significant differences between treatments. Error bars are S.E.

eutrophic wetland species that reported broad tolerances of adult wetland plants for water levels and a reduction of wetland plants at drier conditions by competition rather than abiotic factors (Grace and Wetzel, 1981; Lenssen et al., 1999). Also in oligotrophic wet heathlands, (temporarily) waterlogged sites represent a refuge to escape competition rather than optimal growth conditions for characteristic species of wet heathlands, such as *Erica tetralix* (Berendse and Aerts, 1984).

The two species that had a preference for waterlogged conditions, *Schoenus* and *Samolus*, have several adaptations to waterlogging, including strong oxygen transport to the roots, production of superficial roots and ROL (Armstrong, 1982). While this may explain their high growth at waterlogged conditions, the dry treatment apparently limited growth. *Samolus*

may be vulnerable to drought stress due to its shallow root system (Schat and Van Beckhoven, 1991). *Schoenus*, however, has been reported to tolerate water levels of more than 1 m below the soil surface once it has established (Ernst and Van der Ham, 1988), owing to the ability of this species to make very deep roots. Despite this ability to tolerate low water levels, optimal growth of *Schoenus* in the field generally occurs at wet conditions (Ernst, 1995). The optimal growth of *Carex* in moist rather than waterlogged conditions is in accordance with a previous pot experiment with waterlogged, moist and dry treatments (Jones and Etherington, 1971). The lack of response of the fourth species, *Molinia* indicates both good adaptations to growing in waterlogged conditions and a tolerance for drought, resulting in a broad range of moisture conditions at which this species can grow (Berendse and Aerts, 1984; Runhaar et al., 2004).

For most species, the optimal growth conditions did not change during the experiment. However, for *Samolus* the optimum shifted from a preference for the permanently moist treatment to a preference for the permanently wet treatment. A major changing factor in the course of the experiment was the size of the neighbouring plants and, consequently, competition. *Samolus* is a pioneer species (Van der Meijden, 1996) and may therefore be sensitive to competition for light and/or nutrients. However, the highest biomass of neighbouring species occurred exactly in the treatments where *Samolus* maintained its highest biomass. The strong root oxygen loss of *Schoenus* has been shown to facilitate growth of neighbouring species (Schat, 1984). Oxygen may have been more limiting to *Samolus* than to other species, due to its rosette growth form. Thus, possibly growth of *Samolus* was increasingly facilitated by increasingly large tussocks of *Schoenus* in the wet treatments.

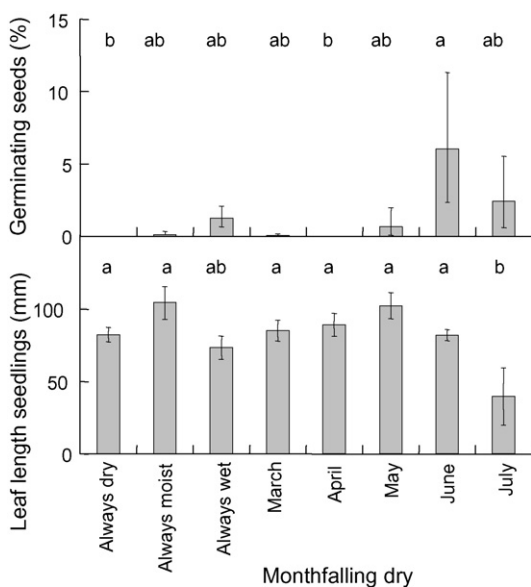


Fig. 5. Germination rate and seedling growth of *Schoenus nigricans* in experimental wetland communities that were exposed to different permanent or fluctuating water level treatments. Letters indicate significant differences between treatments. Error bars are S.E.

4.2. The role of competitive displacement in wetland plant zonation

We found no indications that the restriction of wet dune angiosperms to waterlogged or moist conditions was due to

competitive displacement by dry competitors. The growth of *Calamagrostis* was very low in all treatments and was independent of water level treatments. This was probably caused by the low nutrient content of the soil used, as this species was found to be very responsive to variation in nutrient levels (Van Beckhoven, 1995). The similar response to all water level treatments suggested that, at low nutrient availability, *Calamagrostis* is not very sensitive to the water level. In a previous experiment, however, *Calamagrostis* suppressed biomass production of *Schoenus* within the time span of a year (Van Beckhoven, 1995). This effect was stronger in moist compared to waterlogged conditions and at high nutrient conditions compared to low nutrient conditions. An important difference between that study and our experiment was that Van Beckhoven (1995) had planted *Schoenus* and *Calamagrostis* simultaneously, while in the current experiment the invasion of *Calamagrostis* was simulated after the other species had established. The discrepancy in results therefore indicates that not only nutrient availability, but also the sequence of establishment in a wetland community may change the outcome of competitive interactions among these species after 1 year of competition. The importance of the sequence of invasions for the assembly of communities has repeatedly been shown (e.g., Chase, 2003; Drake, 1990). This suggests that in environments with changing water tables not only the resulting water table determines the composition of a plant community, but also the order of species arrival at a site. The latter is, e.g., affected by the surrounding vegetation (i.e., by seed dispersal) and by seed bank properties.

4.3. The importance of recruitment in wetland plant zonation

Recruitment success is determined by three processes; seed production, germination and seedling survival. Seed production of wet dune species can only potentially contribute to the formation of distinct vegetation zones along moisture gradients if seed production is much more affected by variation in water levels than biomass production and if seed dispersal outside the vegetation zone of the parent plant is very limited. Warwick and Brock (2003) recorded a similarly strong influence of water levels on biomass as on seed production. In a field study (Bakker et al., 2005), we found high numbers of seeds of wetland plants in the seed banks outside the zone of the parent plants. Moreover, in our study *Molinia* was the only species in which seed production appeared to be responsive to water levels. In previous studies, nut production of *Schoenus* appeared to depend on waterlogged conditions, because of the increased availability of silicium (Si) at those conditions (Armstrong, 1982) and the high amounts of Si required for nut development (Ernst et al., 1995). In contrast, waterlogging did not lead to higher seed production of *Schoenus* in this study, indicating sufficient Si availability in the dry treatments. Together, this shows that seed production does not explain the preferential occurrence of wetland plants at (temporarily) waterlogged conditions in dune slacks.

For some species, the water level requirements for adult plant growth were substantially different from those of seed production, germination and seedling recruitment. Therefore, different water level constraints may operate in different stages of the life-cycle for the respective species, e.g., *Schoenus* had narrower water table ranges for germination and seedling growth than for adult growth; germination in seed bags was highest in the treatments that were waterlogged at the start of imbibition (this study; Ernst and Van der Ham, 1988). This might explain why *Schoenus* grows optimally at waterlogged conditions in the field (Ernst, 1995) despite its tolerance to low water levels. Also *Samolus* recruitment of new seedlings showed a much narrower moisture preference than its adult growth.

In contrast to germination requirements, planted seedlings of *Schoenus* grew best at moist to dry conditions. Recruitment of *Molinia* was highest in treatments that had the water level below the soil surface at the time of emergence (i.e., April/May), while its adult growth was independent of water level. The negative effect of submergence on seedling performance of *Schoenus* and recruitment of *Molinia* is in accordance with previous studies, showing that wetland angiosperms may need a drawdown for germination and early establishment, while adult plants of the same species are tolerant to waterlogging (Johnson, 2004; Lenssen et al., 1998). Leaves of small seedlings at the wet position do not emerge above the water level, thus preventing oxygen supply to the plant (Ernst, 1990). Altogether, these results show different growth optima with water level treatment at different stages of the life-cycle and that recruitment may pose a limitation to the distribution of wetland species.

4.4. Fluctuating water tables versus permanent water tables

Total biomass and root biomass were lower in the treatments with fluctuating water tables than in treatments with a permanent water level. A switch between oxic and anoxic conditions is often costly to plants. For instance, waterlogged conditions require roots with aerenchyma that are capable of oxygen transport, while these roots are less efficient in nutrient uptake and vulnerable to mechanical damage especially at dry conditions (Engelaar et al., 1993; Končalová, 1990). Similarly, switching between submerged and emerged conditions requires changes in shoot morphology, e.g., leaf stiffness, cuticle thickness, stomatal density (Robe and Griffiths, 1998; Voesenek et al., 2004). As a result, the switch between dry and wet conditions often increases root- and leaf turnover (Blom and Voesenek, 1996) at the cost of a lower biomass production. This decrease in biomass production was stronger in treatments that fell dry late in the season, suggesting that these costs are higher in the middle of the growing season compared to early in the growing season, possibly due to a difference in temperature and its subsequent effects on plant physiology (Drew, 1983). As a result, biomass production in the treatment that fell dry in July was lowest and thus dissimilar to the permanently waterlogged treatment that had the highest

biomass. While prevailing theory suggests that the occurrence of flooding late in the growing season is most deleterious (Toner and Keddy, 1997; Wheeler, 1999), it may be more correct to state that a change from aerated to waterlogged soil or vice versa late in the growing season has the strongest negative effects on biomass production.

While treatments with fluctuating water tables had a negative or neutral effect on biomass production of the respective species compared to permanent water tables, germination and seedling growth show that there is also a positive effect: *Schoenus* seeds had optimal germination in treatments that fell dry during the germination trial and seedlings performed best at moist to dry conditions. This pattern makes a retreating groundwater table the optimal condition for new recruitment of *Schoenus*: a shallow groundwater level enables imbibition, which is necessary for the onset of germination (Baskin and Baskin, 1998). The consecutive establishment can take place when water tables have further decreased, providing a moist, but aerated soil. Also *Molinia* may profit from water tables that fall in the course of the growing season, providing a waterlogged habitat in winter, which the adult plant is well able to tolerate and a drier habitat in spring summer when establishment takes place. Thus, fluctuations in water tables may be vital for rejuvenation of populations of these wetland species.

4.5. Consequences for predicting wet dune slack communities

While the three hypotheses, investigated in this paper, all predict the highest abundance of wetland angiosperms at (temporarily) waterlogged conditions if the hydrological regime is more or less constant over the years, different bottlenecks among the hypotheses become important in a situation with changing water levels, e.g., when restoring degraded wetlands by rewetting. The auto-ecological and recruitment bottlenecks related to water levels, identified in this paper, may only be resolved by restoration of the hydrological regime whereas competitive displacement could have been resolved by biomass reduction treatments. The importance of each bottleneck may differ among species. Such bottlenecks are not included in current management support models (Latour et al., 1994; Meuleman et al., 1996; Van Ek et al., 2000) and habitat classifications (Runhaar et al., 2004), because these are based on occurrence of adult plants. Especially in the context of ecological restoration, where traditional successional pathways on which these models are built may not be possible (Olde Venterink and Wassen, 1997), incorporation of species recruitment into the models may improve the predictions.

5. Conclusions

Wetland angiosperms of oligotrophic to mesotrophic coastal dune slacks have the highest biomass production at waterlogged conditions. At the low-nutrient conditions of this study, this preference was independent of the competitive effects of *C. epigejos*. Thus, for these species, nutrient-poor wet dune slacks

represent a habitat for optimal growth and not only a refuge to escape from competitive interactions with highly competitive species. For the adult plants, a transition of waterlogged conditions to emerged conditions in spring reduced biomass production, indicating physiological costs associated with fluctuating water levels.

In addition to adult plant performance, recruitment patterns could explain a preference of some wet dune species for conditions of permanent waterlogging or periodic flooding in winter and spring. The narrow water table tolerance of germination and seedling performance of some species compared to broader tolerance in adult plants suggests that predictions of plant community responses to changing water levels may be improved by accounting for recruitment bottlenecks.

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