Macrophytes in drainage ditches

Functioning and perspectives for recovery

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Contents

A typical line shaped drainage ditch with a well-developed vegetation. Photo taken in Dwarsgracht, Overijssel, the Netherlands.

1.   General Introduction

1.1   The paradox of the drainage ditch

As the largest part of the Netherlands is located below sea level, management of water has always been a challenge for its inhabitants. Besides building dikes to prevent sea and river water from flooding the land, drainage systems were constructed to drain for example peat areas to make them suitable for agriculture. As part of drainage systems, ditches can be defined as manmade permanent shallow waters usually less than 8 m in width and not deeper than 1.5 m in which continuous one-directional flow of water is mostly absent (de Lange, 1972). The construction of ditches in the Netherlands already started at the beginning of the common era in the Northern part of the country in the province of Friesland (Rooijendijk, 2009). At present around 250.000 km of drainage ditches can be found resulting in the Netherlands having the highest density of ditches in the world. The network of drainage ditches can be regarded as a typical element of the Dutch polder landscape (Figure 1) and part of the cultural heritage of the Netherlands.

Figure 1. Aerial photo of the typical polder landscape near Kockengen in the Netherlands with a high density of drainage ditches (source: Hoogheemraadschap de Stichtse Rijnlanden)

The main function of drainage ditches is transporting water but they also accommodate a wide variety of plant and animal species and therefore contribute largely to the biodiversity of the agricultural landscape (Painter, 1999; Armitage et al., 2003; Williams et al., 2004). The ecological characteristics of drainage ditches closely resemble those of cut-off channels along rivers. Both are small dimensioned linear water bodies, often with stagnant water and extensive vegetation development resulting in fast terrestrialization. Additionally both systems are influenced by a certain degree of disturbance. In drainage ditches vegetation is removed by maintenance activities while in cut-off channels vegetation is removed by periodic flooding events (Bornette et al., 1998; Roozen et al., 2008). In that sense drainage ditches can be seen as a surrogate for the channels that have disappeared in the Netherlands due to the construction of dikes and the agricultural use of floodplains along rivers. This creates the paradox of the drainage ditch: Although man made and artificial they are important for the ecological quality and biodiversity of the Dutch landscape.

The ecological quality of drainage ditches has deteriorated in many countries the last decades (Herzon and Helenius, 2008). A commonly observed, drastic change in aquatic systems is that from a diverse, mainly submerged vegetation to a dominance of free-floating plants (STOWA, 1992; Janse and Van Puijenbroek, 1998; Kadono, 2004; Gettys et al., 2009). Dense mats of free-floating plants block the

exchange of oxygen from air into water and lower light availability in the water column, the latter causing decreased photosynthesis, limiting oxygen production. With an oxygen consuming sediment at the ditch bottom these conditions often result in anoxia (Villamagna and Murphy, 2010). Anoxic conditions and decreased light availability result in a loss of submerged vegetation and associated macrofauna (Scheffer et al., 2003; Herzon and Helenius, 2008). As a consequence total biodiversity will decrease. From an ecological perspective drainage ditches have been overlooked for a long time with the consequence that research on the ecological functioning and the mechanisms behind deterioration of drainage ditches has lagged behind that of for instance lakes, rivers and streams. Therefore, knowledge on the relations between environmental conditions and vegetation functioning is rather limited which, consequently, makes it difficult to determine good management practices to maintain or restore diversity.

1.2   Macrophytes in drainage ditches

Several studies show that macrophytes are essential for the ecological functioning of aquatic systems. Amongst others they offer habitat for fauna due to their architecture (Waters and San Giovanni, 2002; Christie et al., 2009; Bakker et al., 2010) but also regulate abiotic conditions by for instance removing nutrients from water and sediment (Bouldin et al., 2004; Cooper et al., 2004). Due to the small dimensions of ditches, vegetation development generally occurs throughout the whole width of a drainage ditch. Small ditches therefore can quickly develop from open water to land (Verdonschot et al., 2011). While helophytes usually develop in the ditch bank, the water column is mainly colonized by submerged and floating plants.

In a well-developed aquatic vegetation several submerged and floating plant species are found with biomass production throughout the whole water column. This type of vegetation shows a biomass distribution with a vertical architecture (Figure 2, upper graph) due to the presence of several species occupying different parts of the water column. At elevated nutrient levels the vegetation contains more highly productive, canopy forming, floating leaved and free-floating species that develop their biomass mainly at the water surface (Figure 2, lower graph). This causes the biomass distribution to change to a horizontal architecture (Bloemendaal and Roelofs, 1988).

Whether species remain present in a system not only depends on their growth characteristics but also on their way of reproduction. During the growing season plants produce several reproductive organs like seeds, turions, tubers, rhizomes and detached green plant fragments (together called propagules) that secure the plants establishment the next growing season or after a period of unfavourable conditions (Barrat-Segretain, 1996). Whether plants are able to produce propagules and germinate the next growing season depends on local conditions in the ditch. If species are outcompeted or disturbed during the growing season no propagules will be produced, while suboptimal conditions for germination of propagules (for instance a lack of stratification or low light availability) might prevent the establishment of individuals the next growing season (Barrat-Segretain, 1996; Hilt et al., 2006). Even though the availability of propagules is an important factor in the survival or re-establishment of species, not much is known about their role in drainage ditches.
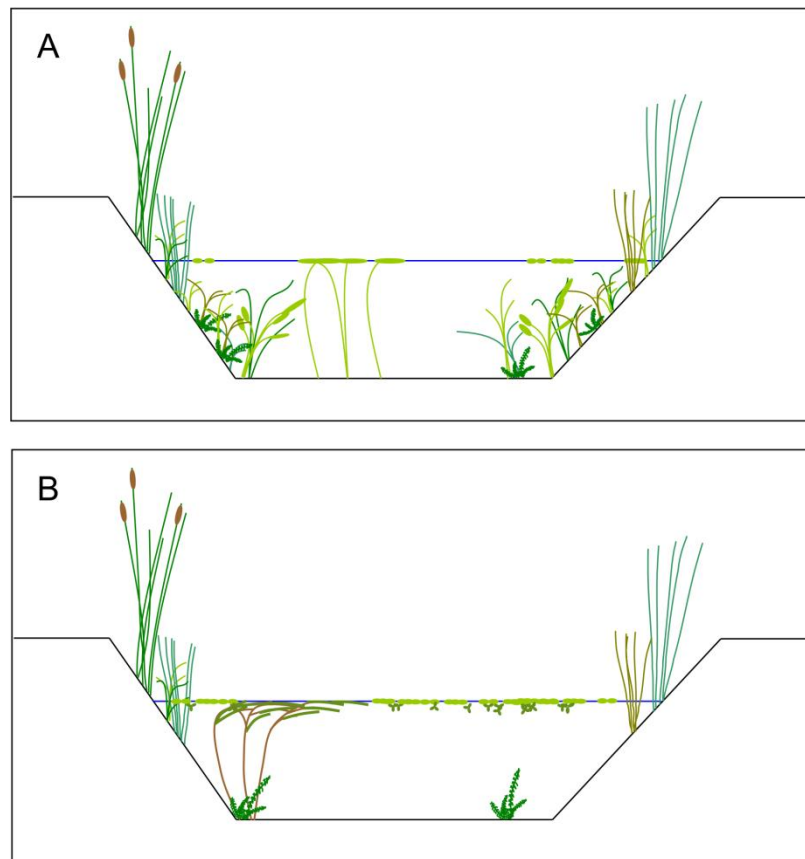
Figure 2. Schematic representation of vertical (A) and horizontal (B) biomass architecture in drainage ditches.

1.3   Environmental conditions and human influence

Nutrients

Although several chemical characteristics influence macrophyte growth in aquatic systems, increased nutrient inputs are considered one of the most important factors affecting productivity in ecosystems around the world (Carpenter et al., 1998; Tilman et al., 2001). Most nutrients enter aquatic systems through surface runoff, atmospheric deposition and groundwater inflow (Lamers et al., 2002). Intensification of agriculture with accompanying increased fertilizer application has caused a strong increase in nutrient inputs to drainage ditches in the past decades (Wolf et al., 2003). This increase in nutrients caused higher productivity of the vegetation and consequently changes in species composition. Free-floating plant dominated systems under hypertrophic conditions for instance are very commonly observed nowadays (Janse and Van Puijenbroek, 1998; Gettys et al., 2009). Knowledge on the nutrient ranges at which different vegetation compositions occur is essential to estimate the required decrease in nutrient levels at which a shift in vegetation composition can be expected.

Although studies in various aquatic systems give insight in the relation between a specific vegetation composition and conditions (Forest, 1977; Ozimek et al., 1990; Hilt et al., 2006; van Liere et al., 2007), not much is known about the specific nutrient ranges at which different vegetation types occur in drainage ditches (but see modelling results of van Liere et al. (2007) on nutrient loadings in drainage ditches at which floating mats occur). Studies in other aquatic systems like lakes show that the availability of nutrients in both sediment and water can play a key role in determining vegetation composition (Mauricio Bini et al., 1999; Squires and Lesack, 2003). It can be assumed these two compartments are also crucial for macrophytes in drainage ditches.

Maintenance

Because plant growth occurs across the full width of drainage ditches, maintenance by means of removing plant biomass and sediment (respectively mowing and dredging) is needed to maintain the drainage function of ditches. As in former days maintenance was done by hand (Figure 3.A), often more

than 20% of the vegetation remained present in non-disturbed patches after each maintenance event (Vernon and Hamilton, 2011). This created a patchy environment with high variability in spots with and without vegetation. Consequently shelter for fauna and remnants of several plant species were always available, likely limiting long-term negative effects on animal and plant life. Nowadays modern, efficient machines are used (Figure 3.B) that remove almost all plant biomass, often including roots, creating an overall disturbed, homogeneous habitat with few remnants from which plants and animals can recolonize the ditch. Consequently mowing can affect plant species composition (Beltman, 1987; Best, 1994) and a decrease in species diversity is observed in systems subject to maintenance (Baattrup-Pedersen et al., 2003).

Figure 3. Ditch cleaning by hand with simple equipment (A) and modern ditch cleaning using powerful machinery with high removal efficiency.(Left photo: J.P. van Zuidam, right photo: H. Hoogenboom.)

Twisk et al. (2003) concluded that in ditches the type of machine used for mowing and dredging affected the floristic value of those ecosystems, while Peeters (2005) showed that the frequency at which mowing was performed influenced the diversity of vegetation in the ditch, with the highest diversity occurring at intermediate mowing frequencies.

The response of vegetation communities to maintenance largely depends on how individual plant species deal with this disturbance. Disturbance tolerant, fast growing species like *Elodea nuttallii* (Planch.) St. John and *Myriophyllum spicatum* L. may profit from a high level of disturbance as they show fast regrowth from small remaining plant fragments, eventually becoming dominant in the system (Bornette et al., 1994; Di Nino et al., 2005). Additionally, eutrophication causes increased productivity of these species resulting in the need to remove vegetation more frequently to prevent drainage problems. Eutrophication and maintenance seem to induce a similar response in the vegetation being a shift towards dominance of fast growing submerged species or free-floating plants (see relations found by for instance Portielje and Roijackers (1995); Scheffer et al. (2003) and Di Nino et al. (2005)). Unfortunately, the effects of maintenance and eutrophication on vegetation often occur simultaneously in the field (see for instance Riis and Sand-Jensen (2001)). Therefore it is difficult to attribute the loss of species to either eutrophication or maintenance. Although the response of species to disturbance may partly be dependent on nutrient levels, additional knowledge on species tolerance to maintenance activities without the effect of eutrophication is needed to improve the estimate of the effectiveness of alternative maintenance methods.

Climatic conditions
Current climate change will likely cause changes in macrophyte community composition (Mooij et al., 2005). In lakes, effects of climate change are often associated with altered nutrient availability, occurrence of anoxia (Mulholland et al., 1997; Jeppesen et al., 2009) and consequently changes in macrophyte distribution and cover (Rooney and Kalff, 2000; Kosten et al., 2009).
In drainage ditches similar relations likely exist. In a warmer climate, increased water temperatures and consequently enhanced eutrophication may act in synergy (Netten et al., 2010), favouring especially free-floating plant development. Climate scenarios for temperate regions predict milder and wetter winters for the future (IPCC, 2007). Therefore, whether free-floating plant dominance will occur more often may also depend on the overwintering strategy of species. Free-floating plants and evergreen

submerged plants such as *Elodea nuttallii* for instance survive winter as green plants or as turions (Jacobs, 1947; Barrat-Segretain and Cellot, 2007) and show fast regeneration at the beginning of the next growing season. Contrastingly, annual submerged macrophytes die back in winter and slowly regenerate from propagules (Renman, 1989, Whiteman and Room, 1991). Although experiments support the idea that climate change may lead to a shift towards free-floating plant dominance (Feuchtmayr et al., 2009, Netten et al., 2010), evidence from field observations in ditches is largely absent.

Environmental factors and spatial scale
In (aquatic) ecosystems often multiple factors operating on different spatial scales affect the conditions for biota. Mowing and dredging as mentioned before operate on a much smaller spatial scale than for instance climate change. Studies showed that indeed multiple spatial scales can contribute in understanding the functioning of an ecosystem. For example, local species richness of invertebrates in headwater streams in Finland was affected by local factors like width and nutrient levels and the regional species richness (Heino et al., 2003), while the quality of downstream located, polluted agricultural streams in France was affected by both the type of local farming and by the presence of non-disturbed natural ecosystems within the surrounding region (Schäfer et al., 2007). In drainage ditches similar relations between vegetation characteristics and environmental conditions at different spatial scales can be expected. At the highest spatial scale water systems and drainage ditches are located in a certain climatic zone, which sets the context for all local and regional factors in terms of for instance temperature and water availability.
An individual drainage ditch is usually part of a larger regional network of well-connected ditches and channels that are used to regulate the hydrology of surrounding land. Consequently, drainage ditches receive water from adjacent pastures through overland flow, from local or regional groundwater flows and from adjacent water bodies. Local processes like the mineralization of organic matter from ditch sediments may increase nutrient levels, while the input of iron rich regional groundwater may limit the availability of phosphorus through binding to iron (Geurts et al., 2008). On the other hand, eutrophication may be enhanced by local shallow groundwater flows, transporting nutrients originating from agricultural land. Additionally, the composition of inflowing water can be determined by the composition of underlying parent material (Wolf et al., 2003). Besides trophic interactions, toxic effects on macrophytes can occur due to inputs of for instance sulphide from soil or groundwater (Lamers et al., 2002). Regional scale characteristics may also be relevant for biotic processes. A high hydrological connectivity of ditches on a regional scale may for instance enhance the dispersal and survival of macrophytes (Demars and Harper, 2005). Considering these examples, it seems likely that relating vegetation composition to both local and regional characteristics of a hydrological unit (polder) will increase insight in the functioning of aquatic vegetation in drainage ditches. This knowledge can eventually be used to determine feasible ecological goals and measures based on the most important characteristics of an area.

1.4   Research questions and approach
Given the loss of ecological quality in drainage ditches in the Netherlands, there is a need for knowledge on how environmental conditions influence the composition and functioning of macrophytes in these ecosystems. This knowledge is essential to identify key mechanisms for restoration of species rich macrophyte communities by means of effective water quality management. Within the PLONS project (see Box 1) trophic level and the magnitude of disturbances are considered two main driving forces for vegetation development in these small aquatic systems and the seed bank is assumed to be the most directly available source for re-establishment of species. Therefore, the main objective of this thesis is:

Identifying conditions and mechanisms that determine macrophyte community composition and functioning in drainage ditches, with focus on effects of nutrient state, maintenance and propagule bank properties

Figure 4 illustrates the components studied in this thesis. Based on analysis of earlier field observations it is hypothesized that three main types of vegetation can be found in the field; a diverse submerged vegetation with mainly annual plant species (A in Figure 4), a vegetation dominated by fast growing, evergreen submerged plants such as *Elodea nuttallii* (B in Figure 4) and a vegetation dominated by

free-floating plants (C in Figure 4). The physical, chemical and biotic conditions as well as maintenance determine vegetation composition and may cause transitions from one vegetation type to the other. In this thesis the vegetation types dominated by evergreen submerged or free-floating plants are sometimes described as 'monocultures'. Although each of these two communities may contain more than one species, this term is used to indicate that the community is generally dominated by a small number of functionally comparable species that influence the ditch ecosystem in a comparable way. A free-floating plant dominated vegetation for instance may contain more than one free-floating plant species. However, most free-floating plant species are fast growing, disturbance tolerant plants that can contribute to low light availability, anoxia and a loss of biodiversity at high coverages.
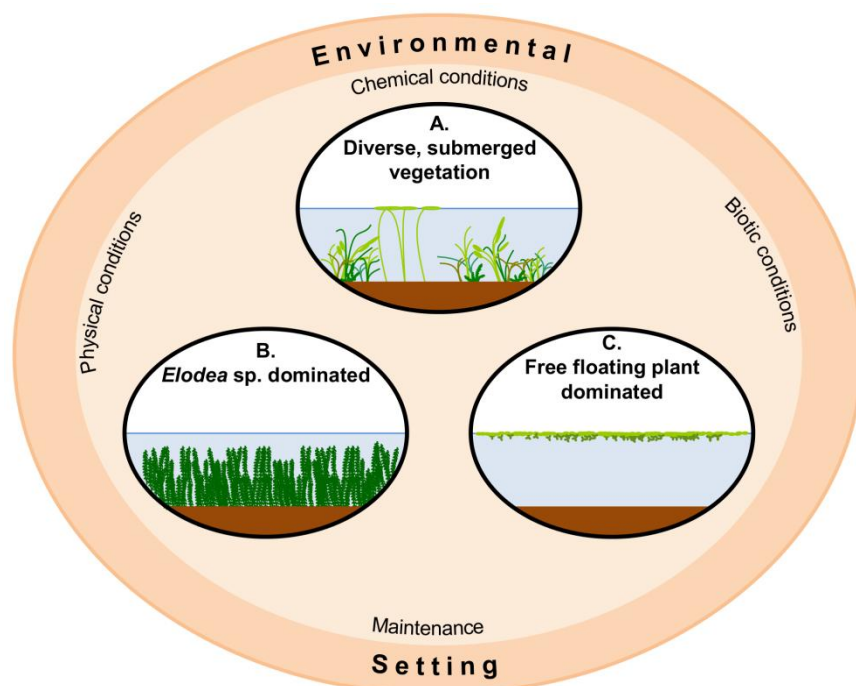
Figure 4. Schematic representation of the hypothesized vegetation types and the environmental setting in which they occur. All four mentioned environmental factors (maintenance, physical, chemical and biotic conditions) are assumed to influence the vegetation composition.

In Chapter 2 environmental factors are determined, operating at different spatial scales, that relate to differences in vegetation composition using a field dataset from 67 ditches. This was done by analysing data on species and biomass composition and the environmental setting. The contribution of factors acting on the local and regional scale was quantified.

Chapter 3 focusses on nutrients as a dominant factor in the functioning of drainage ditches. For this, the most important nutrient fractions (in water or sediment) and levels were determined at which the three vegetation types (Figure 4) will likely develop using biomass and nutrients data from 50 ditches from the same field dataset.

In Chapter 4 the effects of cutting on growth and survival of two Pondweed species is tested. Although water quality might be suitable for species to survive in a ditch, maintenance activities like mowing abruptly remove part of a species' biomass which might endanger completion of the life-cycle or its survival. To determine the direct effect of this cutting, different cutting treatments were applied under experimental conditions to two Pondweed species that are representatives of a diverse drainage ditch vegetation.

Chapter 5 deals with a germination experiment to study the potential of the sediment propagule bank to initiate recovery of aquatic vegetation under suitable conditions for plant growth. Many ditches in the Netherlands show dominance by free-floating plants and restoring suitable site conditions for submerged plants might create opportunities for re-establishment from propagules. The germination experiment was done with sediments from ditches with a submerged vegetation and dominance by free-floating plants.

Climatic change will likely affect many of the above mentioned environmental factors and consequently vegetation functioning. Chapter 6 therefore focusses on the effects of climatic variation on the cover of free-floating and submerged macrophytes. To this end local weather conditions and the North Atlantic Oscillation (NAO) winter index were related to data on macrophyte cover in ditches in the Netherlands. The macrophyte dataset was collected over a period of 26 years by regional waterboards.

Based on the acquired knowledge a synthesis is presented in Chapter 7 in which the perspectives for restoration of macrophyte communities are discussed, considering the findings in this thesis. Furthermore, a vision on water quality management on the polder scale is presented, considering redistribution of functions and ecological goals based on an integrated view on the optimal design of a polder.

Box 1: PLONS research project

Waterboards in the Netherlands are responsible for the management of both water quantity and quality. For effective management of the ecological water quality in drainage ditches there is a need for knowledge on their ecological functioning, more specifically on the relations between nutrient availability, maintenance and the resulting occurrence of macrophytes, macrofauna and denitrification. To gain knowledge on these relations the PLONS project (Dutch acronym for 'Long Term Research Dutch Ditches') was initiated at the Wageningen University and Research Centre through financial support by fourteen waterboards and STOWA (acronym for 'Foundation for Applied Research on Water management'). The project consisted of three PhD researchers studying: (1) nitrogen cycling in drainage ditches with a focus on denitrification, (2) the relations between (a)biotic characteristics of ditches and macrofauna community composition and (3) the effects of nutrients, maintenance and seed bank properties on aquatic vegetations (this thesis).

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Collecting information on vegetation composition during the field survey in 2007. Photo taken close to the Langbroekerwetering, Wijk bij Duurstede, The Netherlands.

2. Macrophyte species composition and biomass in drainage ditches: the importance of both local and regional environmental factors

Van Zuidam, J.P. & Peeters, E.T.H.M. Submitted to PLOS One

Summary

Understanding the relations between macrophyte communities and environmental factors is challenging while factors operating on different scales might be relevant. The objectives of this study were to quantify the contribution of abiotic variables in explaining patterns in macrophyte biomass and species composition from 67 drainage ditches in the Netherlands, to assess the contribution of local and regional factors and to determine whether biomass and species composition data give comparable information on relevant factors. To this end field data was analysed using CCA.

The most important factors related to macrophytes are nutrients, soil type, ditch network characteristics, ditch dimensions and seepage. A moderate fraction of the variation in the macrophytes was explained by all variables (respectively 34% and 46% for species composition and biomass) and the variance explained by each variable was low but significant. This indicates that there is no single factor governing macrophytes in drainage ditches. This result, together with the variety of relevant factors for the functioning of the system seem to be typical characteristics of drainage ditch ecosystems. Local factors (like nutrient availability and ditch dimensions) contributed two times more than regional factors (like total length of ditches and seepage) to the explained variance. A large part of the relevant local factors are associated with eutrophication whereas regional factors are related to hydrological characteristics and land use. The importance of regional factors in both biotic datasets is likely explained by the strong connectivity between ditches and their surroundings, causing intensive exchange of substances and biota.

For effective management of desired macrophyte communities it seems useful to (1) gain thorough knowledge on both local and regional conditions influencing the community in order to determine the potential for a certain vegetation type and (2) consider multiple measures that affect multiple environmental conditions in order to increase the effectiveness.

Introduction

Drainage ditches, as part of the hydrological infrastructure in many countries across Europe [1], largely contribute to the diversity of flora and fauna in especially urban and agricultural environments [2, 3,4,5]. These shallow, man-made waters are characterized by the presence of submerged, emergent and floating vegetation that strongly influence biogeochemical cycling through processes like denitrification [6], uptake of nutrients [1], sedimentation of suspended solids [7] and removal of pesticides [8]. The composition and growth strategy of aquatic vegetation differ between drainage ditches depending on environmental conditions. A well-developed community of different, mainly annual submerged species can be found in undisturbed ditches which tend to show a vertical growth strategy [9]. These communities serve as suitable habitat for macrofauna [1, 5]. Changes in environmental conditions, for instance increased nutrient levels or disturbance frequency, may cause this rather diverse vegetation to be replaced by faster growing, evergreen submerged species (such as *Elodea nuttallii* (Planch.) St. John) that may eventually become dominant in the vegetation. This community often shows a horizontal growth strategy with a large part of the biomass at the water surface. Generally, free floating plants are also part of the community. When these plants occur at high coverage they can outcompete submerged plants, leading to a monoculture of free floating plants with all biomass at the water surface [10,11].

It is suggested that the availability of nutrients and macro-ions are likely the most important factors determining the composition and productivity of the aquatic vegetation [10, 12]. Another characteristic of drainage ditches is the strong connection with the surrounding terrestrial environment [1]. It is therefore likely to suggest that factors like soil type [13] and land use [1] may be of great importance for species composition and productivity. Furthermore, the hydrological unit (through characteristics such as surface area and total length of ditches) influences vegetation development through the dilution and transport of substances. A variety of environmental factors seem to play a role in shaping the macrophyte communities in drainage ditches. Interestingly, those factors may operate on different spatial scales. For example, nutrients, macro-ions, dimensions and oxygen level are typically local whereas hydrological unit, soil type and land-use operate on a much broader, regional scale. Studies in other aquatic ecosystems demonstrated that both local and regional factors may determine local species composition. Macro invertebrate species richness in headwater streams in Finland appeared to be affected by local factors such as width and nutrient level and the regional species richness [14]. The quality in downstream parts of agricultural streams in France was determined by farming in the direct surrounding (= local) and inflow from upstream, non-disturbed natural ecosystems (= regional [15]).

Also in general ecological concepts the importance of factors operating on different spatial scales is incorporated. Concepts such as the metacommunity framework and landscape ecology use different spatial scales to understand community development and functioning, the former focussing on spatial allocation of individual organisms while the latter also focusses on allocation of material [16]. These phenomena are especially important in strongly connected systems such as streams, rivers [17] and likely also drainage ditches. Although there are indications that local and regional factors will likely correlate with macrophyte community composition in drainage ditches, their relative importance is hardly quantified.

Many studies mainly focus on the direct relation between environmental conditions and species composition (for instance [18]). However, it is known that increased nutrient levels lead to shifts in productivity across species [19, 20, 21] and ultimately to changes in species composition. The direct relations between nutrient levels and biomass of vegetation may be used to analyze the trophic status of a system and effects of eutrophication rather quick without the need for time consuming collection of vegetation relevees. However it is important to analyze whether using biomass data results in the same relations with environmental factors compared to using species composition data.

The present study focuses on quantifying the contribution of local and regional factors in explaining differences in vegetation characteristics of macrophytes in drainage ditches in the Netherlands. The objectives of this study are (1) to quantify the contribution of abiotic variables in explaining patterns in biomass and species composition, (2) to assess and compare the contribution of local and regional factors and (3) to determine whether relations with environmental factors are comparable when using biomass and species composition data from the same macrophyte communities. Multivariate analyses (Canonical Correspondence Analyses (CCA)) with variance partitioning [22, 23] were performed on a field dataset containing biomass and species composition data to assess the relative contribution of local and regional factors.

Materials and Methods
Data collection
Information from regional water boards on macrophytes in ditches was used to preliminary select 70 ditches that contained submerged macrophytes and/or free floating plants but were not overgrown by emergents. These ditches were sampled in June and September 2007 on vegetation characteristics and abiotic conditions. During and after fieldwork 3 ditches were removed from the field dataset due to missing data or heavy disturbance during 2007 (for instance reconstruction of the ditch profile). The final 2007 field dataset therefore contained data on 67 ditches (Figure 1).

Vegetation recordings were made with Tansley coverage classes [45] by selecting a part of the ditch, approximately 25 m long, representing the vegetation composition in the ditch. Vascular plants were identified up to species level and Charophytes up to class level. Free floating plants dominated at 19 sites, *Elodea nuttallii* at 16 sites, 11 sites showed a mixture of mainly annual submerged plants and a mixture of the three plant types was found at 21 sites. All present vascular plant species were collected by wading through the transect and were identified up to species level.. Biomass samples of complete plants (roots and shoots) were taken by selecting 1-3 locations in the same 25 m section that together covered all the patches with different species compositions and coverages. From each of the 1-3 selected location(s) biomass was collected from a surface area of 900 cm^2. Total coverage of each patch in the 25 m section was used to calculate a weighted total amount of biomass per m^2. Biomass of free floating plants, *Elodea nuttallii* and other, mainly annual submerged plants was separated from each other in the field in 3 fractions. Biomass (fresh weight in g/m^2) of each fraction was determined after removing attached periphyton and sediment and after removing attached water by spinning each fraction around in a salad spinner for thirty seconds.

Water samples were taken both in June and September. Three samples of the upper 20 cm of the water column were taken with a tube sampler, evenly distributed across the same transect in which vegetation data was collected. The three samples were mixed to one homogenized sample (volume 1 L). From this sample 50 ml was used for analyses on nutrients. Sediment samples were taken once in June as sediment concentrations of most components are assumed to be relatively constant over the year. Three samples from the top 5 cm of the sediment were taken in the 25 m section in which vegetation data was collected and mixed to one homogenized sample (volume 423 cm^3). Water and sediment samples were stored in a freezer directly after collecting.

Water samples were analysed on nutrients using a continuous flow analyzer (Skalar Analytical BV, Breda, The Netherlands). Total phosphorus, orthophosphate, total nitrogen and dissolved nitrogen (ammonium, nitrate and nitrite) were analyzed following standard protocols [46,47,48]. The Griess-Ilosvay reagent was used to determine nitrate and nitrite and ascorbic acid/antimony was used to determine orthophosphate concentrations. Total nitrogen and total phosphorus were determined after a UV/per sulphate destruction. Sediment samples were analysed on total nitrogen and total phosphorus using a segmented flow analyzer after destruction with sulphuric acid/ salicylic acid/ selenium/ hydrogen peroxide, with total nitrogen measurement based on the Berthelot reaction and total phosphorus measured as phosphate molybdenum [49, 50]. Calcium, iron and potassium in water (NEN-6966), sulphate in water (NEN-6604) and iron, calcium and sulphide in sediment (NEN-5709, NEN-6961, NEN-6966) were analyzed according to Dutch standards using an inductively coupled plasma atomic emission spectrometer (Varian Inc, Palo Alto, USA).

Electric conductivity and oxygen level were directly measured in the field during daytime using a Hach HQ40d portable multi-meter with LDO101 (oxygen), CDC401 (conductivity) and PHC101 (pH) electrodes (Hach company, Loveland, Colorado, USA). Local physical characteristics recorded are depth (m), width (m), thickness of the sediment layer (3 thickness classes), and an estimate of the number of days since the last ditch mowing event (3 classes) based on the degree of desiccation of the removed macrophytes on the ditch bank.

Collected regional characteristics are underlying soil type and surrounding land use (observed in the field), while regional hydrological characteristics were collected from a database on the structuring of the Dutch water system [51]. The hydrological characteristics were; surface area (km^2) of the hydrological unit in which a ditch is located, percentage surface water in that hydrological unit, the amount of groundwater seepage/infiltration (mm/day) and the total length of ditches (m) with a width of 0-1m, 1-3m, 3-6m and >6m in the hydrological unit in which a ditch is located.

Figure 1. Location of the sampled ditches (n=67)

Data analysis

The relations between biotic data and environmental variables were analysed by performing Canonical Correspondence Analyses (CCA) with the manual forward selection procedure (p<0.05) using Canoco 4.5 for Windows [52]. To avoid collinearity, the variance inflation factor was checked for each model and was always lower than the critical value of 20 [53]. The net contribution of each variable and net contribution of all local and regional factors were calculated by applying the variance partitioning approach [54] which was successfully applied in other studies (for instance [22]). The net explained variance of a set of local or regional factors was calculated as the sum of the net explained variances of the individual variables included in the set. All analyses were done separately for the biomass and species composition data.

Results

Selected environmental variables

Total variance in the biomass dataset was lower (total inertia: 1.467) than in the species composition dataset (total inertia: 3.211) due to the higher number of biological variables in the latter. The forward selection procedure within CCA resulted in nine and twenty variables included in the model for respectively biomass and species composition (for descriptives of the biotic and environmental variables see Appendix 1A and 1B). The ordination plot for biomass (Figure 2.A) shows the two submerged biomass fractions at the left side and free floating biomass in the right upper quadrant of the plot. The environmental variables plot (Figure 2.B) shows that higher submerged biomass other than *Elodea nuttallii* is often found in deeper ditches on a sandy soil in combination with lower nutrient levels, while higher free floating biomass is found at the highest nutrient levels in more shallow ditches. Higher biomass of *Elodea nuttallii* is found in larger hydrological units at somewhat intermediate nutrient levels compared to ditches with higher biomass of the other two fractions.

The species plot (Figure 2.C) shows that free floating plant species are mainly situated in the upper left quadrant of the plot while submerged species are mainly situated in the right side of the plot. The lower right quadrant contains several submerged species that are favored by eutrophic conditions (for instance *Elodea nuttallii*, *Myriophyllum spicatum* L., *Egeria densa* Link. and *Potamogeton crispus*

L.), while the upper right quadrant contains species that are often found at mesotrophic conditions like *Myriophyllum verticillatum* L., *Potamogeton compressus* L., *Hottonia palustris* L. and *Potamogeton acutifolius* Link. The plot with environmental variables (Figure 2.D) shows that free floating plants mainly occur in shallow ditches at higher N and P levels in both water and sediment and higher S levels in the sediment. The submerged plant species in the right side of the plot mainly occur in deeper ditches at lower nutrient levels, sometimes on sandy soils. Additionally, the submerged species in the upper right quadrant occur in ditches that show relatively high Fe levels in water and sediment and receive seepage water.
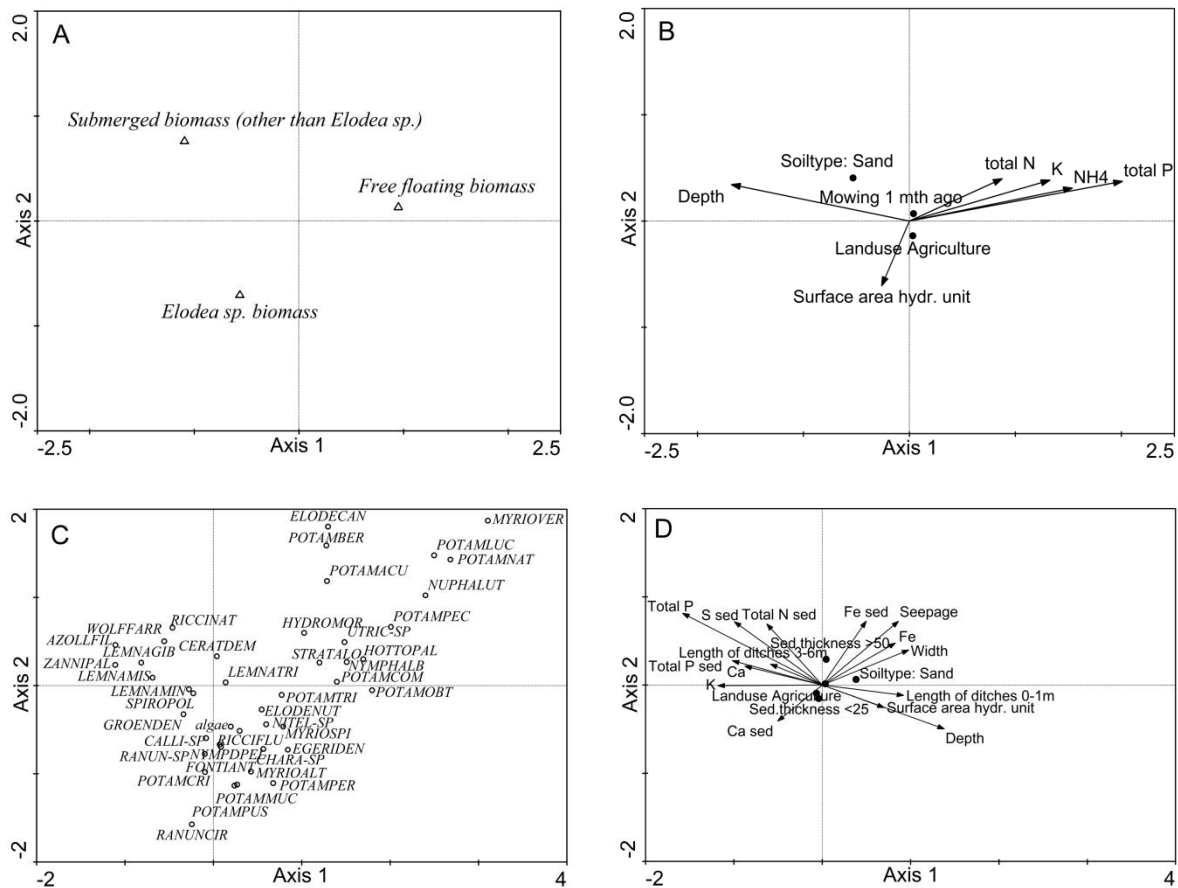
Figure 2. Ordination plots of CCA with biomass and species composition data
Ordination plots of Canonical Correspondence Analysis with Biomass (2.A and 2.B) and Species composition (2.C and 2.D). Biotic data was not transformed and rare species were downweighted. Position of biomass fractions (A), species (C) and environmental variables (B & D) are shown in separate plots with equal axis scaling for each separate CCA. See Appendix 1B for complete plant species names and descriptives. Nominal variables are indicated by solid black circles. The first two axes from the analyses are shown. Eigenvalues for axis 1 and 2 were respectively 0.438 and 0.230 for the CCA with biomass data and 0.290 and 0.140 respectively for species composition data.

Relative contributions
Six variables were included in both the model for biomass and species composition being sand soil, agricultural land use, depth, potassium, surface area of the hydrological unit and total phosphorus in water (Table 1). Three variables were only included in the model based on biomass (ammonium, total nitrogen in water and time since last mowing), whereas the model for species composition contained

fourteen variables that showed no significant contribution when using biomass (among others iron in sediment, width of the ditch and amount of seepage). The net explained variance per variable in the biomass model is quite low, though always above 1.5%. Only two variables contribute more than 5% being agricultural land use and soil type sand. For the species composition data the net explained variance for each variable is always lower than 5%. Individually, the three sediment thickness classes show no net contribution although they contribute to the explained variance of the model possibly due to interaction effects.

Local vs regional variables
The variance in the biomass data was explained by five local and four regional variables while the species composition data was explained by fourteen local and six regional variables (Table 1). Despite the differences in the number and nature of the selected variables, the partitioning of the variance over local and regional factors is quite similar for biomass and species composition data. For both datasets, local factors explained more of the variance than regional factors, being around two third of the total gross and net explained variance (Table 2). The covariance between local and regional factors was in both cases small being respectively 1.8 and 1.9%.

Table 1. Overview of the selected variables by the CCA, using biomass and species composition data. The standard forward selection procedure in Canoco was used with p<0.05 for adding variables. Letter codes indicate if variables are used as local (L) or regional (R) characteristics in further analyses. '**All variables**' indicates the sum of the net explained variances per variable in the final model. Variables denoted in italic are selected in both the model for biomass and species composition data.

Biomass			Species composition		
Variable	**Net explained variance**	**Local (L) /Regional (R) variable**	**Variable**	**Net explained variance**	**Local (L) /Regional (R) variable**
Soiltype: Sand	*0.078*	*R*	Fe sediment [mg/kg]	0.034	L
Landuse Agriculture	*0.059*	*R*	*Total P [mg/l]*	*0.021*	*L*
Depth [cm]	*0.041*	*L*	Width of ditch [cm]	0.020	L
K [mg/l]	*0.039*	*L*	*Soiltype: Sand*	*0.019*	*R*
****Surface area hydro. unit [m^2]*	*0.033*	*R*	Total P sediment [mg/kg]	0.019	L
Total P [mg/l]	*0.029*	*L*	*Length of ditches 0-1m [m]	0.017	R
NH4 [mg/l]	0.019	L	*Landuse Agriculture*	*0.015*	*R*
Total N [mg/l]	0.019	L	*Depth [cm]*	*0.015*	*L*
Last mowing: 1 month ago	0.016	R	**Seepage [mm/day]	0.014	R
			S sediment [mg/kg]	0.014	L
			****Surface area hydro. unit [m^2]*	*0.014*	*R*
			Length of ditches 3-6m [m]	0.014	R
			Total N sediment [mg/kg]	0.012	L
			Ca [mg/l]	0.012	L
			K [mg/l]	*0.012*	*L*
			Ca sediment [mg/kg]	0.011	L
			Fe [mg/l]	0.010	L
			Sediment thickness <25cm	0.000	L
			Sediment thickness 25-50cm	0.000	L
			Sediment thickness >50cm	0.000	L
All variables	**0.333**		**All variables**	**0.273**	

Total model			
Number of variables	9		20
Trace	0.668		1.095
Residual Sum of Squares	0.799		2.116
Explained variance total model	0.455		0.341

* Total length [m] of ditches with the mentioned width in the hydrological unit in which the sampled ditch is located. A hydrological unit is defined as a confined area in the landscape in which free water exchange between ditches occurs, while little water exchange occurs between the unit and the surroundings.

** Groundwater inflow is represented by numbers for the whole hydrological unit in which the sampled ditch is located.

*** Surface area [m^2] of the hydrological unit in which the sampled ditch is located.

Table 2. Gross and net contribution of local and regional factors to the explained variance for biomass and species composition. Gross contribution indicates the explanatory value of the total model with all local/regional factors included. Net contribution is the sum of the net explained variances of each variable separately. The data results from CCA with standard forward selection procedure with $p<0.05$. RSS = Residual Sum of Squares. Covariances between the local and regional factors are shown.

	Biomass		Species composition	
	Local	**Regional**	**Local**	**Regional**
Gross expl. var.				
nr of variables	5	4	14	6
Trace	0.440	0.254	0.795	0.362
RSS	1.027	1.213	2.416	2.849
Expl. variance	**0.300**	**0.173**	**0.248**	**0.113**
Net expl. var.				
Trace	0.414	0.228	0.733	0.300
RSS	1.053	1.239	2.478	2.911
Expl. variance	**0.282**	**0.155**	**0.228**	**0.093**
Covariance	0.018	0.018	0.019	0.019

Discussion

Relevant factors for drainage ditch macrophytes

The total variance in species composition explained by the environmental variables was rather low (34%) in comparison to other studies. For example, in an Australian river 67% of the variation in macrophyte species composition could be explained by environmental variables [24]. Also for other biota such as macroinvertebrates higher explained variances are often found. Both in Dutch lakes and the Rhine-Meuse Delta around 45% of the variation in macroinvertebrates could be explained by environmental variables [22, 25].

Lower explained variances can be obtained when the studied gradients are short (no variation in the database) which is not the case seeing the completely different growth forms. Another reason for low explained variances could be that the relevant factors were not measured or included in the analyses. In our study this is not likely the case, since factors mentioned in the literature as possibly important were included [13, 26, 18, 27]. Therefore, the low values of explained variances are not likely due to flaws or artefacts in our approach.

Interestingly, the number of variables included, especially in our model for species composition, were much higher than in several of the other mentioned studies [22, 28, 25, 29]. The optimal model for species composition included twenty variables with each variable having a net contribution ranging between 0 and 3.5%. These values again are rather low compared to other studies. In calcareous rivers in England for example, 10 variables explained 32.4% of the variance in macrophyte species composition, with individual variables contributing 1 to 11% [29]. In boreal grasslands in Finland, 8 variables explained around 33% of the variance in plant species composition, with individual variables contributing 4 to 7% [30]. The relatively high number of variables together with their relatively low net contributions in the present study indicate that none of the factors is strongly dominating macrophyte communities in drainage systems as was for instance found for the factor current in streams [31, 32] or light-climate in shallow lakes [33, 34]. This lack of dominance of a certain factor therefore likely is a typical characteristic of these kind of ecosystems. Drainage ditches generally have relatively small dimensions and show strong interactions with their surroundings [1]. Consequently, depending on the (spatial) context all kinds of factors may have a large influence on ditch vegetation and the vegetation itself might exert a strong influence on its environment (e.g. increasing P levels under duckweed mats [26]) obstructing clear unidirectional patterns. A high supply of nutrients, being one of the important

factors in this study, may lead to development of faster growing species as a sign of eutrophication. In similar ditches but with high iron concentrations (for instance originating from elevated pleistocene areas [35]) binding of phosphorus to iron may occur inhibiting these eutrophication effects [36]. Therefore, although there is a direct relationship between a certain environmental variable and vegetation, this might be masked by another factor.

Another example of a masking effect might be caused by the degree in which ditches are interconnected (surface area of the hydrological unit and amount of ditches are important factors in this study). A lower degree of species exchange in relatively isolated ditches might prevent a shift to free floating plant dominance when nutrient inputs increase due to the absence of plant exchange with surrounding ditches. Ditches connected to a large network of surrounding ditches free floating plants will likely show fast establishment of new species [29] and may become dominated by free floating plants. A similar function of connectivity was also found for terrestrial species [37].

Another reason for the lack of dominance of a factor might be that the studied ditches are ecologically impoverished. Relatively high nutrient inputs and frequent mowing of aquatic vegetation in most ditches in the Netherlands may have created a relatively uniform environment with hardly any variation. Consequently, only tolerant species dominate the community that survive under a wide range of environmental conditions and thus hardly react to changes in environmental conditions. Additionally it is argued that the generalistic characteristics of macrophyte species (high plasticity and stress tolerance, clonal reproduction and high dispersal rates), cause many species to occur in a broad range of environmental conditions [38]. On the other hand different growth forms were found in drainage ditches (for instance free-floating vs sediment rooting submerged) which show strong differences in competitive abilities (see for instance [39]).

Contribution of local and regional factors
Both local and regional factors contributed substantially to the explanation of the variation in macrophytes in drainage ditches. Although local factors explained the largest part of the variance in this study, regional factors still accounted for approximately one third of the explained variance. A significant contribution of local factors could be expected considering results from previous studies [26, 40], though the present results also confirm the importance of regional factors as observed in other ecosystems. The relative contribution of local and regional factors may differ though depending on the studied ecosystem and biota. In boreal semi-natural grasslands for instance variation in vegetation composition correlated to both local factors (local land use, soil pH, phosphorus content, explaining 33% of the total variance in the data) and regional factors (mainly climate related factors explaining 7%) [30]. Agricultural streams showed a similar pattern with local factors contributing more than regional factors in explaining plant species distribution [15], while the occurrence of invertebrates in streams showed a different pattern with regional factors explaining the largest part of the variance [14]. The results from the present study and those in other ecosystems therefore show that the contribution of local and regional factors in explaining patterns in biota can vary strongly depending on ecosystem type, however mostly knowledge on both local and regional factors is needed to understand the ecological functioning of these systems. This is confirmed by the present study in which local factors associated with causes and effects of eutrophication and regional factors associated with hydrological characteristics of the ditch network both determine macrophyte distribution. The importance of hydrological characteristics is likely explained by the typical strong connectivity between drainage ditches and the surrounding terrestrial and aquatic system (1) causing intensive exchange of substances and biota.

Biomass versus species composition
Both biotic datasets describe different aspects of the vegetation since species composition data contains detailed information on coverages of 44 individual species, while biomass data only distinguishes three groups of plants. Biomass though might give more detailed information on actual

standing stock in contrast to the estimate of horizontal coverage in the species composition data. Although the models based on biomass and species composition had the variables soil type sand, agricultural landuse, depth, K, total P water and surface area of the hydrological unit in common there were also differences which were not associated with a certain group of variables/characteristics. For example, information on species composition indicated a relation between occurrence of species of mesotrophic conditions and the occurrence of seepage and high iron levels (which may limit phosphorus availability).This pattern was not retrieved using biomass data which might be explained by the lack of differentiation in biomass of different species within the submerged biomass other than from *Elodea nuttallii*.

From literature (for instance [19, 20]) it was expected that biomass would be mostly related to nutrient levels. Nutrients indeed had a relatively large influence when considering the final model including all selected environmental variables. However, the net explained variances found in the present study hardly confirm the importance of nutrients individually. Alternatively, soil type and land use had the strongest net impact on biomass. For species composition levels of iron and total phosphorus were most important. Also several sediment characteristics were only included when using species composition. The availability of nutrients from the sediment might cause differences in species composition [41], even though biomass within each of the three distinguished plant groups might remain comparable (only the distribution of biomass over the species within a group may for instance change). Additionally, the total length of available ditches (with different widths) may affect the available species pool in a hydrological unit and consequently the local species composition [42, 43].

A variable characterizing the disturbance by mowing is only included in the biomass dataset. This is likely caused by the time the vegetation had to produce new biomass since the last mowing event, while species composition did not change due to a mowing event a month earlier. Information on mowing frequency and method across several years is likely more related to differences in species composition.

Overall, each approach had its own merits as there were several characteristics that were taken into account by only one of the two biotic datasets. It might be useful though to explore a biomass sampling method that generates (part of) the additional information found when using vegetation recordings since biomass can be sampled quite easily without extensive knowledge on the appearance of all individual species in a ditch. Part of the additional information might be generated for instance by grouping biomass of other competitive, fast-growing species with that of *Elodea nuttallii*. Alternatively, categorizing species and their biomass according to specific functional characteristics might also be a method to further clarify the relations with environmental conditions [44].

In summary, the present study clearly showed that there is not one single factor dominating the functioning of macrophytes in drainage ditch ecosystems. This is likely a characteristic of these small dimensioned ecosystems with strong interactions with their surroundings. Several factors influence vegetation composition, depending on the local and regional context. Important factors found in this study mainly relate to nutrient availability, soil type, characteristics of the ditch network, dimensions of the ditch and seepage. The interaction with its surroundings is visible in the net contribution of regional factors which is around one third of the total explained variance, comparable to studies in some other ecosystems.
Considering these results, management of desired macrophyte communities may become more effective when both the local and regional context are taken into account when determining measures. To this end, first the potential for development of a certain vegetation type can be estimated by determining the local and regional factors that predominantly influence the community. Secondly, to effectively influence the community, several measures likely need to be considered that influence multiple environmental conditions, each with their own moderate influence on vegetation development.

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Appendix 1A. Descriptives of the environmental variables and vegetation characteristics

Vegetation characteristics	Mean	Standard error	Minimum	Maximum
Biomass				
Free-floating (gr FW/m^2)	493.84	68.91	0	3811.11
Elodea sp (gr FW/m^2)	352.18	59.27	0	4707.78
Submerged (other than *Elodea* sp) (gr FW/m^2)	242.96	56.15	0	4578.89
Total biomass free-floating & submerged (gr FW/m^2)	1085.29	90.35	6.67	4707.78
Species composition				
nr of free-floating plant species	3	0.13	0	7
nr of submerged plant species	3.69	0.22	0	12
Total number of species	6.69	0.21	1	14

Environmental variables	Mean	Standard error	Minimum	Maximum
Water				
NO$_3$ + NO$_2$ (mg N/l)	0.4	0.1	0	9.09
NH$_4$ (mg N/l)	0.36	0.05	0	3.35
Total N (mg/l)	2.61	0.22	0.02	22.92
Total P (mg/l)	0.37	0.04	0	2.89
K (mg/l)	9.73	0.71	0	47.9
Ca (mg/l)	77.95	3.87	10.7	226
Fe (mg/l)	0.51	0.07	0	4.52
SO$_4$ (mg/l)	58.43	5.9	1.68	339.39
TIC (µg/l)	42.84	2.28	3.46	125.18
TOC (µg/l)	24.75	1.86	0.32	162.23
EC (µS/cm)	825.72	63.46	93.6	6200
Sediment				
Total N sediment (mg/kg DW)	6290	441	530	22500
Total P sediment (mg/kg DW)	1008	62	144	3025
Fe sediment (mg/kg DW)	25180	2509	1386	236230
Ca sediment (mg/kg DW)	30432	1954	1063	104300
S sediment (mg/kg DW)	8498	678	365	35022
Physical characteristics				
Depth sampled ditch (cm)	43.05	1.67	15	100
Width sampled ditch (cm)	365.22	12.74	130	750
Thickness sediment layer (>25cm, 25-50cm, >50cm)*				
Soiltype (Sand, Peat, Clay)*				
Landuse (Nature/Agriculture)*				
Time since last mowing (<1wk, 2-4wks, >1month)*				
Hydrological characteristics				
Surface area of hydrological unit (km^2)**	30	3	1	150
Total length ditches >6m width (m) ***	3.71	0.36	0	19.33
Total length ditches 0-1m width (m) ***	62.01	6.55	0	300.68
Total length ditches 1-3m width (m) ***	596.4	29.1	85.87	1301.95
Total length ditches 3-6m width (m)***	165.03	12.71	34.85	723.9
Percentage surface water in hydrological unit (%)	6.86	0.44	0.77	24.73
Seepage (mm/day)****	0.08	0.03	0.3	1.94

* Nominal variables

** Surface area [m^2] of the hydrological unit in which the sampled ditch is located.

*** Total length [m] of ditches with the mentioned width in the hydrological unit in which the sampled ditch is located. A hydrological unit is defined as a confined area in the landscape in which free water exchange between ditches occurs, while little water exchange occurs between the unit and the surroundings.

**** Groundwater inflow is represented by numbers for the whole hydrological unit in which the sampled ditch is located.

Appendix 1B. Observed plant species and nr. of observations per sampling round

Species name	Code in ordination	Total nr. of observations	Highest observed coverage (Tansley class)
Filamentous algae	algae	62	9
Azolla filiculoides Lam.	AZOLLFIL	30	9
Fontinalis antipyretica Hedw.	FONTIANT	8	5
Callitriche sp. L.	CALLI-SP	26	7
Ceratophyllum demersum L.	CERATDEM	64	9
Chara sp. L.	CHARA-SP	17	8
Egeria densa Planch.	EGERIDEN	2	2
Elodea canadensis Michx.	ELODECAN	11	9
Elodea nuttallii (Planch.) H. St. John	ELODENUT	86	9
Groenlandia densa L.	GROENDEN	1	1
Hottonia palustris L.	HOTTOPAL	2	2
Hydrocharis morsus-ranae L.	HYDROMOR	38	8
Lemna gibba L.	LEMNAGIB	54	9
Lemna minor L.	LEMNAMIN	111	9
Lemna minuta Kunth.	LEMNAMIS	30	9
Lemna trisulca L.	LEMNATRI	75	9
Myriophyllum alterniflorum DC.	MYRIOALT	1	6
Myriophyllum spicatum L.	MYRIOSPI	19	9
Myriophyllum verticillatum L.	MYRIOVER	4	2
Nitella sp. C. Agardh.	NITEL-SP	12	9
Nuphar lutea (L.) Sm.	NUPHALUT	9	5
Nymphoides peltata (S.G.Gmel.) Kuntze	NYMPDPEL	8	8
Nymphaea alba L.	NYMPHALB	4	7
Potamogeton acutifolius Link	POTAMACU	3	3
Potamogeton berchtoldii Fieber	POTAMBER	1	5
Potamogeton compressus L.	POTAMCOM	3	6
Potamogeton crispus L.	POTAMCRI	9	5
Potamogeton lucens L.	POTAMLUC	8	8
Potamogeton mucronatus Sonder	POTAMMUC	2	2
Potamogeton natans L.	POTAMNAT	11	6
Potamogeton obtusifolius Mert. & Koch	POTAMOBT	9	6
Potamogeton pectinatus L.	POTAMPEC	6	5
Potamogeton perfoliatus L.	POTAMPER	3	2
Potamogeton pusillus L.	POTAMPUS	1	2
Potamogeton trichoides Cham. & Schltdl.	POTAMTRI	18	7
Ranunculus circinatus Sibth.	RANUNCIR	8	6
Ranunculus sp. L.	RANUN-SP	7	2
Riccia fluitans L.	RICCIFLU	16	7
Ricciocarpos natans L.	RICCINAT	2	7
*Spirodela polyrhiza (*L.) Schleid.	SPIROPOL	81	6
Stratiotes aloides L.	STRATALO	5	9
Utricularia sp. L.	UTRIC-SP	4	8
*Wolffia arrhiza (*L.) Horkel ex Wimm.	WOLFFARR	19	8
Zannichellia palustris L.	ZANNIPAL	6	5

Biomass sampling during 2007 fieldwork. Photo taken in de Wieden-Weerribben, Overijssel, the Netherlands

3. Occurrence of macrophyte monocultures in drainage ditches relates to phosphorus in both sediment and water

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Abstract

Monocultures often negatively affect the quality of aquatic ecosystems. The importance of water and sediment nutrients for the occurrence of monocultures of certain species in aquatic vegetations was analyzed using field data from drainage ditches. Ranges of nutrients were identified that best explained the occurrence of monocultures of *Elodea nuttallii* (Planch.) st. John (Waterweed type), monocultures of free floating plants (Free floating type) and the occurrence of a diverse submerged vegetation (Mixed type). The results indicated these three vegetation types occurred at distinctive ranges of especially phosphorus in water and sediment. Sediment phosphorus distinguished monocultures from the Mixed type, with the two monocultures occurring at two to four times higher concentrations. Highly competitive *Elodea nuttallii* likely outcompetes other submerged plants at high sediment phosphorus levels, illustrated by the lower diversity of the Waterweed type. Phosphorus concentrations in water were four to six times higher in the Free floating type compared to the Waterweed or Mixed type. The three vegetation types had comparable total biomass which was unexpected. This comparability was likely caused by free floating plants only growing at the water surface at the highest nutrient levels and the limited space in drainage ditches for increased submerged biomass development at high nutrient availability. Possible measures to limit the occurrence of monocultures, and thereby increasing the ecological quality, are discussed focussing on lowering phosphorus concentrations in both water and sediment and on removal of plant species that develop into monocultures.

Introduction

Environmental change in ecosystems due to anthropogenic stressors generally leads to a loss of community diversity and is often combined with an increased dominance of one or a few species (Hillebrand et al. 2008). Since monocultures might be difficult to mitigate due to their resilience (Scheffer et al. 2001), they often cause undesired changes in ecosystem functioning. In Argentinian grasslands for instance, dominant exotic plant species may produce easier decomposable litter resulting in increased soil decomposer activity, supporting continued dominance of the exotic species (Spirito et al. 2012). In wetlands the dominance of species like *Juncus effuses* may lead to altered light conditions, negatively affecting species richness and abundance (Ervin and Wetzel 2002).

In aquatic systems similar negative effects of dominance are found. In lakes for example, eutrophication and related phytoplankton dominance prevents submerged macrophyte development which leads to an overall loss of biodiversity (Scheffer et al. 1993). Alternatively, small aquatic systems such as streams and drainage ditches can develop monocultures of fast growing submerged species like *Elodea nuttallii* (Planch.) St. John. or free floating plants (Peeters et al. 2013) which can affect nutrient cycling and plant diversity (Janse and Van Puijenbroek 1998; Di Nino et al. 2005).

Changes in species composition of aquatic systems often result from increased productivity following elevated nutrient availabilities (see for instance Squires and Lesack 2003). For instance, oligo- to mesotrophic lakes and ditches contain a well-developed vegetation with different submerged, mainly annual plant species (Forest 1977; Netten et al. 2010). Standing biomass typically ranges from 100-150 g DW/m^2 or lower in oligotrophic conditions (Downing and Anderson 1985; Bloemendaal and Roelofs 1988) to 200-400 g DW/m^2 at mesotrophic conditions (Forest 1977; van Wijk 1988). At eutrophic conditions the submerged vegetation may become dominated by a monoculture of fast growing,

evergreen submerged species like *Elodea nuttallii* (Planch.) St. John that outcompete other submerged plants (Portielje and Roijackers 1995; Kadono 2004; Arts and Leenders 2006) with a standing biomass between 500 – 1000 g DW/m^2 (Bloemendaal and Roelofs 1988; Ozimek et al. 1990; Di Nino et al. 2005). At very high nutrient concentrations a free floating plant dominated vegetation may develop in shallow and sheltered aquatic systems with a standing biomass of 100-200 g DW/m^2 (Bloemendaal and Roelofs 1988; Janse and Van Puijenbroek 1998; Driever et al. 2005).

Dominance of Elodea or free floating plants is frequently found in drainage ditches in the Netherlands as well as the diverse vegetation composition (Netten et al. 2010). Studies analysing the relations between macrophyte species composition and nutrient concentrations mainly focus on large aquatic systems (e.g. lakes) and often only take into account one source of nutrients (either water or sediment). It appeared that in those large aquatic systems vegetation composition is both influenced by water and sediment nutrient levels (see for instance Squires and Lesack 2003; James et al. 2005; Sayer et al. 2010). In smaller sized aquatic ecosystems such as drainage ditches a positive relation was found between P loading and the degree of free floating plant dominance in early successional stages of vegetation development in experimental drainage ditches (Portielje and Roijackers 1995). Furthermore, a shift from submerged to free floating plants could be modelled through increased N levels in water (Janse and Van Puijenbroek 1998; Scheffer et al. 2003). The study by van Liere et al. (2007) showed that critical nutrient levels at which those shifts may occur were 0.19-0.42 mg P/L and 1.3-3.3 mg N/L. Although there is general consensus that nutrients play a crucial role in changing plant community compositions of aquatic systems (Carpenter et al. 1998), hardly any field studies exist that investigated the importance of nutrients from both water and sediment for the occurrence of monocultures in small aquatic systems. The present study therefore relates both water and sediment nutrient concentrations to the occurrence of a diverse submerged vegetation type and two frequently observed monocultures in drainage ditches. The vegetation types are characterized by their biomass since biomass is a direct result of nutrient availability. Central in this study is the question which nutrients in water and sediment correlate best with differences in biomass composition of drainage ditch vegetation. The objectives are (1) to identify nutrient fractions in water and sediment that best explain the occurrence of monocultures (of *Elodea nuttallii* or free floating plants) and diverse submerged vegetation and (2) to determine the nutrient ranges at which the three vegetation compositions occur.

Materials and Methods

Drainage ditch characteristics
Ditches in the Netherlands are mainly found in agricultural areas. Average width of these ditches is around 4m and depth is around 50cm with water levels being mostly constant. Generally both free floating (such as duckweeds) and submerged plants (such as *Elodea nuttallii* and *Potamogeton* sp.) occur all through the ditch profile. Most variation in species distribution is usually found within a stretch of 25 m. In the Netherlands, plant growth shows a seasonal pattern starting around april and reaching peak biomass around the end of august. During autumn and winter die back of most biomass occurs (except for evergreen plants). Ditches are usually mown yearly in autumn using a mowing bucket while dredging is performed once every 5-10 years.

Data collection
Based on knowledge of regional water boards 90 ditches across the Netherlands were selected from which was known they either were dominated by free floating plants or by *Elodea nuttallii* or had a mixed vegetation in the previous 5 years. Field measurements were performed in June and September 2007 including sampling of water, biomass and determining species composition. Sediment samples were taken once in June (for descriptives see Table 1). Vegetation recordings were made with Tansley

coverage classes (Tansley 1946) by selecting a part of the ditch, approximately 25 m long, representing the vegetation composition in the ditch. All present vascular plant species were collected by wading through the transect and were identified up to species level. Biomass samples were taken in the same 25 m section. Biomass samples of complete plants (roots and shoots) were taken by selecting 1-3 patches in the ditch that together covered all variation in species composition and coverage. Vegetation was collected from a surface area of 900 cm^2. Total coverage of each patch in the ditch was used to calculate a weighted total amount of biomass per m^2. Biomass of free floating plants, *Elodea nuttallii* and other submerged plants was separated from each other in the field. Biomass of each of these subsamples was determined after removing any attached periphyton and sediment by rinsing with water and removing attached water by spinning the biomass around in a salad spinner for thirty seconds. To compare measured biomasses with those in literature, dry weights were estimated as being 10% of fresh weight (Forest 1977; Hasan and Chakrabarti 2009). Water samples were taken both in June and September. Three samples of the upper 20 cm of the water column were taken with a tube sampler, evenly distributed across the same transect in which vegetation data was collected and were mixed to one homogenized sample (volume 1 L). From this sample 50 ml was used for analyses on nutrients. Sediment was collected by taking a subsample from a homogenized sample consisting of three sediment cores, taken from the top 5 cm of the sediment along the transect used for collecting vegetation data. Water and sediment samples were stored in a freezer directly after collecting.

Chemical analysis
Water samples were analyzed for nutrients using a continuous flow analyser (Skalar Analytical BV, Breda, The Netherlands). Total phosphorus (P), total nitrogen (N), orthophosphate (PO_4^{3-}) and dissolved nitrogen ($NO_3^- + NO_2^-$) were analyzed following standard protocols (NNI 1986; NNI 1990; NNI 1997). $NO_3^- + NO_2^-$ and PO_4^{3-} were determined using the Griess-Ilosvay reagent ($NO_3^- + NO_2^-$ analysis) and ascorbic acid/antimony (PO_4^{3-} analysis). Total N and P were determined after a UV/per sulphate destruction. Concentrations of total N and P in sediment were determined on a segmented flow analyser after destruction with sulphuric acid/salicylic acid/ selenium/ hydrogen peroxide, with total N measurement based on the Berthelot reaction and total P measured as phosphate molybdenum (Novozamsky et al. 1983; Novozamsky et al. 1984).

Vegetation pre-analysis
From the 90 sampled locations, 23 ditches were removed from the dataset due to missing data or heavy disturbance during 2007 (for instance large scale reconstruction of ditch banks). The remaining data on 67 ditches was used to appoint ditches to one of the three vegetation types; dominated by *Elodea nuttallii* (hereafter called *Waterweed type)* or free floating plants *(Free floating type)* or being divers *(Mixed type.)* This was done by evaluating the amounts of the three sampled biomass fractions relative to the total biomass. Similar to Tansley's coverage classes 8 and 9, indicated as (co-)dominance with coverage ranging from 50 to 100% (Tansley 1946), a ditch was labelled as Free floating type or Waterweed type when more than 50% of the total biomass was made up of free floating plants or *Elodea nuttallii* respectively. It was assumed that Mixed type ditches contained biomass of a mixture of several species but with lower biomass of the ones responsible for monocultures. To this end ditches were selected that showed more than 50% submerged biomass other than *Elodea nuttallii*. Ditches at least had to meet these criteria at the peak of the growing season (September), when the vegetation was fully developed. 17 out of 67 ditches could not be properly classified and were left out of further analysis. Figure 1 shows the distribution in the Netherlands of the final 50 ditches involved in the data analysis described below.

Figure 1. Location of the sampled drainage ditches in the Netherlands (n=50)

Diversity measures and the number of red list species (species that are sensitive to disturbances and have decreased considerably in the last decades (LNV 2004)) were calculated for each vegetation type. Alpha diversity (diversity within a habitat) was calculated as the mean number of species per vegetation type. This was calculated as the total number of unique observed species in June and September per ditch, reflecting all species that can occur in the ditch throughout the growing season. Gamma diversity (total diversity on the landscape level) was calculated as the total number of species found in all ditches within each vegetation type. Beta diversity (the degree of differences in diversity between habitats) was calculated as Whittaker's measure $\beta_w = (\gamma/\alpha)-1$ (Magurran 1988). The degree of dominance in the vegetation relevees was calculated as 1- Simpson's index (D) with;

$$D = \sum_i \left(\frac{n_i}{n}\right)^2$$ where n_i is the coverage of taxon *i* and n is the total macrophyte coverage in the relevee (Magurran 1988). The index ranges from 0 (all taxa are equally present) to 1 (one taxon dominates the community).

Data analysis
The vegetation types were analyzed for differences in nutrient concentrations, total biomass and diversity measures (α-diversity and dominance index) by performing Kruskal-Wallis tests with posthoc comparisons of vegetation types (Bonferroni corrected). Kruskal-Wallis tests were used due to non-homogeneous variances. Patterns arising from statistical analyses on data from the 1st and 2nd sampling round were similar and therefore only results from the 1st round are presented. A Pearson's correlation matrix was used to identify strongly correlated nutrient fractions. A multinomial logistic regression was done with the nutrient fractions that differed significantly (according to the Kruskal-Wallis test) and were not strongly correlated (according to the Pearson correlation) to determine the contribution of the various nutrient fractions in explaining the differences between vegetation types. To determine at what

ranges of nutrient concentrations the vegetation types occur 95% confidence intervals were calculated per vegetation type for the nutrient fractions that contributed most in the multinomial logistic regression. To test whether the three vegetation types occurred at significantly different combinations of water and sediment P concentrations the level of group separation was tested with an ANOSIM with the Bray-Curtis distance measure and 10000 permutations, using PAST 1.91 (Hammer et al. 2001). All other statistical analyses were done using SPSS 18 (IBM 2009).

Results

Characteristics of vegetation types
Based on biomass composition respectively 20, 17 and 13 ditches were appointed to the Free floating, Waterweed and Mixed type. Each vegetation type contained the highest biomass of the similar named biomass fraction, both in June and September (Table 1). Ditches in the Free floating and Waterweed type on average contained respectively 97% (S.E.= 1.5) free floating plant biomass and 91% (S.E.= 2.3) *Elodea nuttallii* biomass in both sampling rounds. The Mixed type contained on average 61% (S.E.= 6.6) submerged biomass (other than from *Elodea nuttallii*), while average biomass of the other two biomass fractions was 19% (S.E. = 3.7) of the total biomass. Total biomass was comparable between the vegetation types for both months (Kruskal-Wallis, χ^2=0.682, df=2, p=.711).

Free floating type ditches showed a lower α-diversity compared to the Mixed type ditches (Table 2, Kruskal-Wallis, χ^2=10.132, df=2, p=.006), but was comparable to the Waterweed type (for observed species see Appendix 1). The dominance index was higher for the Waterweed type than for the Free floating and Mixed type (Kruskal-Wallis χ^2=6.839, df=2, p=.033) indicating a higher degree of dominance in the species composition of Waterweed dominated ditches. Both beta and gamma diversity were lowest for the Free floating type and highest for the Mixed type. Additionally, from the total of five recorded red list species none were found in the Free floating type, only one species was found in the Waterweed type while five out of thirteen ditches within the Mixed type contained one or more (maximum four) red list species.

3. *Occurrence of macrophyte monocultures in drainage ditches relates to phosphorus in both sediment and water*

Table 1. Distribution of the three biomass fractions (g fresh weight/m^2) for the defined vegetation types.

		Free floating type (n=20)	Waterweed type (n=17)	Mixed type (n=13)
Juni				
Free floating plants	**mean**	**1080**	**27**	**307**
	standard error	240	15	155
	minimum	14	0	0
	maximum	3411	231	2056
Elodea nuttallii	**mean**	**16**	**1102**	**233**
	standard error	16	302	104
	minimum	0	18	0
	maximum	318	4708	1078
Other submerged plants	**mean**	**0**	**91**	**794**
	standard error	0	58	317
	minimum	0	0	0
	maximum	3	833	3444
Total	**mean**	**1096**	**1219**	**1335**
	standard error	239	320	319
	minimum	14	18	150
	maximum	3411	4708	3444
September				
Free floating plants	**mean**	**1120**	**61**	**202**
	standard error	224	38	84
	minimum	7	0	0
	maximum	3811	572	866
Elodea nuttallii	**mean**	**15**	**757**	**149**
	standard error	15	149	60
	minimum	0	11	0
	maximum	300	2328	607
Other submerged plants	**mean**	**11**	**43**	**1174**
	standard error	11	29	336
	minimum	0	0	67
	maximum	210	502	4579
Total	**mean**	**1146**	**860**	**1525**
	standard error	221	165	376
	minimum	7	11	79
	maximum	3811	2385	4676

Table 2. Diversity measures for the three vegetation types. For α-diversity and Dominance mean values are shown with standard errors in parentheses. Letter codes (a,b) in superscript indicate the subgroup to which the vegetation types belong according to the Kruskal-Wallis posthoc comparison. For test statistics see results section. Dominance calculation is described in the methods section.

| Diversity measure	Free floating type (n=20)	Waterweed type (n=17)	Mixed type (n=13)
α-diversity (number of species per ditch)	6.65 (0.65)[a]	8.53 (0.55)[a,b]	9.46 (0.69)[b]
β-diversity (γ/α-1)	2.46	2.52	2.91
γ-diversity (total nr. of species in vegetation type)	23	30	37
Dominance (1-Simpson's index (D))	0.38 (0.04)[a]	0.52 (0.05)[b]	0.36 (0.04)[a]
Number of red list species	0	1	5
Number of ditches containing red list species	0	1	5

Differences in nutrient concentrations between vegetation types

Figure 2A shows that the Free floating type was found at PO_4^{3-} concentrations in water around ten to thirty times higher than the Waterweed type and the Mixed type (Kruskal-Wallis, χ^2=28.597, df=2, p<.001) whereas total P concentrations in water (Figure 2B) were four to six times higher in the Free floating type than in the Waterweed and Mixed type (Kruskal-Wallis, χ^2=23.760, df=2, p<.001). Total P concentrations in the sediment (Figure 2C) were almost two times higher in the Free floating type than in the Waterweed type, while concentrations in the Waterweed type were also around two times higher than those in the Mixed type (Kruskal-Wallis, χ^2=22.112, df=2, p<.001). NO_3 + NO_2 (Figure 2D) and total N (Figure 2E) concentrations in water did not show any significant differences (NO_3^- + NO_2^- : Kruskal-Wallis, χ^2=2.473, df=2, p=.290; total N: Kruskal-Wallis, χ^2=2.873, df=2, p=.238), while total N in sediment (Figure 2F) differed between the Free floating and Mixed type. Total N sediment concentrations in the Waterweed type were comparable to both the Free floating and Mixed type (Kruskal-Wallis, χ^2=8.823, df=2, p=.012).

Weak correlations were found between total N - NO_3^- + NO_2^- in water, total P sediment – total P water and total P sediment – total N sediment, values ranging between .450 and .500 (Table 3). A moderately high correlation was found for PO_4^{3-} and total P in water. Therefore, the multinomial logistic regression was done with total P in water and sediment and total N in sediment as explaining variables. The resulting regression model explained 45% more of the variance compared to the model with only the intercept (χ^2=48.769, df=6, p<.001). Total P in water (χ^2=20.255, df=2, p<.001) and total P in sediment (χ^2=12.039, df=2, p=.002) contributed significantly to this explained variance with net contributions of respectively 41.5% and 24.7%. Total N in sediment contributed 2.6%, which was not significant (χ^2=1.288, df=2, p=.525). Therefore total P in water and sediment were used to determine the 95% confidence intervals as these two nutrient fractions performed best in the regression model.

Figure 3 shows that the 95% confidence intervals for total P in water and sediment are rather separated for the three vegetation types, even though there is some overlap in the locations of individual ditches. The ANOSIM resulted in significant group separation between all vegetation types (ANOSIM, R=0.285, mean rank within= 496.1, mean rank between= 670.5, p<.001). Each vegetation type belonged to an inherent 'group' with p-values for each comparison of two vegetation types ranging from .000 to .020. The Mixed type mainly occurred at total P sediment concentrations between 236 and 482 mg/kg (respectively lower and upper boundary of 95% confidence interval) while the Waterweed type is mainly found at higher concentrations (between 551 and 1052 mg/kg). The 95% confidence interval of the Free floating type shows some overlap with that of the Waterweed type but is mainly restricted to the highest values, ranging from 1008 to1614 mg/kg. The Free floating type occurs at higher total P concentrations in water (between 0.42 and 0.73 mg/L) than a submerged vegetation (Waterweed or Mixed type). Both the Waterweed and Mixed type are mainly found at values between 0.10 and 0.22 mg/L.
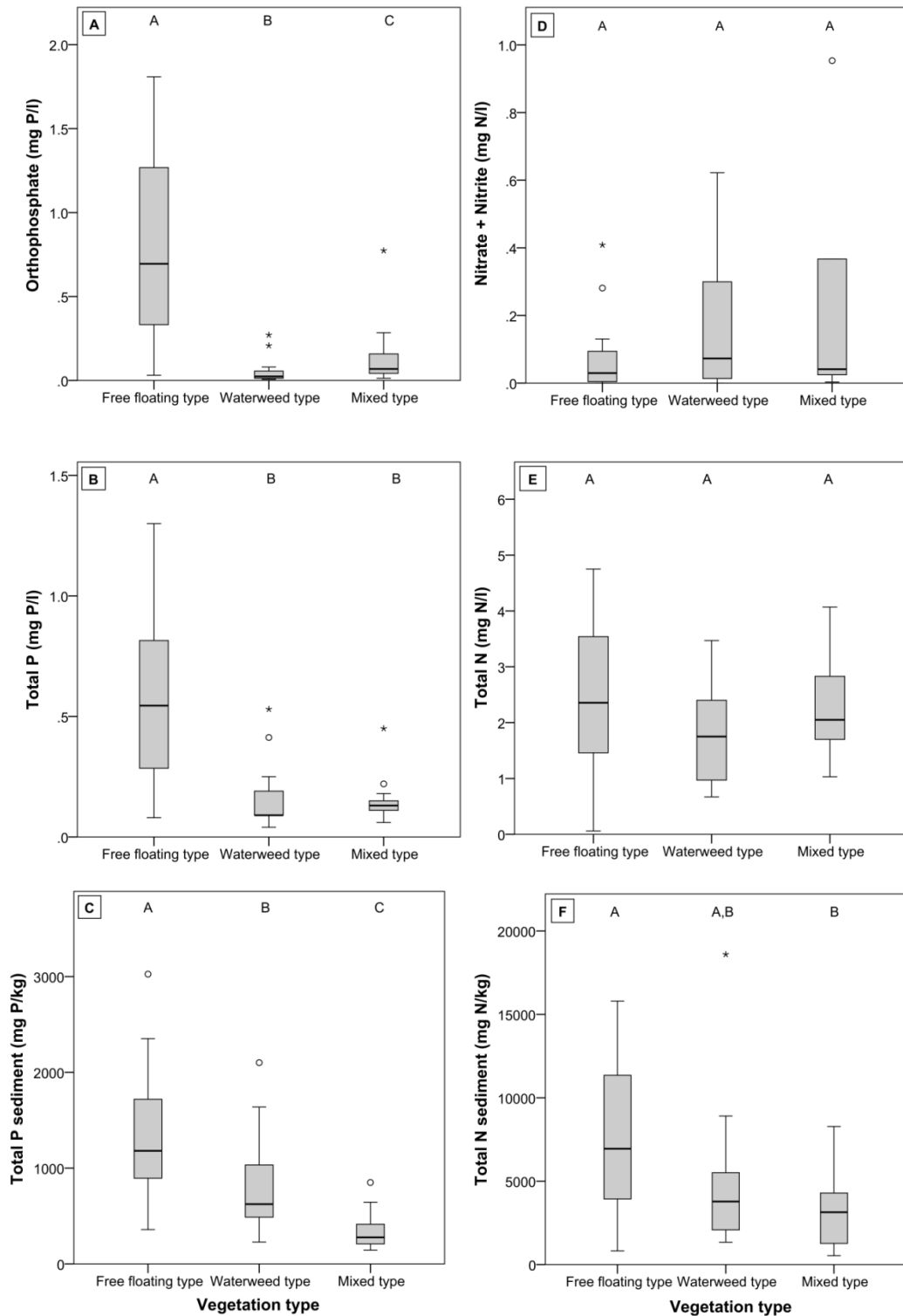
Figure 2. Boxplots with ranges of nutrient concentrations of the three vegetation types, measured in June 2007. The horizontal line within the grey box represents the median value. Grey box contains 50% of all values. Whiskers contain 75% of all values. Circles indicate outliers, asterisks indicate extremes. Letter codes on top of the boxplots indicate similar or significantly different groups according to Kruskal-Wallis tests with posthoc comparisons (Bonferroni corrected). For test statistics see Results.
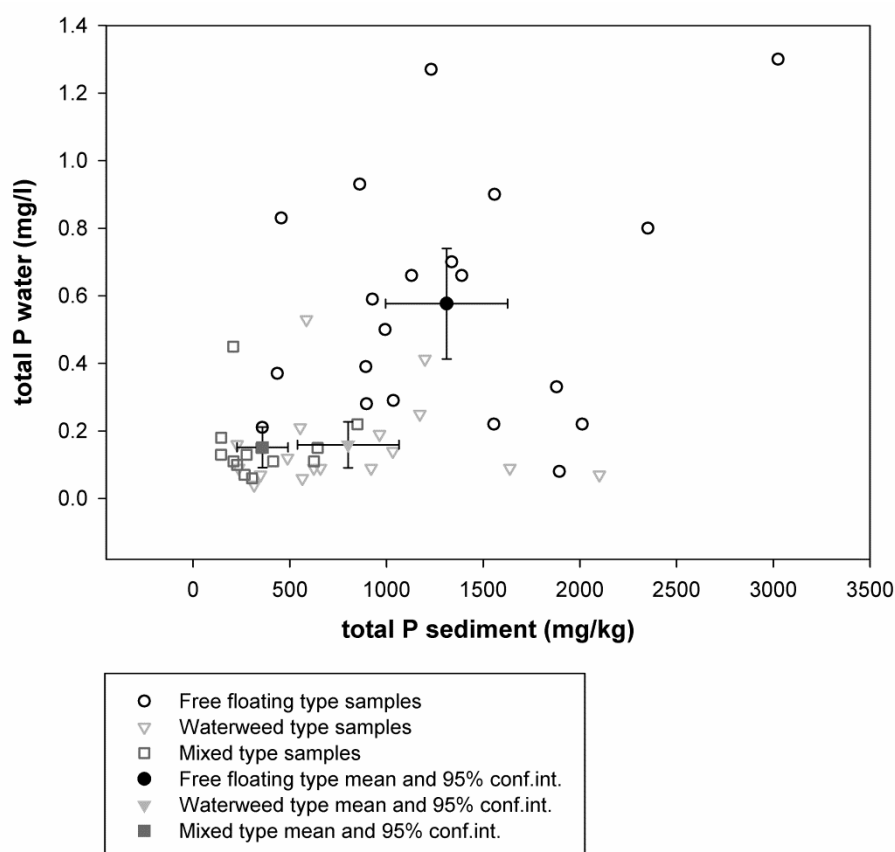
Figure 3. Scatter biplot for total P in water and sediment, measured in June 2007. Individual samples (n=50) are shown together with the mean and 95% confidence interval for each of the three vegetation types.

Table 3. Pearson correlation matrix for the nutrient fractions (n=50). Significant correlations (α=0.05) are indicated by *.

		PO_4	Total P	$NO_3 + NO_2$	Total N	Total P sediment
Total P	Pearson Correlation	.641*				
	Sig. (2-tailed)	.000				
$NO_3 + NO_2$	Pearson Correlation	-.067	-.024			
	Sig. (2-tailed)	.644	.868			
Total N	Pearson Correlation	.017	.146	.483*		
	Sig. (2-tailed)	.904	.311	.000		
Total P sediment	Pearson Correlation	.141	.479*	-.023	-.055	
	Sig. (2-tailed)	.327	.000	.872	.703	
Total N sediment	Pearson Correlation	-.010	.270	-.115	.191	.455*
	Sig. (2-tailed)	.946	.058	.425	.184	.001

Discussion

Nutrients and occurrence of monocultures

The results show that P in both water and sediment contribute to explaining the occurrence of monocultures in shallow aquatic systems. Total P in water only differed between the dominance of free floating plants and ditches with one of the two submerged vegetation types, while sediment P concentrations especially play an important role in distinguishing the Waterweed monocultures from the Mixed type. Although minerals such as iron and manganese may also play a role in macrophyte growth (see for instance Steinberg 1946), the results of the present study confirm the importance of P found for

lakes, streams and in some drainage ditch studies (Portielje and Roijackers 1995; Thiébaut and Muller 1998; Hilt et al. 2006; van Liere et al. 2007). The role of nutrients in both water and sediment is in line with the large influence of soil-water interactions found in shallow aquatic systems (Herzon and Helenius 2008). Although limitation by both N and P may occur frequently in aquatic systems (Elser et al. 2007), N limitation does not seem to occur in the present study since N fractions showed weak relations with the vegetation types. The continuous high input of N from agricultural fields into surface water (Lamers et al. 2002) may cause a non-limiting availability, while high uptake rates may cause low measured concentrations in water.

The three vegetation types occur in distinctive ranges of nutrient concentrations. The occurrence of the two monocultures is related to higher P concentrations in water (for the Free floating type) and sediment (for both the Free floating and Waterweed type) compared to the Mixed type. Chambers (1987) also found that increased nutrient concentrations in the sediment led to a shift from rosette and bottom dwelling species like *Chara* sp. to canopy forming species like *Elodea canadensis* Michx. The transition from a diverse submerged vegetation to *Elodea nuttallii* dominance at higher sediment P concentrations may occur when *Elodea nuttallii* outcompetes other submerged plants due to its higher uptake efficiency and growth rate at high nutrient availability (Nichols and Shaw 1986). The high competitive ability of *Elodea nuttallii* is illustrated by the higher degree of dominance and lower number of red list species in the Waterweed type, compared to the more heterogeneous Mixed type. The lack of a clear relation between higher water P concentrations and the occurrence of the Waterweed and Mixed type might result from the preferred uptake of nutrients from the sediment by submerged plants, irrespective of the nutrient concentrations in water (Carignan and Kalff 1980). The relation between the Free floating type and higher water P concentrations can be expected as free floating plants only have access to the water phase as a nutrient source while simultaneously having the primacy for light, enabling them to outcompete submerged plants at high water nutrient levels (Portielje and Roijackers 1995; Scheffer et al. 2003; van Liere et al. 2007; Herzon and Helenius 2008). The positive relation with sediment P concentrations is likely caused by the release of P from the anoxic but nutrient rich sediments into the water phase through which it becomes available for free floating plants (Janse and Van Puijenbroek 1998).

The Mixed type is mostly found in ditches with sediment that can be classified as oligo- to mesotrophic, while both the Waterweed and Free floating type are found in ditches with sediments classified as eutrophic (Bloemendaal and Roelofs 1988). The lower range of total P concentrations in water at which free floating plant dominance was found in this study are comparable to the model predictions by van Liere et al. (2007) who indicated that a shift from submerged vegetation to free floating plant dominance in ditches would occur at water P concentrations between 0.2 and 0.4 mg/L. Most ditches with free floating plant dominance are found at higher total water P concentrations though.

Biomass
No differences in total biomass were found between the vegetation types. This is in contrast with Bloemendaal and Roelofs (1988), who describe an optimum curve for the relation between water P levels and macrophyte biomass. They describe that the highest biomass (up to 1200 g DW/m^2) is found at meso- to eutrophic conditions at which a submerged vegetation produces biomass throughout the whole water column. At eutrophic to hypertrophic conditions, when only free floating plants dominate, the total biomass is lower (up to 200 g DW/m^2) as production is only located at the top of the water column. In the present study the total biomass of the Mixed type confirms the ranges described for mesotrophic systems with a mixed vegetation or with *Potamogeton* species (Forest 1977; van Wijk 1988) and also the total biomass in the Free floating type is in accordance with previous studies (for instance Janse and Van Puijenbroek 1998; Driever et al. 2005). Interestingly, the total biomass of the Waterweed type is approximately 5 times lower compared to other studies by for instance Di Nino et al.

(2005) and Ozimek et al. (1990) who report values from 500 to more than 800 g DW/m^2. A possible explanation for this relatively low *Elodea nuttallii* biomass in drainage ditches might be the limited depth of most drainage ditches (depths are comparable between the Waterweed and Mixed type). The high biomasses reported in literature (for instance Ozimek et al. (1990) and Pokorný et al. (1984)) for *Elodea* species were obtained in deeper water systems. Due to the limited depth *Elodea nuttallii* might not be able to use additional available nutrients to produce more biomass when all available space is already filled. Thus, if all space in the water column is already used, additional available nutrients will not lead to more biomass. A second and alternative explanation could be the increased P-uptake efficiency of *Elodea nuttallii* at higher P availability leading to faster growth (Garbey et al. 2004; James et al. 2006) and increased P concentrations in plant tissue (Sterner and Elser 2002; Garbey et al. 2004). This higher uptake efficiency at higher P availability may consequently be reflected in higher tissue P concentrations rather than in higher total biomass. The stored P may for example be used to produce vegetative reproductive organs or to maintain growth if nutrient concentrations in the water decrease. Garbey et al. (2004) showed that *Callitriche platycarpa* Kütz. and *C. hamulata* Kütz. ex Koch displayed lower nutrient use efficiencies and tissue P content at increased nutrient availability compared to *Elodea nuttallii*. Several other species characteristic for a more diverse vegetation such as *Chara vulgaris* L., *Potamogeton zosteriformis* Fernald (Hough et al. 1989), *Potamogeton lucens* L. (Mazej and Germ 2008) and *Myriophyllum alterniflorum* DC. (Fernández-Aláez et al. 1999) also show relatively low tissue P concentrations. If these species are less able to profit from higher nutrient availability by additional growth or storage (see for instance Demars and Edwards (2007)) they may be outcompeted by species like *Elodea nuttallii*. This way higher P concentrations may result in the development of the Waterweed type at comparable total biomass. However, for many of the mentioned species from more diverse vegetation little is known about the plasticity in nutrient uptake efficiency. This might be caused by a lack of studies on this subject, though several of these species might hardly be found under highly eutrophic conditions. A possible third explanation for the low biomass of the Waterweed type could be the effect of mowing which is common in the Netherlands to secure the drainage function of highly productive ditches (Peeters 2005). Di Nino et al. (2005) for instance found a maximum standing stock of *Elodea nuttallii* in a stream of 822 g DW/m^2 without cutting and 180 g DW/m^2 with cutting early in the growing season. However, *Elodea nuttallii* will likely remain dominant in these disturbed systems due to its fast regrowth and regeneration from stem fragments (Di Nino et al. 2005).

Implications for water quality management
Considering the negative effects of dominance by both free floating plants and *Elodea nuttallii* on ecosystem functioning (Di Nino et al. 2005; Janse and Van Puijenbroek 1998) it seems necessary for water managers to lower both water and sediment P levels in drainage ditches with a monoculture to values at which the Mixed type was found in this study. However, to cause a shift towards the Mixed type even lower nutrient levels might be needed to overcome the possible resilience of for instance the Free floating type (Scheffer et al. 2001). Rigorous additional measures such as removal of the propagule bank of free floating plants or reintroduction of previously present submerged species might further support reestablishment of the Mixed type (van Zuidam et al. 2012; Hilt et al. 2006).

The focus of present water quality legislation in the Netherlands is only on nutrient levels in water with targets for total P in water being around 0.2 mg P/L (Evers et al. 2007). Considering the present study, lowering P levels of inflowing water to concentrations below 0.2 mg/L will probably be insufficient to prevent free floating plant dominance when sediment P concentrations are still higher than 1000 mg/kg. Exchange of P from the sediment to the water will likely elevate the P concentrations in water (Roelofs 1991), supporting free floating plant dominance, thereby raising the need for additional removal of P rich sediments. To suppress excessive growth of *Elodea nuttallii* and promote development of the Mixed type a reduction of P in sediment to concentrations below 500 mg/kg is likely needed. It seems useful to include targets for sediment P concentrations in current water quality

legislation although negative effects of dredging should be taken into account when considering large scale sediment removal. Among possible negative effects are loss of aquatic fauna (Twisk et al. 2000), decreased nutrient removal by benthic biota and increased nutrient fluxes from newly exposed, nutrient rich layers (Smith and Pappas 2007).

Even though reduced nutrient concentrations might create favourable conditions for restoration of the Mixed type, frequent mowing might still cause persistence of the Waterweed type as *Elodea nuttallii* is capable of showing fast regeneration and spreading after disturbance (Barrat-Segretain et al. 1998). Since Peeters (2005) showed that the highest species richness in ditches was found at intermediate mowing frequencies, lowering mowing frequency as an additional measure might further stimulate recolonisation by other submerged species.

Acknowledgements

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3. *Occurrence of macrophyte monocultures in drainage ditches relates to phosphorus in both sediment and water*

Appendix 1. Observed plant species and nr. of observations

Species name	Total nr. of observations	Highest observed coverage (Tansley class)
Filamentous algae	62	9
Azolla filiculoides Lam.	30	9
Fontinalis antipyretica Hedw.	8	5
Callitriche sp. L.	26	7
Ceratophyllum demersum L.	64	9
Chara sp. L.	17	8
Egeria densa Planch.	2	2
Elodea canadensis Michx.	11	9
Elodea nuttallii (Planch.) H. St. John	86	9
Groenlandia densa L.	1	1
Hottonia palustris L.	2	2
Hydrocharis morsus-ranae L.	38	8
Lemna gibba L.	54	9
Lemna minor L.	111	9
Lemna minuta Kunth.	30	9
Lemna trisulca L.	75	9
Myriophyllum alterniflorum DC.	1	6
Myriophyllum spicatum L.	19	9
Myriophyllum verticillatum L.	4	2
Nitella sp. C. Agardh.	12	9
Nuphar lutea (L.) Sm.	9	5
Nymphoides peltata (S.G.Gmel.) Kuntze	8	8
Nymphaea alba L.	4	7
Potamogeton acutifolius Link	3	3
Potamogeton berchtoldii Fieber	1	5
Potamogeton compressus L.	3	6
Potamogeton crispus L.	9	5
Potamogeton lucens L.	8	8
Potamogeton mucronatus Sonder	2	2
Potamogeton natans L.	11	6
Potamogeton obtusifolius Mert. & Koch	9	6
Potamogeton pectinatus L.	6	5
Potamogeton perfoliatus L.	3	2
Potamogeton pusillus L.	1	2
Potamogeton trichoides Cham. & Schltdl.	18	7
Ranunculus circinatus Sibth.	8	6
Ranunculus sp. L.	7	2
Riccia fluitans L.	16	7
Ricciocarpos natans L.	2	7
*Spirodela polyrhiza (*L.) Schleid.	81	6
Stratiotes aloides L.	5	9
Utricularia sp. L.	4	8
*Wolffia arrhiza (*L.) Horkel ex Wimm.	19	8
Zannichellia palustris L.	6	5
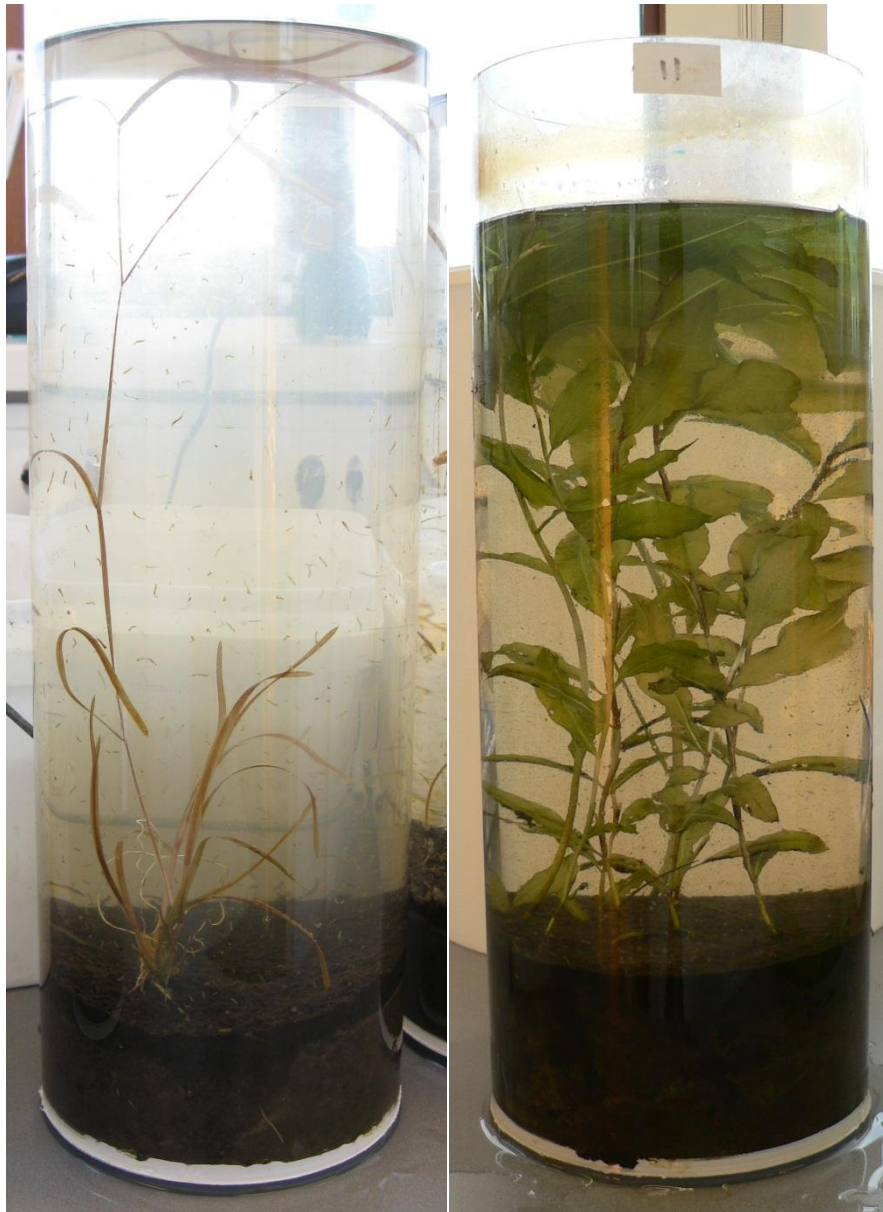
Transparant cylinders used for the cutting experiment described in chapter 4, with *Potamogeton compressus* (left) and *Potamogeton lucens* (right).

4. Cutting affects growth of *Potamogeton lucens* L. and *Potamogeton compressus* L.

Abstract
Effects of cutting on the growth of *Potamogeton lucens* L. and *Potamogeton compressus* L. were studied indoor under experimental conditions. Plants were cut every time they reached the water surface, applying three depth treatments at which the plants were cut; halfway down the water column, at three-quarters down the water column and at the sediment-water interface. For both species short term negative effects of cutting on biomass production and survival were observed. *P. lucens* seemed to be the more tolerant species as only below-ground biomass was significantly lower when cutting biomass at the sediment-water interface together with a downward trend in shoot biomass at increasing cutting depth. The low below-ground biomass (less than 20% of that in the controls) was caused by the death of most plants in this treatment. *P. compressus* was more vulnerable with every treatment resulting in significantly lower below-ground and green shoot biomass production. The lowest biomass for *P. compressus* was observed when plants were cut at the sediment-water interface with values more than 80% lower compared to the controls, while cutting halfway and at three-quarters resulted in values 30-50% lower compared to the controls. Long term effects of cutting on *P. lucens* might occur through decreased development of the rhizome network. Long term effects on reproduction of *P. compressus* might be expected as flowering decreased when cut at the sediment-water interface, while turion formation only occurred in the uncut controls. Additionally, the decreased biomass production by *P. compressus* may lead to a competitive disadvantage in the field as fast-growing, disturbance tolerant species such as *Elodea nuttallii* (Planch.) St. John may outcompete the species. Creating patchiness in mowing height and frequency or applying a mowing regime that leads to reduced biomass development while species still survive might create opportunities to both maintain the water transporting function of drainage ditches while preserving the species in the system.

Introduction

Macrophytes are essential for the ecological functioning of aquatic systems since, amongst others, they offer habitat for fauna due to their architecture (Waters and San Giovanni, 2002; Christie et al., 2009; Bakker et al., 2010) and remove nutrients from water and sediment (Bouldin et al., 2004; Cooper et al., 2004). Eutrophication has led to a decreased plant diversity in many systems (Thiébaut and Muller, 1998; Hilt et al., 2006; Bakker et al., 2010) while the development of fast-growing species like *Elodea* nuttallii (Planch.) St. John and *Myriophyllum spicatum* L. is often promoted (Nichols and Shaw, 1986; Mesters, 1995), especially in small and shallow aquatic ecosystems like drainage ditches. This increased productivity of fast-growing species under eutrophic conditions results in the need to remove vegetation more frequently to prevent drainage problems. Mowing can affect plant species composition (Beltman, 1987; Best, 1994) and a decrease in species diversity is often observed in systems subject to maintenance (Baattrup-Pedersen et al., 2003; Peeters, 2005). Mowing damages green parts of the plant and may also uproot plants. If below-ground parts and green shoots do not remain present after mowing this will lead to the disappearance of species during the growing season. Maintenance may also restrict the possibilities for species to produce propagules for the next growing season such as seeds and turions, thereby possibly jeopardizing long term survival of species. Contrastingly, disturbance tolerant species may profit from a high level of disturbance by expanding and eventually becoming dominant in the system (Bornette et al., 1994; Di Nino et al., 2005), accelerating the decrease in biodiversity of the system.

Potamogeton species (Pondweeds) are a major component in many macrophyte communities, are found worldwide with around 100 different species (Pip, 1987; Wiegleb and Kaplan, 1998) but have also declined in parts of Europe due to human influences among which maintenance is one of them (Wiegleb et al., 1991). The genus contains species that are indicators for different levels of water quality (Sastroutomo, 1981) and disturbance (Wiegleb et al., 1991). Some species for instance occur at eutrophic conditions and invest a large part of their energy in subsurface overwintering parts such as rhizomes (e.g. *P. lucens* L., *P. gramineus* L. and *P. natans* L.) (Wiegleb et al., 1991) while other species

may occur as annuals at mesotrophic conditions and produce above ground reproductive parts such as seeds and turions (e.g. *P. compressus* L. and *P. acutifolius* Link. (Wiegleb and Kaplan, 1998; Pot, 2003)). In both Britain and the Netherlands this species is endangered and in the latter it has a protected status.

In the field, eutrophication and increased maintenance intensity often occur simultaneously. Therefore, the disappearance of species is difficult to attribute to either eutrophication or maintenance. In this paper focus is on the effects of maintenance and the effects of cutting on the performance of two Pondweed species is investigated. The main objective of the study is to quantify the effects of cutting on the growth of *P. lucens* L. and *P. compressus* L. It is hypothesized that (1) cutting will result in decreased biomass production, (2) cutting away more biomass will cause less regrowth and (3) *P. lucens* will be more tolerant to cutting than *P. compressus* due to the differences in growth form (respectively high and low root:shoot ratio). To test these hypotheses an experiment was conducted in which 4 different cutting treatments were applied to both species. This was done under comparable conditions during a period of 6 months.

Materials and methods
Setup
Transparent cylinders with a closed bottom, 45 cm high and 14 cm in diameter were used as test microcosms. Each microcosm was filled with five cm of sediment and five L of Smart and Barko culture solution without nutrients (Smart & Barko, 1985). All microcosms were kept at a water temperature of 20 $^{\circ}$C and a photoperiod of sixteen hours light: eight hours dark. Philips Son Agro 430W HPS lights were used at a mean light intensity of 64 W/m^2 (Philips, 2012). Water levels were checked weekly and were kept constant by adding demineralized water. All microcosms were aerated continuously and pH was measured every two weeks. pH was kept at a value between six and eight by adding drops of sodium hydroxide or hydrogen chloride solution if needed while measuring the change in pH. Adjustments of pH were only needed occasionally. Therefore pH fluctuations likely had limited effect on the results of the experiment. To suppress phytoplankton bloom 20 individuals of *Daphnia magna* were added, which were replenished if necessary. Biomass of filamentous algae was removed by hand.

Sediment was collected from a drainage ditch in the Netherlands that accommodated both species and was located in the Natura 2000 area 'De Wieden' (52°45'49.81"N, 6°5'59.58"E). Prior to the experiment, plants of both species were cultivated under the same conditions as the main experiment to obtain sufficient material. For the main experiment, *P. lucens* plants with a horizontal rhizome of nine cm long and an attached vertical shoot of five cm long were used. For *P. compressus* turions with a mean length of six cm were used. One plant fragment was planted in each of the microcosms. The Smart and Barko solution contained no nutrients to prevent algal blooms, assuming the Pondweeds would acquire nutrients from the sediment. It was assumed that nutrient supply did not influence the experimental results as sediment N and P concentrations hardly changed during the experiment.

Treatments
Four treatments were applied: 1) control in which no cutting was applied, 2) cutting halfway the water column at approximately 17.5 cm depth, 3) cutting at three-quarter of the water column at approximately 26 cm depth and 4) cutting at the bottom without disturbing sediment and below-ground parts. All plant shoots were cut each time a single shoot reached the water surface. This implies that the number of cuttings was different between treatments. Four replicates per treatment were used resulting in 16 microcosms per plant species. The experiment was ended when plants in the control treatment started to show decay of leaves and stems which was after 160 d and 187 d for respectively *P. lucens* and *P. compressus.*

Data collection and analyses
Plant development was monitored by measuring the total length of all standing green shoots several times during the experimental period. This was done by placing a ruler in the microcosm and measuring all vertical shoots. On average this was done every 25 days.

Dry mass (g DW) was determined of shoots cut during the experiment, total shoots (sum of the shoots cut and shoots removed at the end of the experiment) and below-ground parts at the end of the experiment. Also total length (cm) of the shoots produced during the experiment was measured and the

number of flowers and turions that developed during the experiment were recorded. Additionally mean dry mass per cm shoot was calculated for all collected green shoots. The data was analysed using ANOVA and Tukey-b posthoc tests in SPSS 17 (SPSS, 2009).

Results
Course of the experiment
Within one month after the start of the experiment all plants of *P. lucens* (Figure 1A) started growing and within three months they all reached the water surface. Insufficient data was available for the period between the 6th of October 2009 and 11th of January 2010 to illustrate this development (Figure 1). Total length of the shoots at 11th January was still comparable for all treatments. Thereafter total length of plants cut at the sediment-water interface hardly increased, while in the other treatments shoots continued their growth. Plants cut at three-quarters down the water column showed moderately lower values compared to the controls and plant cut halfway down the water column although standard errors were rather high. *P. compressus* (Figure 1B) developed faster as within one month all plants had reached the water surface. From the 3rd of May, plants cut at the sediment-water interface showed less shoot development compared to the other treatments. At the final monitoring date some treatments had a lower mean value compared to the previous date (Figure 1). This seems to be caused by a measuring error as all lengths of shoots were measured under water in the microcosms, except for the final measurement when lengths were measured after all shoots had been removed from the microcosms.

The first cuttings of *P. lucens* were on average performed after 85 days while for *P. compressus* this was after 31 d. After the first cutting, the average time in between cuttings was comparable for *P. lucens* and *P. compressus* being respectively 31 and 28 d. Compared to *P. lucens,* the number of cuttings was higher for *P. compressus* for cutting halfway and at three-quarters down the water column (Table 1).

Nutrient concentrations in the sediment were moderate (Bloemendaal and Roelofs, 1988) and hardly changed during the experiment (Table 2). The difference in total N in the sediment between the two experiments was caused by the two separate field visits in which the sediment for the two species was collected, although the sediment was collected at the same location.
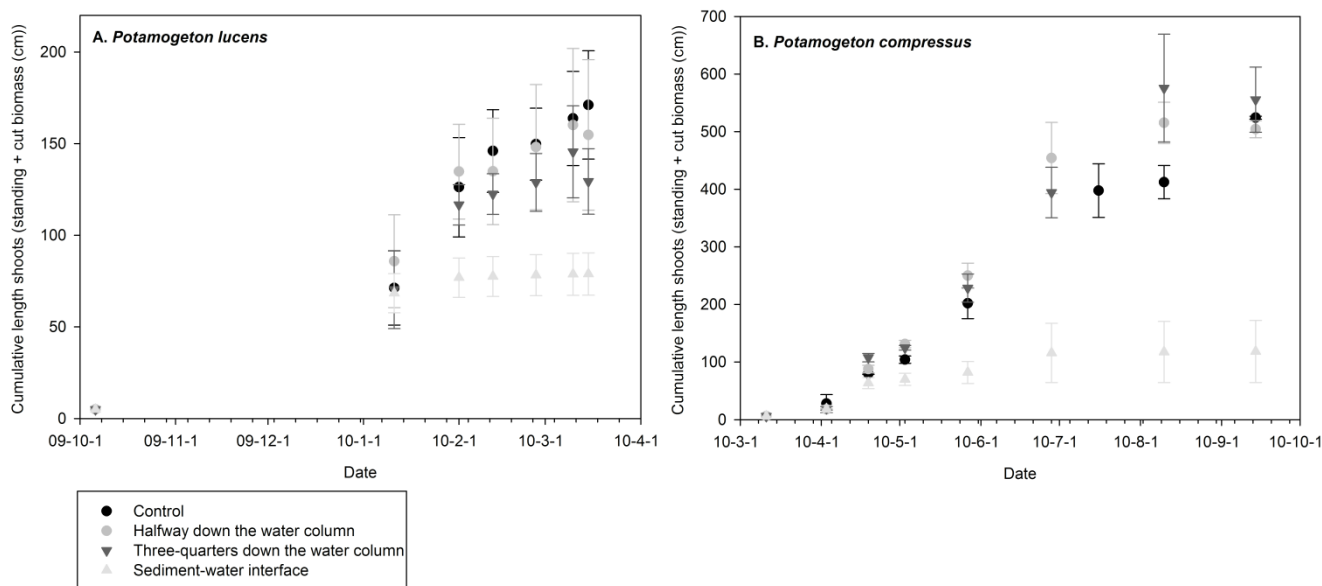
Figure 1. Development of cumulative shoot length per treatment during the experiment for *Potamogeton lucens* (A) and *P. compressus* (B). Cumulative shoot length was calculated as the sum of all meristems in the microcosm and the total length of cut meristems till each date. Mean values and standard error are shown per treatment. Each point in the figure represents at least three replicates. Data from the same replicates was used for every monitoring date in each treatment. The values at the first date represent the mean length of the green shoot attached to the rhizome fragment and mean length of the turions that were planted for respectively *P. lucens* ad *P. compressus*.

Table 1. Descriptives of the number of cuttings per treatment. n=4 per treatment.

Treatment	*Potamogeton lucens* L.				*Potamogeton compressus* L.			
	Mean	Standard error	Min	Max	Mean	Standard error	Min	Max
Control	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Halfway	2.50	0.87	0.00	4.00	4.75	0.48	4.00	6.00
Three-quarters	2.00	0.41	1.00	3.00	4.25	0.85	2.00	6.00
Water-sediment interface	1.25	0.25	1.00	2.00	1.50	0.50	1.00	3.00

Table 2. Nutrient levels in water and sediment at the start and end of the experiment for both Pondweed species. Mean concentrations are given with standard errors in parentheses. For total N and P in sediment no standard errors are available for the start concentrations as these were determined in one sample from the homogeneous sediment stock with which the microcosms of a species were filled. For each species a separate sediment stock was used, both collected at the same location. Total N and P in water at the start was always zero as no nutrients were added to the culture solution.

	Potamogeton lucens L.		*Potamogeton compressus* L.	
	Start	End	Start	End
Sediment:				
total N (mg/kg)	5020 (n.a.)	5030 (120)	3400 (n.a.)	3500 (70)
total P (mg/kg)	317 (n.a.)	292 (7)	239 (n.a.)	223 (5)
Water:				
total N (mg/L)	0 (0)	1.23 (0.08)	0 (0)	1.27 (0.06)
total P (mg/L)	0 (0)	0.06 (0.01)	0 (0)	0.04 (0.00)

Produced biomass

The dry mass of the cut shoots during the experiment (Table 3) showed significant differences between the treatments for both species. Especially cutting at the sediment-water interface resulted in a lower yield compared to the other treatments, caused by the death of three out of four replicates after the first cut for both species. Interestingly, dry mass was comparable for cutting halfway and at three-quarters down the water column for both species.

The total dry mass of shoots (yield from cutting + standing biomass at the end of the experiment) in *P. lucens* showed a negative trend with decreasing yield when more biomass was removed at each cutting. Differences were not statistically different for the treatments though, partly due to the relatively large variation. For *P. compressus* cutting halfway and at three-quarters down the water column gave comparable results while the control and cutting at the sediment-water interface respectively resulted in about five times higher and one and a half times lower values.

The below-ground biomass in *P. compressus* showed a similar pattern in differences between the treatments as was found for total shoot biomass while for *P. lucens* only cutting at the sediment-water interface resulted in about five times lower values compared to the control although this difference was not significant according to the ANOVA (Table 3).

Total length of shoots produced during the experiment was not statistically different between the treatments for *P. lucens* (Table 3) but a negative trend is visible with decreasing yield when more biomass was removed per cut (Figure 1A). The controls showed higher values compared to cutting at three-quarters down the water column during the second half of the experimental period, while cutting at the sediment-water interface resulted in lower values compared to cutting at three-quarters during that same period. For *P. compressus* cutting at the sediment-water interface resulted in significantly lower total length, caused by the death of three out of four replicates. The dry mass per cm shoot of *P. compressus* was significantly higher (approximately one and a half times) for the control compared to the other three treatments whereas for *P. lucens* no significant differences were found (Table 3).

Flowering and turion formation

Flowering was only observed for *P. compressus* and did not occur in *P. lucens* (Table 3). The number of flowers was significantly lower when plants were cut at the sediment-water interface (only one flower in one replicate) compared to cutting halfway down the water column which had on average two to five flowers. Turion formation only occurred in the controls of *P. compressus*.

Table 3. Mean values and standard errors (in parentheses) for produced biomass and reproductive organs by *Potamogeton lucens* and *P. compressus.* Asterisks (*) indicate significant differences between treatments (p<0.05). Letter codes in superscript indicate different subsets according to Tukey-b posthoc tests.

	Treatment				Statistics ANOVA (df = 15)	
	Control	Halfway	Three-quarters	Sediment-water interface	F	p
P. lucens						
Dry mass cut shoots (g)	0 (0)[A]	0.65 (0.20)[B]	0.68 (0.15)[B]	0.45 (0.09)[A,B]	5.728	0.011*
Total dry mass shoots (g)	1.04 (0.24)[A]	1.00 (0.26)[A]	0.79 (0.14)[A]	0.46 (0.10)[A]	1.779	0.205
Dry mass below-ground parts (g)	0.56 (0.19)[A]	0.30 (0.11)[A,B]	0.22 (0.08)[A,B]	0.07 (0.03)[B]	3.191	0.063
Total length shoots (cm)	171 (29.55)[A]	155 (41.04)[A]	129 (17.88)[A]	79 (11.51)[A]	2.156	0.146
Dry mass per cm shoot (g)	5.83 (0.48)[A]	5.86 (0.55)[A]	6.08 (0.36)[A]	5.58 (0.62)[A]	0.159	0.922
P. compressus						
Dry mass cut shoots (g)	0 (0)[A]	1.02 (0.04)[B]	1.02 (0.16)[B]	0.33 (0.11)[A]	26.153	0.000*
Total dry mass shoots (g)	2.52 (0.16)[A]	1.75 (0.05)[B]	1.69 (0.18)[B]	0.34 (0.12)[C]	43.645	0.000*
Dry mass below-ground parts (g)	0.88 (0.15)[A]	0.43 (0.06)[B]	0.51 (0.06)[B]	0.02 (0.02)[C]	16.969	0.000*
Total length shoots (cm)	512 (12.79)[A]	532 (29.23)[A]	509 (61.38)[A]	118 (53.92)[B]	20.741	0.000*
Dry mass per cm shoot (g)	4.93 (0.28)[A]	3.31 (0.12)[B]	3.36 (0.21)[B]	3.26 (0.30)[B]	11.606	0.001*
number of flowers	2.50 (1.19)[A,B]	3.50 (0.65)[B]	1.00 (0.71)[A,B]	0.25 (0.25)[A]	3.574	0.047*
number of turions	18.50 (4.25)	0 (0)	0 (0)	0 (0)		

Discussion

Short term effects

Short term negative effects of cutting on biomass production and survival are observed for both species. *P. lucens* seems to be more tolerant to cutting. Total shoot biomass is comparable between treatments, partly due to the large variation in the data. The results do indicate a downward trend with removal of more biomass leading to a lower cumulative length of shoots. However, this downward trend is not significant. Additionally, cutting at the sediment-water interface caused most plants to die and this is reflected in the low biomass yield from the cuttings and the lower below-ground biomass. Possibly the negative effect of cutting at the sediment-water interface would be less pronounced if the plants could have developed a more extensive system of below-ground parts before being cut which was not possible in the microcosms used in the present experiment. In that case it seems likely that the additional biomass stored in the sediment would more easily lead to growth of new shoots and therefore to less pronounced effects on survival. It is known that several macrophyte species evade disturbances by developing an extensive network of below-ground parts from which they can regenerate (Murphy et al., 1990; Willby et al., 2001). *P. compressus* is more vulnerable than *P. lucens* as cutting resulted in lower biomass production than in the uncut controls, with the lowest total shoot and below-ground biomass for the plants cut at the sediment-water interface.

Increase in the relative growth rate of plants as a response to herbivore damage is a widespread compensatory mechanism in terrestrial species but also in Seagrass (*Posidonia oceanica* L.) (Vergés et al., 2008). It might be argued that herbivory and mowing, especially cutting halfway down the water column, might affect plants in a similar way: damaging the green parts and thus triggering a compensatory mechanism. However, the Pondweeds used in the present study did not show such a mechanism which may be due to the larger damage that mowing causes by complete removal of the cut parts, whereas parts of stems and leaves often survive herbivory.

The current practice in mowing drainage ditches is usually mowing all vegetation just above the sediment. It seems likely that this method will increase the risk of losing *P. compressus* (and possibly other plant species with similar survival mechanisms) for the remainder of the growing season as most replicates in the present study died when cut at the sediment-water interface.

The difference in total shoot biomass between treatments cutting halfway/at three-quarters down the water column and the controls is caused by differences in plant morphology as the dry mass per cm shoot is higher for the controls. Apparently, while the total produced length of shoots is comparable, characteristics like the density of stem and leaf material or the number and length of leaves decrease as the plants are disturbed by cutting. Changes in plant morphology due to biomass removal have been reported for different plant species like increased growth rates and leaf production for Eel grass (*Vallisneria spiralis* L.) (Li et al., 2010). In the present study, changes in morphology are also observed but no increased productivity . The decreased productivity of the two Pondweeds in the

present study is similar to the results from cutting Red Bushwillow (*Combretum apiculatum* Sond.*)* in Botswana, as this resulted in the production of fewer annual shoots which were lower in biomass and leaf area (Bergström et al., 2000). Furthermore, as Li et al. (2010) reported a greater compensatory ability of Eel grass at higher nutrient availability in the sediment, it is possible that the Pondweed species used here would show a different response to cutting at different levels of nutrient availability.

Long term effects
Although the experiment had a limited duration, it might be expected that mowing leads to long term effects through changes in reproduction. The experiment clearly showed that flowering decreased when *P. compressus* was cut at the sediment-water interface and no turion formation occurred in all treatments where *P. compressus* was cut. As turion formation is a very important way of reproduction in this species (Preston and Croft, 1997; Markwell and Halls, 2008), depletion of these organs in the propagule bank on the longer term might also cause the species to disappear. In *P. lucens* rhizomes are important for long term survival. The results show that cutting caused a reduction in rhizome biomass that can overwinter into the next year, possibly leading to a smaller population size in the second year. Subsequent cuts in following years may further reduce the population towards extinction.
While cutting results in direct effects on growth and survival of Pondweeds it might be argued that this can also lead to changes in competitive abilities of species. Analogous to over-grazing of grasslands leading to a loss in species diversity as discussed for instance by Howe (1999), also in aquatic systems high frequent plant removal may cause a shift in species composition. Disturbance tolerant, fast growing species like *Elodea nuttallii* and *Myriophyllum spicatum* are known to show fast regrowth after cutting and can regenerate from small plant fragments that remain in the water (Nichols and Shaw, 1986; Di Nino et al., 2005; Vernon and Hamilton, 2011). If these species establish in the system and availability of nutrients is high enough these species may outcompete *P. compressus* or *P. lucens* after mowing, leading to a loss of these species. Sastroutomo (1981) for example observed in a lake with a well-developed population of *Potamogeton crispus* that this species could not develop in the presence of *Elodea nuttallii*. Together with a loss of species, the fast biomass development of disturbance tolerant species might cause a higher risk of decreased drainage. This way maintenance may have the opposite effect to what it is intended for.

Implications for management
The current mowing practice is aimed at removing all above ground biomass in the complete drainage ditch at least once a year. In the present study complete removal of green shoots lead to death of most plants. Therefore it seems likely that the current maintenance practice should be changed to enhance survival of *Potamogeton* species, even though results generated under experimental conditions can only partly be applied to actual field conditions. Under field conditions effects of cutting might be even more pronounced though if for instance competition (with disturbance tolerant species) influences regeneration of species.
        Total dry mass of shoots showed a decreasing trend at increasing biomass removal per cut for both studied *Potamogeton* species, while plants survived when cut halfway and at three-quarters down the water column. A mowing regime in the field cutting maximally at three-quarters down the water column might generate opportunities to both maintain the water transporting function of drainage ditches (as a result of lower biomass production) and preserving the species in the system.
        Following the intermediate disturbance hypothesis (Huston, 1979), which was illustrated by for instance Peeters (2005) and Greulich and Bornette (1999), creating patchiness in mowing height and frequency might also be considered to enhance the survival of Pondweed species while maintaining sufficient unvegetated water for drainage purposes.

Acknowledgements

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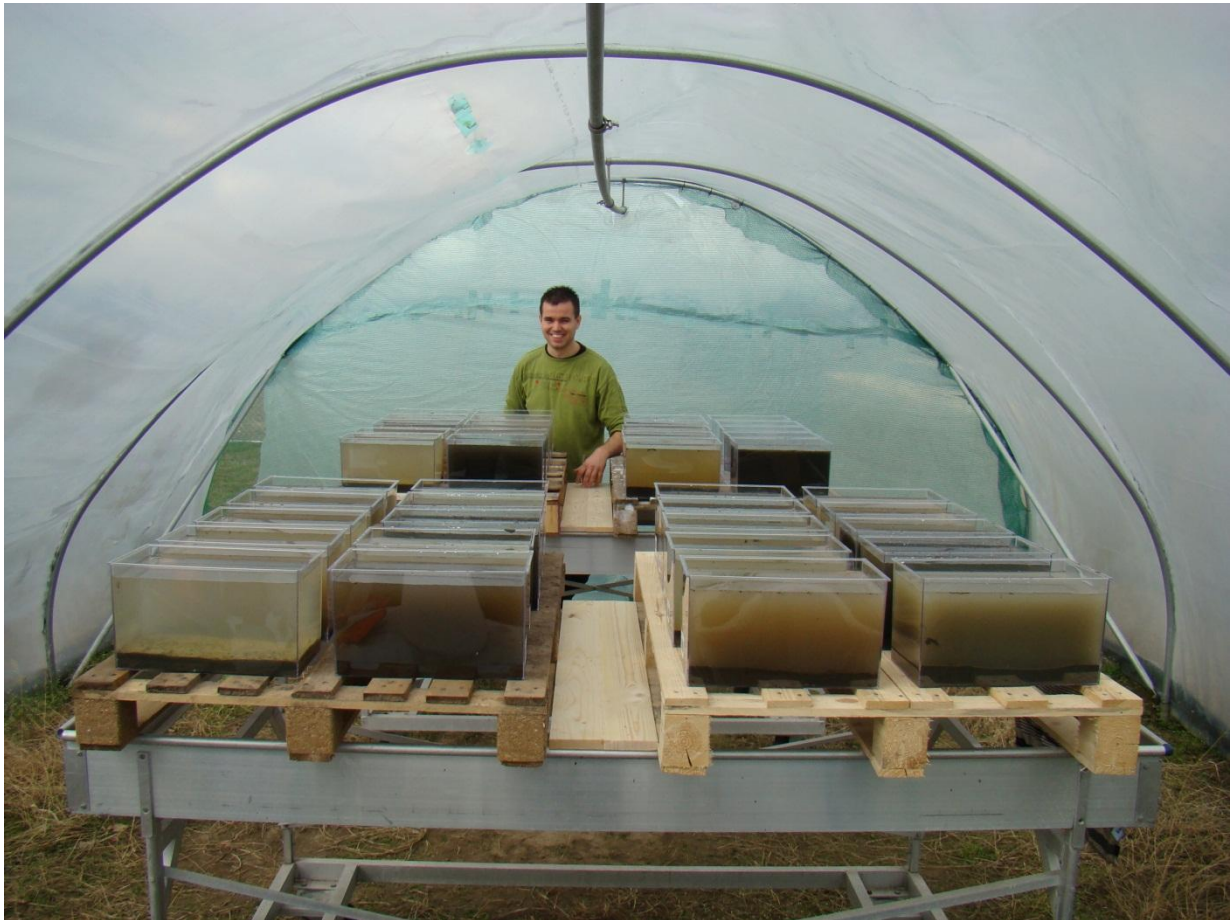
Experimental setup to study propagule germination from sediments of ditches with different vegetation compositions.

5. The role of propagule banks from drainage ditches dominated by free-floating or submerged plants in vegetation restoration

Abstract

Dominance by free-floating plants results in a loss of plant species in many waters. An important source for re-establishment of non-floating aquatic plants can be the propagule bank. This study focuses on whether the propagule bank of free-floating plant dominated ditch sediments can serve as potential source for recovery of a diverse plant community. The first objective was to determine differences in propagule germination from sediments of ditches in the Netherlands that differ in vegetation composition through a seedling-emergence experiment. The second objective was to analyze the effect of sediment disturbance on the number of germinating propagules.

The results show that, compared to sediments from ditches with submerged vegetation, sediments from free-floating plant dominated ditches produced significantly lower numbers of individuals and species of submerged + emergent plants, while numbers of individuals and species of free-floating plants were higher. These results suggest that sediments from free-floating plant dominated ditches have lower potential to recover a diverse plant community probably resulting from positive feedback mechanisms caused by the vegetation present, maintaining the free-floating plant dominated state. Sediment disturbance strongly favors the germination of free-floating plant propagules, especially from free-floating plant dominated ditch sediments. Ditch maintenance activities like mowing and dredging will therefore likely favor persistence of the free-floating plant dominated state.

To shift from dominance by free-floating plants to a more diverse plant community alternative maintenance methods should be considered that cause less sediment disturbance together with measures that promote colonization like temporary drawdown or re-introduction of species.

Introduction

Drainage ditches can be found in many countries across the world and several authors have shown the importance of ditch vegetation in biogeochemical cycling (Coulson et al. 1990; Nguyen & Sukias 2002; Bouldin et al. 2004; Cooper et al. 2004; Ecke 2009). Besides being an important hydrological infrastructure, ditches also largely contribute to the diversity of flora and fauna in the agricultural landscape (Painter 1999; Armitage et al. 2003; Williams et al. 2004; Herzon & Helenius 2008).

In general, different compositions of aquatic vegetation can be found in ditches, mainly as a result of differences in nutrient state. Low to intermediate nutrient levels generally lead to the development of a submerged diverse plant community with various submerged and emergent species that serve as suitable habitat for macrofauna communities (Painter 1999, Herzon & Helenius 2008). When nutrient levels increase, a submerged diverse plant community is replaced by a submerged monoculture of a fast growing submerged species like *Elodea nuttallii* (Planch) H. St John (Nuttall's waterweed*).* Ultimately, at high nutrient levels, all submerged vegetation is replaced by a free-floating plant dominated vegetation (Portielje & Roijackers 1995; Arts & Leenders 2006). Scheffer et al. 2003 concluded that systems dominated by either free-floating plants or submerged plants can be considered as alternative stable states and both systems show the tendency to stay in that same state despite changes in external conditions. This tendency is caused by positive feedback mechanisms: conditions or processes - promoted by the vegetation - that favor the existence of the present vegetation.

Eutrophication has resulted in dominance by free-floating plants in many shallow waters across the world (Douglas Oliver 1993; Janse & Puijenbroek 1998; Kadono 2004; Gettys et al. 2009). Dense layers of free-floating plants cause dark, anoxic conditions, restricting the growth of submerged plants and deteriorating the conditions for aquatic fauna (Morris & Barker 1977; Scheffer et al. 2003; Herzon & Helenius 2008; Villamagna & Murphy 2009). Modeling approaches and several field experiments (Scheffer et al. 2003; Arts & Leenders 2006) indicated that lowering water nutrient levels did not result in the return of a species rich plant community, making nutrient reductions less effective.

An important source from which macrophytes can re-establish is the propagule bank. Propagules being present in the sediment (seeds, turions, tubers, roots and fragments from the green plant) are produced to ensure the species regeneration or establishment the next growing season or after a period of unfavorable conditions (Barrat-Segretain 1996). The extent of re-establishment through germination of propagules depends on several factors like presence and dormancy of seeds (Teltscherová & Hejný 1973), stratification of turions (Barrat-Segretain 1996), occurrence of a drawdown period (Jutila 2001) and suitability of site conditions (Hilt et al. 2006).

Most ditches in agricultural areas are subject to yearly mowing of all macrophytes in summer and frequent mowing can lead to a loss of plant diversity in ditches (Wade 1993; Twisk et al. 2003; Peeters 2005). As mowing and dredging cause disturbance of the sediment, this will likely influence production, presence, and germination of propagules during the growing season. Alternatively, maintenance can also be aimed at reducing only the free-floating plant coverage by means of superficial removal of free-floating biomass. This may lead to improved conditions for submerged and emergent plants to re-establish or expand but a viable propagule bank will likely be essential for a successful restoration of a diverse plant community. To date, it is unknown whether, and to what extent, ditch sediments contain viable propagules that may contribute to the establishment of a diverse plant community and what the effect of disturbance by maintenance is on germination success.

The main question of the present study is whether the propagule bank of free-floating plant dominated ditch sediments can serve as a potential source for the recovery of a submerged diverse plant community. The first objective is to determine differences in propagule germination from sediments of 9 ditches in the Netherlands that differ in vegetation composition (free-floating plant dominated, submerged monoculture and submerged diverse plant communities) through a seedling-emergence experiment in a semi-controlled environment. The second objective is to analyze the effect of sediment disturbance at the end of the experiment on the number of germinating propagules.

Methods
Sampling locations
Sampling locations were selected by analyzing monitoring data on vegetation composition collected by us in previous years. Free-floating plant dominated ditches contained vegetation mainly dominated by duckweeds, Submerged monoculture ditches contained a monoculture of *Elodea nuttallii* and ditches with a submerged diverse vegetation contained several submerged species. The selected ditches contain water year round, have shown the respective vegetation for several years and have been in the present morphological state for at least 25 years. All ditches are located in an agricultural area and are surrounded by grasslands used for hay-making or grazing by cattle. The aquatic vegetation is mown once a year or once every two years. No further disturbances occur. The average distance between the ditches is 58 km. Details on the location and characteristics are shown in Table 1.

Table 1. Characteristics of the sampling locations. Water depths were measured in July. The hydrological unit in which a ditch is located is defined as a confined area in the landscape in which free water exchange between ditches occurs, while little water exchange occurs between the unit and it's surroundings. Often the water levels in a hydrological unit are managed from one central pumping station. Numbers on groundwater inflow are given for the mentioned hydrological unit. Negative numbers represent a net loss to the groundwater.

Nr	Vegetation composition	Width (cm)	Depth (cm)	Surface Area hydrological unit (ha)	Surface water area in hydrological unit (%)	Ground-water inflow (mm/day)	Latitude	Longitude
1	Submerged monoculture	300	65	2578	3.09	-0.08	51°57'15.28"	5°43'51.04"
2	Free-floating plant dominated	320	25	1026	6.17	-0.08	52° 7'0.55"	4°54'56.24"
3	Submerged diverse	150	30	272	6.36	0.48	52°36'26.03"	6° 0'35.60"
4	Submerged monoculture	280	33	15335	17.52	0.13	52°41'53.26"	5°58'53.37"
5	Free-floating plant dominated	350	30	5142	8.92	0.28	51°56'56.24"	4°54'38.40"
6	Submerged diverse	200	25	2186	5.53	0.33	52°29'35.94"	5°57'20.17"
7	Submerged monoculture	220	30	2393	6.17	-0.48	52°35'8.86"	5°54'41.55"
8	Free-floating plant dominated	210	30	7007	1.83	0.02	52° 1'6.19"	5°20'49.72"
9	Submerged diverse	320	46	15335	17.52	0.13	52°40'49.38"	6° 0'34.11"

Sampling

Sediment was collected in 9 ditches in the Netherlands, with 3 ditches for each vegetation composition. As there are species from which the propagules show increased germination after lower temperatures during winter (Van Wijk & Trompenaars 1985), samples were collected after winter in the 3rd week of March 2008 to ensure this stratification took place. Sampling was done using a clear Perspex corer tube (Ø 12.2 cm). In each ditch a 14 m stretch was selected from which two samples were taken every two meters; one from the middle of the ditch and one from the zone close to the ditch bank, resulting in 16 samples per ditch. As the upper 5 cm of the sediment is considered to be the most important part for propagules to germinate from (Dugdale et al. 2001), this part of the core was used for the experiment, resulting in a total sample volume per ditch of 9.3 L. Samples were transported in dark containers and stored in the dark at 10 ^{o}C for 12 days before being used in the experimental setup.

Experimental setup

The seedling-emergence technique was applied under ambient weather conditions from April 2nd until September 15th 2008. The experiment was performed in an 'open' greenhouse with a plastic roof and two open sides. The two open sides were covered by wire mesh to allow free gas exchange, regulate temperature and to keep out birds. Measurements showed that the plastic cover blocked around 20% of the Photosynthetically Available Radiation.

The sediment from each ditch was first homogenized and then four plastic aquaria (l:w:h = 34x19x19 cm) were each filled with 1.5 L sediment resulting in a total volume of 6 L. per ditch, representing a surface area of 0.12 m^{2}. Afterwards, all 36 aquaria (9 ditches, 4 subsamples per ditch) were gently filled with Dutch Standard Water (Maas et al. 1993). All aquaria were aerated continuously and water levels were maintained during the experiment using demineralized water. Disturbance of the experiment by growth of filamentous algae or grazing by macrofauna was prevented by removal of both on a daily basis. Water fleas (*Daphnia magna)* were added to suppress algal bloom, maintaining at least ten individuals per aquarium.

As soon as germinated plants could be identified they were removed from the aquaria, disturbing the sediment as little as possible to maintain enough space and light for germination of as much propagules as possible to assess the overall responsiveness of the propagule bank.

Four weeks before the end of the experiment (August 21st) the complete sediment layer was stirred to mimic sediment disturbance by mowing, after having removed all individuals.

Measurements

Oxygen level, water temperature and pH were measured weekly. Germination was assessed at approximately weekly intervals by counting the number of germinated individuals and species per subsample. All individuals were in principle identified up to species level following nomenclature according to Raam 1998; Tamis et al. 2004 and Heukels et al. 2005. Floating plants were identified and removed as soon as possible thereby preventing any clonal reproduction. 3.5 Weeks after disturbance the experiment was ended (September 15th) since water temperatures became too low for germination (<15 ^{o}C), which generally occurs in ditches in the Netherlands in the second half of September according to an analysis of 3500 water temperature records from the period 1980-2005 (STOWA, 2010). All new seedlings were identified and counted at the end.

Data analysis

The data of the period before and after the sediment disturbance were analysed separately. The counting data from before the disturbance was used to calculate weekly cumulative numbers of individuals and species per ditch from the four subsamples. For each vegetation composition (consisting of data from three ditches) mean values and standard errors were plotted against time to detect temporal patterns in seedling emergence.

For each ditch the mean number of days after the start of the experiment was calculated at which the first individual of each plant type (free-floating, submerged and emergent) appeared, as well as the day at which the maximum amount of individuals and species were reached. Wilcoxon Signed Ranks tests were performed to detect differences in the start and ending of germination between plant types for both numbers of individuals and species.

The total numbers of germinated individuals per species per ditch (totals from four subsamples) were used to compare the ditches in a Detrended Correspondence Analysis using Canoco 4.5 (ter Braak & Smilauer 2002). The differences in position of the ditches in the ordination diagram (grouped according to vegetation composition) were analysed using Independent samples T-tests.

For each ditch the total number of free-floating, submerged and emergent plant species and individuals were calculated from the four subsamples to test for differences between ditches with a different vegetation composition in the field using Mann-Whitney tests. This was done both for the data from before and after the sediment disturbance. All statistical tests other than the Detrended Correspondance Analysis were done using SPSS 17 (SPSS 2009).

Data on germinated propagules after the disturbance event were standardized to number of individuals/m^2. The corresponding coverages were also calculated, based on the surface area size of the observed species from Weeda et al. 2003.

Results

Experimental conditions

Average oxygen level in the aquaria during daytime was 12.4 mg/L with the lowest measured concentration being 4.9 mg/L. Water temperatures mostly ranged between 15 and 30 ^{o}C, with an average water temperature of 24.3 ^{o}C. pH ranged between 5.2 and 10.6.

Germination during the experiment

Figure 1.A, C and E illustrate the early start of the germination of individuals of free-floating plants, while germination of submerged and emergent plants started after some weeks in all nine ditches (For the total number of germinated individuals per species see Appendix 1). On average, the germination of free-floating plants started 17 days after the start of the experiment, which is significantly earlier than germination of submerged and emergent plants which started after resp. 74 days (Wilcoxon signed ranks: Z=-2.67, p=0.008) and 80 days (Wilcoxon signed ranks: Z=-2.52, p=0.012).

After the early start, the total number of free-floating plants hardly increased from June until August (Figure 1.A), while the numbers of submerged and emergent plants still increased (Figure 1.C and 1.E). On average, germination of free-floating plants ended after 40 days, which is significantly earlier than for submerged plants (97 days, Wilcoxon signed ranks: Z=-2.67, p=0.008) and emergent plants (100 days, Wilcoxon signed ranks: Z=-2.52, p=0.012).

The early development of free-floating plants is also reflected in the observed number of species (Figure 1.B, D and F). While in the first four weeks four out of five free-floating plant species have emerged, most submerged and emergent species start to appear later and their numbers increase until the end of July. The maximum number of free-floating plant species was on average reached after 29 days which is significantly earlier than for submerged (68 days, Wilcoxon signed ranks: Z=-2.67, p=0.008) and emergent species (94 days, Wilcoxon signed ranks: Z=-2.52, p=0.012). No significant differences existed in the start and end of germination between submerged and emergent plants. After four months - end of July 2008 - germination had ended.
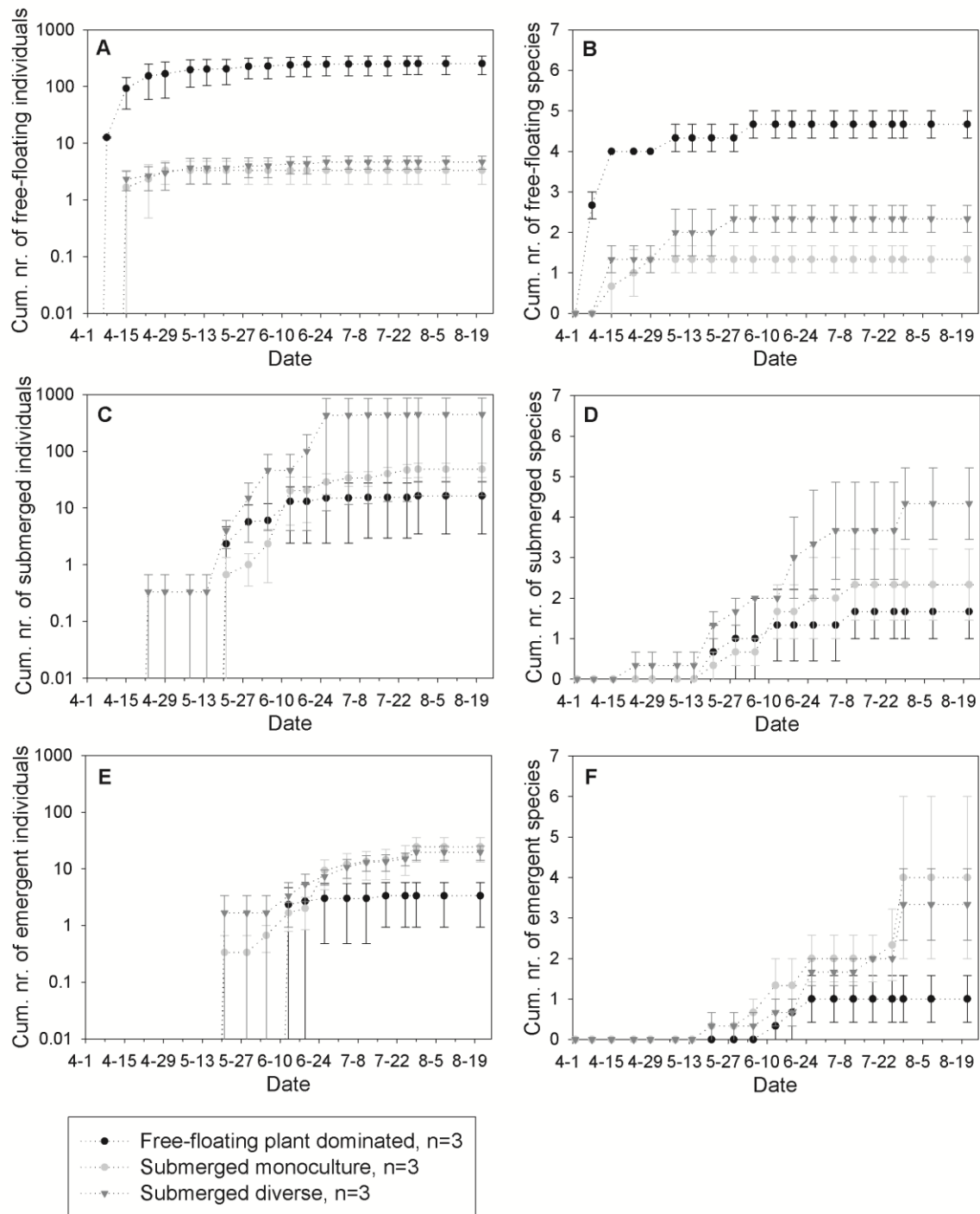
Figure 1. Number of emerging individuals and species from the sediment during the experiment. Each point represents the mean number from three ditches. Per ditch the total number was calculated from four subsamples. Whiskers show the standard errors. All graphs show separate lines for results from free-floating plant dominated, submerged monoculture and submerged diverse ditch sediments. Separate graphs are shown for the number of emerged free-floating individuals (A) and free-floating species (B), submerged individuals (C) and submerged species (D), emergent individuals (E) and emergent species (F). For each vegetation composition n=3.

Germinated species composition
The first two axes of the DCA explained 38.5 % of the variance in the species data (Figure 2). A rather clear division in plant species can be observed in the species plot (Figure 2A) with free-floating species located on the left side of the figure and the submerged and emergent species on the right side. *Elodea nuttallii* was located within the cloud of other submerged and emergent species, therefore not strongly responsible for differences in germinated species composition between submerged monoculture and submerged diverse ditches. This can also be concluded from Figure 2B, in which submerged monoculture (M1 – M3) and submerged diverse ditches (D1 – D3) were not separated but located together on the right side of the plot. Free-floating plant dominated ditches (F1 – F3) located on the left side, had significantly different positions on the first axis than submerged monoculture ditches (T-test, scores axis 1: t= -3.989, p= 0.016) and submerged diverse ditches (T-test, scores axis 1: t= -3.215, p= 0.032), indicating their different species composition. Submerged monoculture ditches had a similar position in the diagram as submerged diverse ditches (T-test, scores axis 1: t=0.203, p= 0.849). For further analysis, submerged monocultures and submerged diverse ditches were therefore combined and referred to as submerged plant dominated ditches.
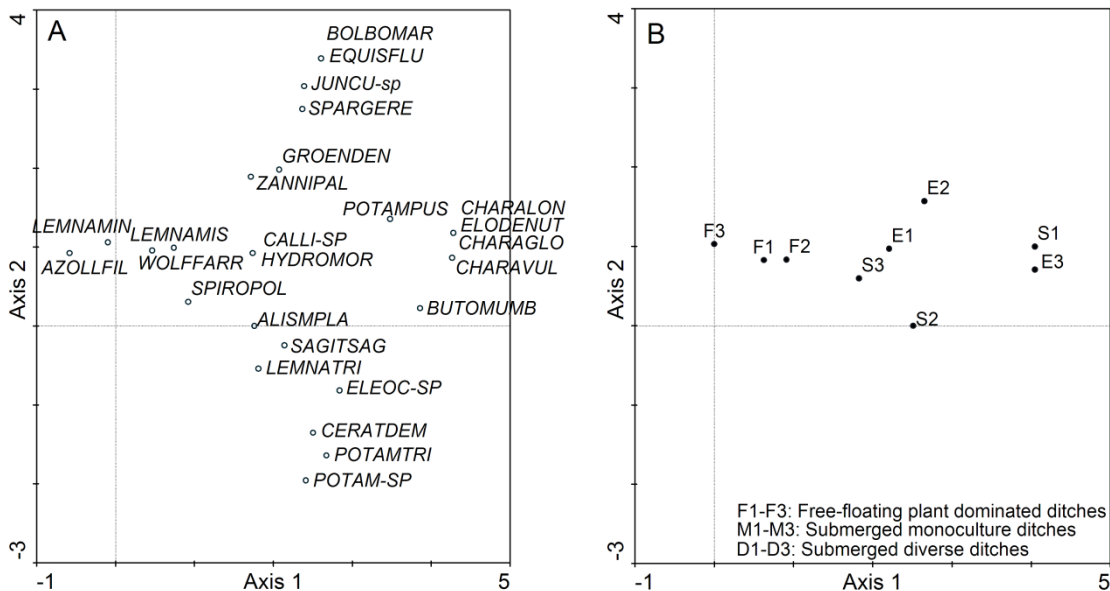
Figure 2. Ordination plots from detrended correspondence analysis with the total number of emerged individuals per species per ditch for the period before the sediment disturbance. Species data was not transformed, rare species were downweighted and detrending was done by segments. Position of species (A) and the ditches (B) are shown in separate plots with equal axis scaling (for complete species names, see Appendix 1). The first two axes from the analysis are shown. Plot with the ditches (B) shows separate labels (referring to the vegetation composition in the field) for ditches with free-floating plant dominance (F1 - F3), a submerged monoculture (M1 - M3) and a submerged diverse plant community (D1 - D3). Eigenvalues were 0.899 and 0.174 for respectively axis 1 and axis 2.

Total number of individuals and species
The germinated number of free-floating plant species from free-floating plant dominated ditches (Figure 3.A) was more than 2 fold higher than from submerged plant dominated ditches (Mann-Whitney, U = 0.000, p= .017), while the number of individuals (Figure 3.B) was even more than 20 fold higher for free-floating plant dominated ditches (Mann-Whitney, U = 0.000, p= .020). For the distribution of these numbers over the different species see appendix 1. Contrastingly, although the number of submerged species (Figure 3.C) and individuals (Figure 3.D) showed no significant differences between the free-floating plant dominated and submerged plant dominated ditches (Mann-Whitney: species: U= 3.500, p= .145; individuals: U= 3.000, p= .121), the number of emergent species (Figure 3.E) and individuals (Figure 3.F) were significantly lower for the free-floating plant dominated ditches (Mann-Whitney:

species: U = 1.500, p=.043; individuals: U = 1.000, p=.039). Summing up the number of submerged and emergent individuals and species (Figure 3.F and 3.G) resulted in a more pronounced difference (lower p-value) in species number between the free-floating plant dominated and submerged plant dominated ditches (Mann-Whitney: U = 0.000, p= .019) while the difference in the number of individuals did not change (Mann-Whitney: U = 1.000, p= .039).

Sediment disturbance
After the sediment disturbance only new free-floating individuals appeared (Table 2). The species that contributed most to the increase after the disturbance was *Spirodela polyrhiza* (L.) Schleid. (Greater Duckweed). Sediment from free-floating plant dominated ditches produced a significantly higher (Mann-Whitney, U = 4.000, p= .015) number of free-floating individuals than sediment from submerged plant dominated ditches. The average of 2825 collected individuals/m^2 since the disturbance is the highest found during the experiment and would represent a coverage of around 16% only from propagules.
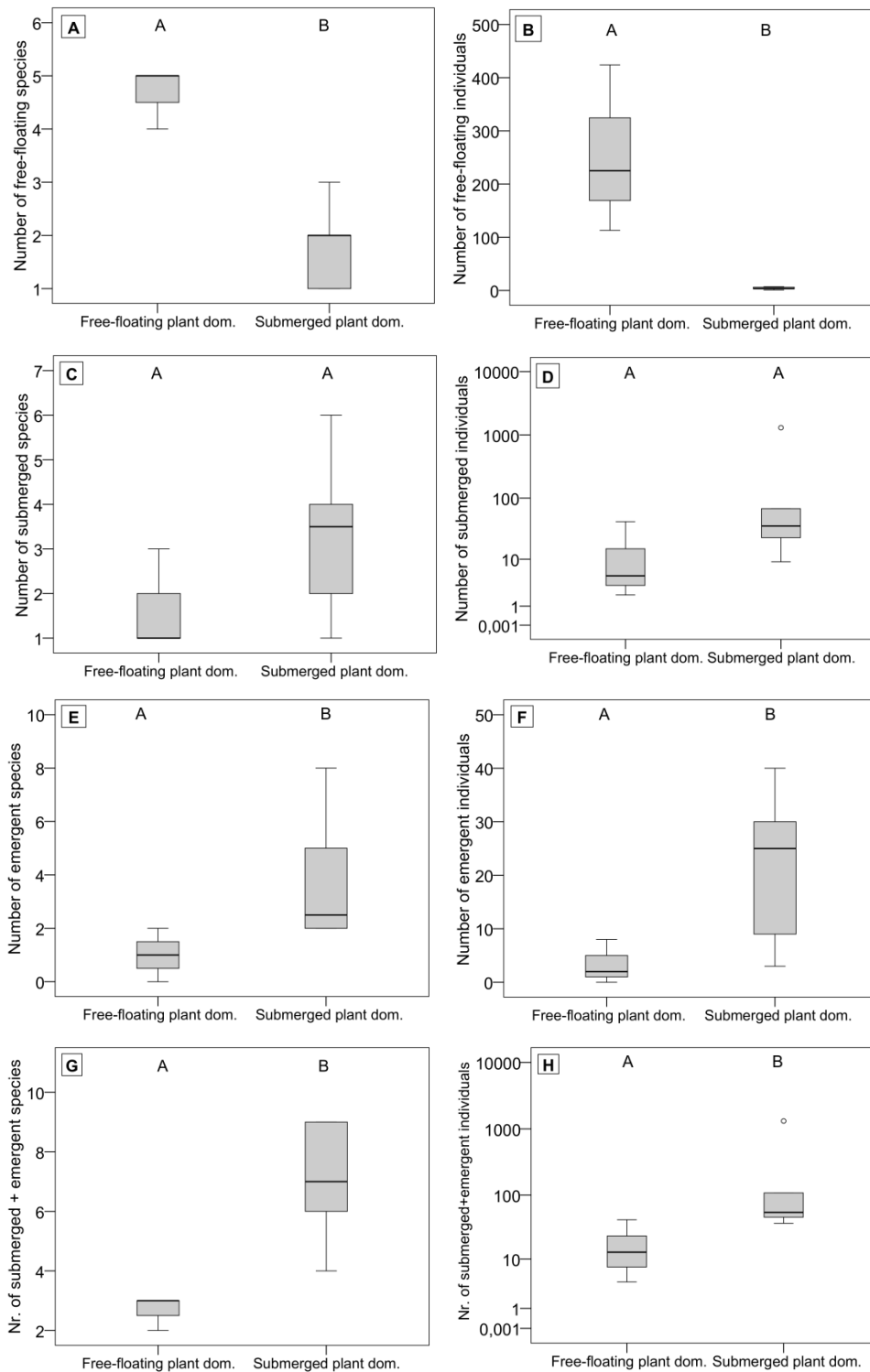
Figure 3. Boxplots with ranges of total number of germinated species and individuals from the sediment of the two vegetation compositions. For free-floating plant dominated ditches: n = 3, Submerged plant dominated ditches: n = 6. Horizontal line within the grey box represents the median value. Grey box contains 50% of all values. Whiskers contain 75% of all values. Circles indicate outliers. Figures are shown for free-floating (A & B), submerged (C & D), emergent (E & F) and submerged + emergent (G & H) plants. Letter codes on top of the boxplots indicate similar or significantly different groups according to Mann-Whitney tests (α = 0.05).

Table 2. Number of individuals/m^2 and corresponding coverage (%) for each of the free-floating plant species that germinated in the 112 days before and 24 days after the sediment stirring (stirring performed on August 21st). For the number of individuals/m^2 mean values are shown, calculated from the ditches within each vegetation composition. Surface area of sediment used in the experiment was 0.12 m^2 per ditch thus observed number of individuals*8.33 results in individuals/m^2. The coverage was calculated from the number of individuals/m^2, multiplied by the surface area of the species, shown in parentheses next to the species name in mm^2 (after Weeda et al. 2003).

Before disturbance: April-August (112 days)	Free-floating plant dominated n=3		Submerged plant dominated n=6	
	number of individuals/m^2	coverage (%)	number of individuals/m^2	coverage (%)
Spirodela polyrhiza (84.5)	350	2.95	10	0.08
Wolffia arrhiza (1)	189	0.02	1	0.00
Lemna sp. (11.5)	1564	1.80	22	0.03
Azolla filiculoides (100)	14	0.14	0	0
Total	2116	4.91	33	0.11
After disturbance: August-September (24 days)	number of individuals/m^2	coverage (%)	number of individuals/m^2	coverage (%)
Spirodela polyrhiza (84.5)	1747	14.76	7	0.06
Wolffia arrhiza (1)	181	0.02	0	0.00
Lemna sp. (11.5)	897	1.03	0	0.00
Total	2825	15.81	7	0.06

Discussion

This study clearly demonstrates that the potential to regain a diverse plant community from sediments of free-floating plant dominated ditches is rather low. Differences in the number of germinated individuals and species from free-floating plants were pronounced with very high numbers in free-floating plant dominated ditches. Contrastingly the number of individuals and species of emergent species remained lower than from submerged plant dominated ditches, with submerged species adding modestly to this difference. The results further demonstrate differences in timing of germination between free-floating, submerged and emergent plants. Free-floating plants quickly start to emerge whereas it took submerged and emergent plants significantly more time before germinating. Therefore, it seems likely that even if other than free-floating plants could start to develop in a free-floating plant dominated ditch, the sediment will increase the chance of keeping the vegetation dominated by free-floating plants as free-floating plants develop earlier to a high number.

Several processes may cause the low germination numbers of submerged and emergent plants in free-floating plant dominated ditches. Firstly, the propagule bank of free-floating plant dominated ditches might contain hardly any viable propagules of submerged and emergent plants as prolonged dominance by free-floating plants hampers the propagule bank buildup of other plants (Boedeltje et al. 2005). Blanckenhagen & Poschlod 2005 observed a similar pattern in grasslands restoration efforts where only 25% of the former species richness was present. Secondly, the presence of dense layers of free-floating plants in ditches results in anoxic conditions that may cause increased decay of propagules of other species, produced in former years (Klimesova & Klimes 2007). Thirdly, besides absence of propagules, burial of older but viable propagules might occur which hampers germination as the most active part of the propagules is often restricted to the upper 5 cm of the sediment (Dugdale et al. 2001). Finally, free-floating plants started growing directly at the start of the experiment which might give them a competitive advantage as they can use the available nutrients first and can limit the development of submerged and emergent propagules by shading the water and sediment (Netten et al. 2010).

The mentioned four processes might act as positive feedback mechanisms, promoting the persistence of free-floating plant dominance. Removing only free-floating plant biomass as a measure to restore submerged vegetation will probably be less effective if positive feedback mechanisms have resulted in a sediment poor in submerged and emergent plant propagules and rich in floating plant propagules. Decreased propagule bank functioning has been found in many other degraded aquatic systems across the world. de Winton & Clayton 1996 concluded from a study in 21 New Zealand lakes

that lakes invaded by adventive weeds showed lower numbers of seeds in the seed bank, together with lower species diversity. A study on germination of wetland species in the Everglades U.S.A. (Smith et al. 2002) also showed that germination of the seed bank did not facilitate the return of target species of the former vegetation. Furthermore, in terrestrial systems the seed bank is often also impoverished at sites with a species poor vegetation. This was found in semi-arid rangelands subject to intensive grazing in South Africa (Jones & Esler 2004) but also in grasslands in which restoration efforts often show low success (Bakker & Berendse 1999; Donath et al. 2003). More insight in the relevant processes in drainage ditches is required to understand which positive feedback mechanisms are involved and what the impact of restoration measures might be.

Besides processes within the system, maintenance may also be important in explaining the differences in the germinated number of individuals and species of emergent (and submerged) plants. When a system becomes eutrophic, plant biomass increases and the vegetation may eventually shift towards free-floating plant dominance. As a consequence of higher biomass production more intensive/frequent mowing is also needed to maintain the drainage function of ditches. By mowing frequently, emergent plants may be damaged and removed more often which may reduce their chances to re-establish yearly and produce sufficient propagules to survive, eventually lowering emergent plant diversity in these systems (Peeters 2005).

The results from the sediment disturbance experiment indicate that disturbance during summer strongly favors the germination of propagules from free-floating plants, especially in free-floating plant dominated ditches. The amount of free-floating individuals that germinated in the period after the sediment disturbance was much higher than from the period prior to the disturbance and not a single submerged or emergent plant germinated. The mixing of the sediment - also caused by maintenance in the field through mowing and dredging - probably causes new, viable duckweed propagules to be transported towards the top of the sediment, where they germinate after the sediment has settled. This will give free-floating plants a strong competitive advantage and hamper the re-establishment of submerged vegetation.

Dredging, on the other hand may lead to removal of nutrients and might bring propagules to the surface of the sediment that were buried deeper. One might argue that the combination of lower nutrient levels - limiting extensive free-floating plant development - and the increased availability of submerged plant propagules might lead to the re-establishment of non-floating species. However, Boedeltje et al. 2005 showed that a decrease of water nutrient levels indeed caused lower coverage by duckweeds originating from the propagule bank but unfortunately also that no increased germination of submerged or emergent plants took place.

When looking at the perspectives for restoring aquatic vegetations in ditches, some considerations can be pointed out. Many ditches in agricultural areas have become eutrophic in the past resulting in the presence of dense layers of free-floating plants and absence of habitat forming submerged and emergent vegetation (Painter 1999; Herzon & Helenius 2008). The present study shows that the potential to recover a diverse vegetation in these systems from the propagule bank is rather low, probably due to feedback mechanisms. Furthermore, reducing nutrient levels alone does not seem effective (Scheffer et al. 2003; Arts & Leenders 2006) besides the huge efforts that are needed for such a reduction. Additionally, the current maintenance practices also seem to promote free-floating plant dominance. Unfortunately, changing the current maintenance practice to removing free-floating plant layers without disturbing the sediment will probably not be sufficient to regain a diverse plant community. Therefore, to induce a shift from free-floating plant dominance to a more diverse plant community an external perturbation is probably needed. The germination of propagules that are locally present might for instance be stimulated by creating a drawdown period which can increase germination of propagules from (mainly) emergent plant species (Jutila 2001, Boedeltje et al. 2002). Another promising measure could be the introduction of propagules from an external source by means of introducing plant material as was successfully applied in a grassland (Donath et al. 2003) and a floodplain meadow (Hölzel & Otte 2003), but also in some shallow lakes (Hilt et al. 2006). Introducing propagules of formerly present aquatic plants in ditches could be a very promising measure and should therefore be investigated.

Implications for Practice
- Creating favorable site conditions by removing free-floating plant biomass during summer in free-floating plant dominated drainage ditches will probably not be effective to recover a diverse plant community from the propagule bank.
- Additional measures like temporary draw down and re-introduction of plant species are needed and should be investigated.
- Alternative maintenance methods should focus on preventing high coverages by free-floating plant propagules early in the growing season and on preventing sediment disturbance as this stimulates the germination of free-floating plant propagules.

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Appendix 1. Germinated number of individuals and species per m^2 per ditch during the experiment. Per ditch, the number of individuals per m^2 was calculated from four subsamples: 4 * 1.5 L = 6 L of sediment from the top 5cm of the sediment. This represents a surface area of 0.12 m^2. number of individuals from 4 subsamples * 8,33 resulted in the shown numbers of individuals/ m^2. The used abbreviations in figure 2A are also shown, together with the division in plant types used for calculating the total number of individuals and species per plant type (F = free-floating, S = submerged and E = emergent). Last eight rows show the totals for the three plant types and the total number of individuals and species per ditch.

| | | | Ditch number & field vegetation composition | | | | | | | | |
| | | | 2 | 5 | 8 | 1 | 4 | 7 | 3 | 6 | 9 |
Name	Code	Type	Free-floating plant dominated			Submerged monoculture			Submerged diverse		
Alisma plantago-aquatica	*ALISMPLA*	E	0	0	58	58	58	0	0	67	208
Azolla filiculoides	*AZOLLFIL*	F	0	0	42	0	0	0	0	0	0
Bolboschoenus maritimus	*BOLBOMAR*	E	0	0	0	0	8	0	0	0	0
Butomus umbellatus	*BUTOMUMB*	E	0	0	0	0	8	0	67	8	0
Callitriche sp.	*CALLI-SP*	S	0	0	0	0	0	0	0	0	8
Ceratophyllum demersum	*CERATDEM*	S	0	8	0	0	0	17	0	42	0
Chara globularis	*CHARAGLO*	S	0	0	0	0	0	0	8	0	0
Chara longibracteata	*CHARALON*	S	0	0	0	0	0	0	375	0	0
Chara vulgaris	*CHARAVUL*	S	0	0	0	33	0	425	7575	0	0
Eleocharis sp.	*ELEOC-SP*	E	0	0	0	0	8	8	0	17	0
Elodea nuttallii	*ELODENUT*	S	0	0	0	0	0	0	8	0	0
Equisetum fluviatilis	*EQUISFLU*	E	0	0	0	0	8	0	0	0	0
Groenlandia densa	*GROENDEN*	S	0	0	0	25	0	0	0	0	0
Hydrocharis morsus-ranae	*HYDROMOR*	S	0	0	0	0	0	0	0	0	8
Juncus sp.	*JUNCU-sp*	E	0	0	0	0	33	0	0	0	8
Lemna minor/gibba	*LEMNAMIN*	F	150	692	3267	42	25	0	0	0	33
Lemna minuta	*LEMNAMIS*	F	325	133	108	0	0	0	0	0	17
Lemna trisulca	*LEMNATRI*	F	0	17	0	0	0	0	8	8	0
Potamogeton pusillus	*POTAMPUS*	S	17	283	0	192	192	0	2892	108	58
Potamogeton sp.	*POTAM-SP*	S	0	0	0	0	0	0	0	8	0
Potamogeton trichoides	*POTAMTRI*	S	0	0	0	0	0	0	8	42	0
Sagittaria sagittifolia	*SAGITSAG*	S	17	0	0	275	17	17	0	83	0
Sparganium erectum	*SPARGERE*	S	0	0	8	0	108	0	8	8	17
Spirodela polyrhiza	*SPIROPOL*	F	208	733	108	0	0	8	17	25	8
Wolffia arrhiza	*WOLFFARR*	F	258	300	8	8	0	0	0	0	0
Zannichellia palustris	*ZANNIPAL*	S	0	58	42	317	0	0	0	0	0
Floating: number of individuals/m2			942	1875	3533	50	25	8	25	33	58
Floating: number of species			4	5	5	2	1	1	2	2	3
Submerged: number of individuals/m2			17	350	42	567	192	442	10867	200	75
Submerged: number of species			1	3	1	4	1	2	6	4	3
Emergent: number of individuals/m2			17	0	67	333	250	25	75	183	233
Emergent: number of species			1	0	2	2	8	2	2	5	3
Total number of individuals/m2			975	2225	3642	950	467	475	10967	417	367
Total number of species			6	8	8	8	10	5	10	11	9

Close-up of a dense monoculture of free-floating plants with *Wolffia arrhiza* (smallest plants), *Lemna minor/gibba* and *Spirodela polyrhiza* (largest plants)

6. Differential response to climatic variation of free-floating and submerged macrophytes in ditches

Abstract
1. Experimental studies have indicated in freshwater ecosystems that a shift in dominance from submerged to free-floating macrophytes may occur with climate change due to increased water surface temperatures and eutrophication. Field evidence is, however, rare.
2. Here we analyzed long-term (26 years) dynamics of macrophyte cover in Dutch ditches in relation to Dutch weather variables and the North Atlantic Oscillation (NAO) winter index. The latter appears to be a good proxy for Dutch weather conditions.
3. Cover of both free-floating macrophytes and evergreen overwintering submerged macrophytes was positively related to mild winters (positive NAO winter index). On the other hand, high cover of submerged macrophytes that die back in winter coincided with cold winters (negative NAO winter index). Our results therefore suggest that the effect of weather on macrophyte species depends strongly on their overwintering strategy.
4. The positive relation of free-floating macrophytes with the NAO winter index was significantly stronger in ditches in organic soil than in those in inorganic soil. This may be due to increased nutrient loading associated with increased decomposition of organic matter and increased run-off to these ditches during mild wet winters.
5. Our results suggest that mild winters in a changing climate may cause submerged macrophytes with an evergreen overwintering strategy and free-floating macrophytes to outcompete submerged macrophytes that die back in winter.

Introduction
Climate change may directly or indirectly cause a change in species distribution, phenology and ecosystem structure in both the terrestrial and aquatic realms (Hughes 2000, Winder & Schindler 2004; Mooij *et al.* 2005). Much of the research dealing with the effect of climate change on aquatic ecosystems has focused on lakes. Here climate change may affect nutrient dynamics through internal (enhanced mineralization and increased anoxia due to warming) and external loading (increased run-off through precipitation) (Mulholland *et al.* 1997; Jeppesen *et al.* 2009). Climate change also influences trophic dynamics between communities (Winder & Schindler 2004) and, specifically in shallow lakes, it may influence macrophyte distribution (Rooney & Kalff 2000) and cover (Kosten *et al.* 2009).

Small water bodies such as ditches differ strongly in biological composition and functioning from shallow lakes (Janse 1997 and 1998) and although ditches occur worldwide, they have been studied relatively little (Herzon & Helenius 2008). It is, for instance, uncertain how they will react to climate change. Ditches in the Netherlands are generally nutrient-rich because they often drain fertilized agricultural fields. Additionally, aquatic ecosystems on organic soils usually have a higher potential for internal loading than systems on inorganic soils (Fisher *et al.* 2005). Furthermore, ditches are characterized by high bottom surface area to volume ratios with the consequence that the sediment strongly influences nutrient availability in the overlaying water column (Bloemendaal & Roelofs 1988).

High nutrient loading and low exposure to wind make ditches susceptible to free-floating macrophyte dominance. On the other hand, the low water depth may favour growth of submerged macrophytes, resulting in ditches totally covered by these macrophytes. In general, three functional macrophyte groups can be distinguished in ditches based on their main overwintering strategy; free-floating macrophytes, evergreen submerged macrophytes and submerged macrophytes that die back in winter. Free-floating macrophytes can survive the winter period as green plants or as turions (Jacobs 1947). Evergreen submerged macrophytes often survive winter with green parts but can also overwinter as propagules such as turions or tubers (Barrat-Segretain & Cellot 2007). Both macrophyte types allow fast regeneration at the start of the growing season. Submerged macrophytes that die back in winter only produce propagules from which to regenerate after winter (e.g. Renman 1989; Whiteman & Room 1991). Examples of species commonly found in Dutch ditches are *Lemna* sp., *Wolffia* sp., *Spirodela* sp. (free-floating macrophytes), *Elodea* sp., *Potamogeton crispus* L., *Myriophyllum alterniflorum* DC.

(evergreen overwintering submerged macrophytes) and *Potamogeton pectinatus* L., *Potamogeton lucens* L. *and, Myriophyllum spicatum* L. (submerged macrophytes that die back in winter).

Scheffer *et al.* (2003) suggested that dominance by free-floating and submerged macrophytes may represent alternative stable states. This is supposed to be due to asymmetric competition as free-floating macrophytes have a primacy for light, whereas submerged macrophytes can grow at lower water column nutrient concentrations. Increased water surface temperatures in a warming climate could favour free-floating macrophytes disproportionally in view of their position in the water column. Likewise, free-floating macrophytes will profit most from eutrophication enhanced by climate change. These effects are reinforced if variables act in synergy (Netten *et al.* 2010). Experimental work (Feuchtmayr *et al.* 2009; Netten *et al.* 2010) supports the idea of a shift towards free-floating macrophyte dominance under climate change, but up to now supporting field observations have been lacking. Increased dominance by free-floating plants will result in a loss of functioning and reduced biodiversity in aquatic systems (Janse & Van Puijenbroek 1998).

Climate scenarios of temperate regions predict future winters to be milder and wetter (IPCC 2007). In parts of Western Europe including The Netherlands, mild and wet winters coincide with high NAO winter index values (Ottersen *et al.* 2001). The correlation of the NAO winter index with ecosystem dynamics in the Northern Hemisphere is broadly recognized as a climate proxy (summarized in Ottersen *et al.* 2001 and Hurrell *et al.* 2003). The NAO winter index has already been related to biological components in lake ecosystems ranging from plankton (George & Taylor 1995; Müller-Navarra *et al.* 1997; Gerten & Adrian 2000; Straile & Adrian 2000), macrophytes (Rip 2007) to zoobenthos and vertebrate predators (Straile *et al.* 2003), but has not yet been related to free-floating macrophyte cover, overwintering strategy of macrophytes or to small water bodies such as ditches.

Here, we relate 26 years of field data on macrophyte cover in Dutch drainage ditches to yearly climatic variations using local weather variables and the North Atlantic Oscillation (NAO) winter index. The objective is to study the effect of climatic variation on the cover of free-floating and submerged macrophytes, which are common competitors in ditch ecosystems. We specifically focus on winter conditions and overwintering strategy as climate change is expected to have a stronger influence on Dutch winter conditions than on summer conditions (Sigmond 2003). We hypothesize that mild winter conditions will promote macrophytes with an evergreen overwintering strategy. Additionally, soil type may influence nutrient availability in the water column, which is the primary limiting factor for free-floating macrophytes.

Methods
Study site
We used biological and physicochemical data from the Limnodata Neerlandica (STOWA 2010), an ecological monitoring database that has included many freshwater sites in the Netherlands since the 1970s until the present collected by water boards and provinces. Our subset contained data of 2274 ditches with in total 22961 observations between 1981 and 2006 (n=26). These years had sufficiently large numbers of observations to conduct the analysis. Unfortunately, the dataset did not include complete time series for individual ditches. On average each ditch was visited twice in these 26 years. We, therefore, refrained from analyzing climate impact on vegetation in individual ditches. Instead we calculated for each year an average cover for all ditches sampled. The ditches were distributed throughout the Netherlands (Fig. 1) and situated on organic (n=530; peat) and inorganic (n=1744; sand/clay) soils. No data were available on the dimensions of the studied ditches but in general they have a mean width of 2 m and a maximum width of 8 m with a maximum depth of 1.5 m. Because their dimensions are generally homogenous we expect these to have no or only minor influence on the outcome of our results. The nutrient data available for the studied ditches were very limited. To analyze the possible relationship between climate and nutrient concentrations we therefore used nutrient data from the studied ditches and from closely related water bodies such as canals and ponds. Unfortunately this aggregation did not allow for a division into soil types. Because nitrogen concentrations were not measured in a consistent way we focused on total phosphorus.
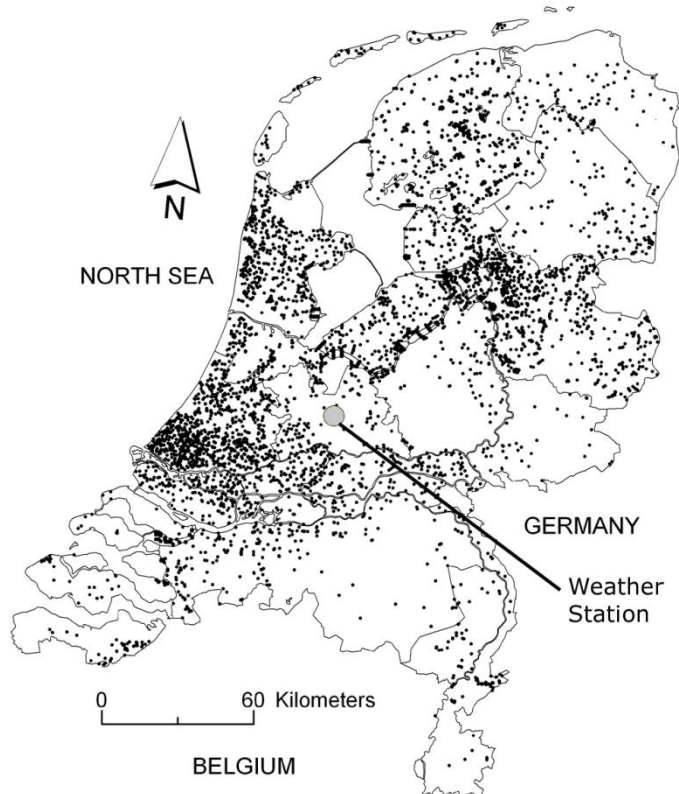
Figure 1. Sampling locations of macrophyte cover in Dutch drainage ditches

Climate data

Local weather variables used in the analyses were the number of frost days (days with minimum temperature below 0°C), temperature (daily average and daily minimum), precipitation (daily sum) and solar radiation (global radiation and solar duration). As a proxy for winter severity we used the Hellmann number, which is defined by summing the absolute value of all daily averages of below 0°C temperatures over the period November (previous year) through March (Hellmann 1883). Weather variables were averaged for two periods per year: (1) Half year period: October (previous year) to March and (2) NAO winter period: December (previous year) to March. Data were provided by the Royal Netherlands Meteorological Institute (KNMI 2010) for a central and representative location in the Netherlands (De Bilt/Utrecht , 52°06'N, 05°11'E).

The North Atlantic Oscillation (NAO) describes the difference of normalized sea-level pressure between Lisbon, Portugal and Stykkisholmur, Iceland (Hurrell 1995). The NAO winter index is the mean value from December (previous year) to March and was obtained from the National Center of Atmospheric Research, Boulder, USA (NCAR 2010).

Macrophyte data

Macrophyte data were retrieved from the Limnodata Neerlandica. Macrophyte cover recordings (Braun-Blanquet scale) were collected during the growing season (April – September). Species in the dataset were assigned to one of three macrophyte types based on growth and overwintering strategy: free-floating species, evergreen overwintering submerged species, and submerged macrophyte species that die back in winter.

We calculated the average cover per year for each macrophyte type, using the maximum class values of the Braun-Blanquet scale. When a macrophyte type was not encountered in a ditch we used a cover of 0% for that type. Additionally, the first four Braun-Blanquet classes were grouped resulting in a cover class ranging from 0-5%. Subsequently we split the recordings according to their soil type into either ditches in inorganic soil or ditches in organic soil.

Statistics
Pearson correlation was used to test for relationships between the NAO winter index and weather variables. Stepwise linear regression was conducted to determine the primary climate predictor(s) for macrophyte cover. Our independent variables were highly correlated, but we had small confidence intervals. Therefore we had degrading collinearity, which only causes minor problems (Belsley *et al.* 2004). In our case this collinearity affects the ability of estimating the contributions of individual predictors, but it does not affect the ability of the multiple regression model to predict the response. Then linear regression (Enter method) was conducted between the primary climate predictor (independent) and macrophyte covers (dependent) per soil type. Multiple factor and single factor slope comparisons were done with Analysis of Covariance (ANCOVA) with the primary climate predictor as covariate and soil type and/or macrophyte type as fixed factor. Student t-tests were used for intercept comparisons. Pearson correlation was used to test for a relationship between the primary climate predictor and total phosphorus concentrations of resembling water body types. Statistical analyses were performed using PASW Statistics 17.0 (SPSS Inc., Chicago, IL, USA). Statistically significant difference was defined as $P < 0.05$ (* at 0.05 level and ** at 0.01 level).

Results
NAO winter index was negatively correlated with Hellmann number, number of frost days and solar radiation (global radiation and solar duration). It was positively correlated with temperature (daily average and daily minimum) and precipitation (sum) (Table 1).

Table 1. Pearson correlations between NAO$_{winter}$ and weather variables (n=26)

Variable	Dimension	Pearson r	p
Hellmann number[a]	-	-0.544	<0.001**
# Frost days[b]	-	-0.692	<0.001**
# Frost days[c]	-	-0.695	<0.001**
Precipitation (sum)[b]	mm	0.339	0.045*
Temperature (average)[b]	ºC	0.558	0.003**
Temperature (minimum)[b]	ºC	0.538	0.005**
Solar duration[c]	hour	-0.428	0.029*
Global radiation[c]	Joule cm^{-2}	-0.384	0.053

[a] For the Hellmann period (Nov-Mar)
[b] For the Half Year period (Oct-Mar)
[c] For the NAO period (Dec-Mar)

In stepwise linear regressions the NAO winter index was the single significant predictor related to free-floating and evergreen submerged macrophyte cover, respectively (R^2=0.38, F=14.85, p=0.001** and R^2=0.45, F=6.10, p=0.003**). The NAO winter index together with average temperature explained most of the variance in cover of submerged macrophytes that die back in winter (R^2=0.40, F=7.67, p=0.003**). Free-floating and evergreen submerged macrophyte covers were both positively linearly related to the NAO winter index. Winter die-back macrophyte cover was negatively related to the NAO winter index (Fig. 2).
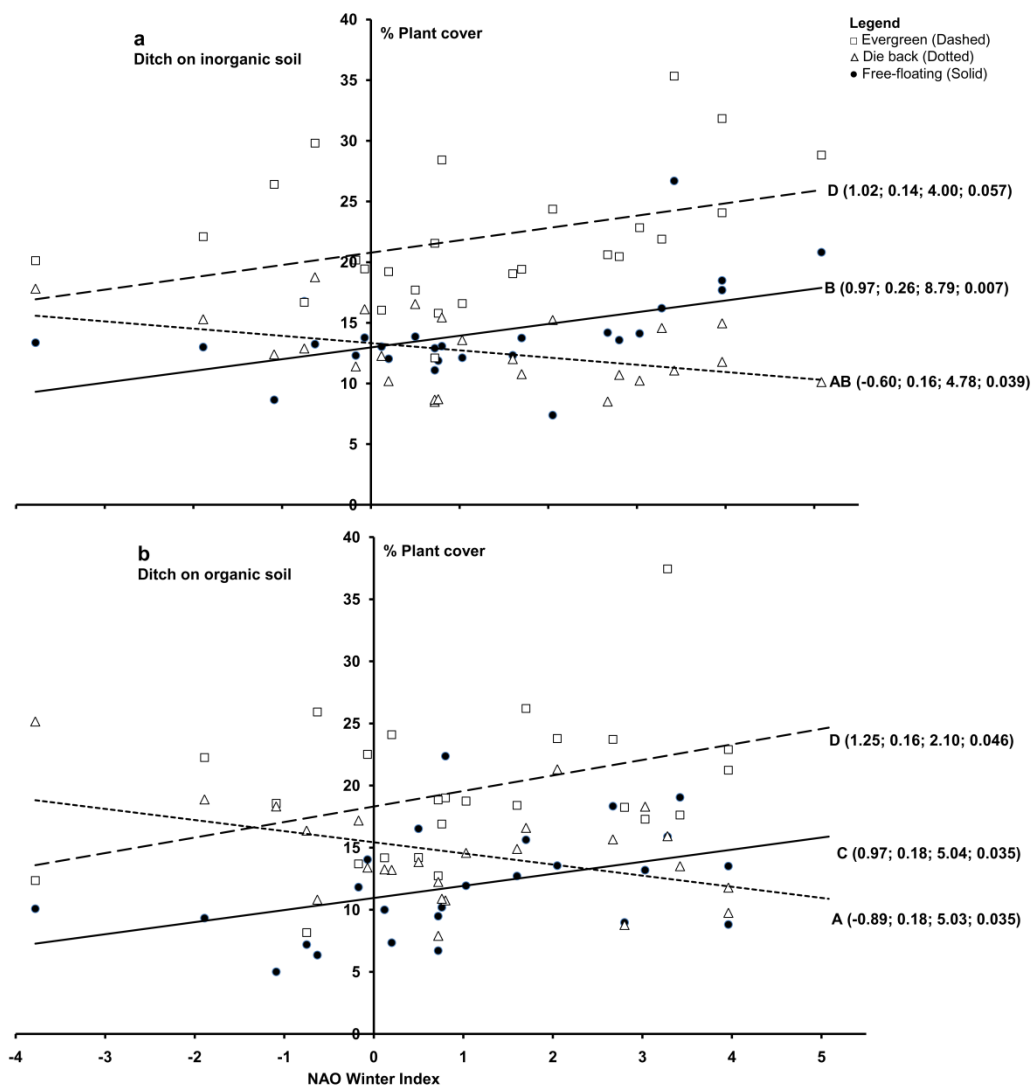
Figure 2. NAO winter index and macrophyte responses of free-floating, evergreen submerged and winter die-back submerged macrophytes in ditches in inorganic (**a**) and organic (**b**) soils. Capitals indicate significant differences in slopes across panels. Results of the linear regression analyses can be found between brackets (Slope; R^2; F, p).

Multiple factor slope comparisons (ANCOVA) showed that differences between slopes were mainly determined by macrophyte type (F=47.44, p<0.001**), NAO winter index (F=5.04, p=0.026*) and the interaction between macrophyte type and soil type (F=3.64, p=0.029*). Single factor slope comparisons showed that, in both soil types, evergreen submerged macrophytes were more steeply related to NAO winter index than free-floating macrophytes or submerged macrophytes that die back in winter. Generally slopes of the regression models of different growth and overwintering strategies differed significantly except for free-floating and submerged macrophytes that die back in winter in ditches on organic soil (Fig. 2 & Table 2).

The relation between free-floating macrophyte cover and NAO winter index was significantly stronger in ditches on organic soil than in ditches on inorganic soil. There was no significant difference in response between soil types for evergreen submerged and winter die-back submerged macrophytes (Table 2).

We found a positive correlation (Pearson r=0.53, p=0.014*) between NAO winter index and total phosphorus concentrations of our lumped nutrient data (ditches, canals and ponds).

Table 2. Slope comparisons (ANCOVA) and intercept comparisons (Student t-test) between free-floating macrophytes, evergreen submerged macrophytes and submerged macrophytes that die back in winter in relation to soil type (n=26).

	Slope		Intercept	
Evergreen vs. Winter die back	**F**	**Significance**	**t**	**p**
Ditches on organic soil	58.06	<0.001**	-	-
Ditches on inorganic soil	12.24	0.001**	-	-
Free-floating vs. Evergreen				
Ditches on organic soil	43.90	<0.001**	-	-
Ditches on inorganic soil	31.95	<0.001**	-	-
Free-floating vs. Winter die back				
Ditches on organic soil	4.80	0.034*	-	-
Ditches on inorganic soil	2.36	0.131	1.54	0.130
Ditches on organic soil vs. Ditches on inorganic soil				
Free-floating	10.20	0.002**	-	-
Evergreen	2.25	0.14	1.51	0.138
Winter die-back	3.87	0.055	-1.93	0.059

Discussion

Our analyses demonstrate that the NAO winter index is related to the cover of macrophytes with different overwintering strategies in drainage ditch ecosystems. Free-floating and evergreen submerged macrophytes were positively related and submerged macrophytes that die back in winter were negatively related to the NAO winter index. The NAO winter index was the best predictor of macrophyte cover and can be regarded as a good proxy for the general pattern in weather conditions in the Netherlands as it is negatively correlated with Hellman number, number of frost days and solar duration and positively correlated with precipitation and temperature.

Our analysis suggests that cold winters favour submerged macrophytes that die back in winter, while warm winters favour free-floating and evergreen submerged macrophytes. This differential winter effect may be explained by the increased frost damage on free-floating and submerged evergreen plants in colder winters (negative NAO winter index), while submerged macrophytes that die back in winter are less vulnerable for winter damage because they overwinter in the sediments as specialized structures like seeds, tubers and turions (e.g. Renman 1989; Whiteman & Room 1991). In the absence of other macrophytes after a cold winter the submerged macrophytes that die back may take advantage of available resources, resulting in higher cover. Additionally, increased stratification of turions during colder conditions may result in increased germination rates or germination success (Van Wijk & Trompenaars 1985).

In line with results from experimental studies, our analysis of field data also suggests that when climate change causes warmer winter conditions, higher cover of free-floating or evergreen submerged macrophytes during the next growing season might occur more often. The positive relation between the NAO winter index and total phosphorus concentration may imply that after a mild winter an increased nutrient concentration creates opportunities for fast growing macrophytes to expand their cover early in the growing season, especially free-floating species such as duckweed (*Lemna* sp.) that are more affected by nutrient availability in the water column. Rooted submerged macrophytes are less affected since nutrients are often not the limiting resource. The relation between free-floating macrophyte cover and the NAO winter index is stronger in ditches on organic soil. This supports the idea that mild and wet winters can possibly lead to a relatively strong increases in nutrient availability in these ditches caused by the strong temperature dependence of mineralization of organic matter (internal loading) (Fisher *et al.* 2005). Phosphorus loadings from organic soils to aquatic systems may be especially high after dry periods with increased mineralization followed by periods with high precipitation and high run-off resulting in increased external phosphorus loading (Rip 2007).

With the alternative stable states theory in mind (Scheffer *et al.* 2003), higher NAO winter indices might increase the probability of a shift from a diverse vegetation to a state of dominance by free-floating macrophytes. To prevent a shift towards dominance of free-floating macrophytes,

management efforts could focus on reducing nutrient levels. As many ditches are situated in fertilized agricultural areas this would not, however, be an easy task.

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Two important human activities influencing ditch vegetation: nutrient addition and maintenance

7.   Synthesis

7.1   Perspectives for management of drainage ditches

Although drainage ditches are artificial, manmade infrastructures to transport water, the ecological characteristics of these ditches resemble those of cut-off channels along rivers. Both are small dimensioned water bodies with extensive vegetation development and are influenced by disturbances. Manmade drainage ditches can be seen as a surrogate for disappeared biodiverse cut-off channels in floodplains and, therefore, have an important ecological function in the Dutch landscape (Verdonschot et al., 2011).

Heterogeneity of the habitat is often crucial to maintain diversity in ecosystems since diverse environmental conditions create niches for multiple species (Brose, 2001; Kreft and Jetz, 2007). Cut-off channels in floodplains of larger rivers are very heterogeneous (Bornette et al., 1998) and different successional stages of the vegetation can be found in cut-off channels at any point in time. Disturbance events caused by river flooding set back succession in some parts and create variations in for instance nutrient availability, resulting in heterogeneous habitats with many different plant species (Bornette et al., 1998; Roozen et al., 2008). Heterogeneity should therefore also be considered an important characteristic to restore and maintain plant diversity in drainage ditches. However, modern maintenance methods used in drainage ditches nowadays, together with extensive eutrophication cause a loss of heterogeneity and consequently a loss in biodiversity.

This thesis shows that heterogeneity in environmental conditions creates differences in composition of drainage ditch vegetation across the Netherlands. The occurrence of the three different vegetation types described in the introduction (Chapter 1) was correlated to several factors operating at different spatial scales (Figure 1). Analyses of the data gathered in 2007 showed that hydrological characteristics of the drainage system, land use, soil type and groundwater flow were the main driving forces on the regional scale. Important local factors included ditch dimensions, chemical composition of water and sediment (including nutrient levels) and physical disturbance of the vegetation. It can therefore be concluded that functioning of vegetation in drainage ditches is better understood when considering local factors in the context of the regional setting. The additional value of including regional factors is in line with studies from other aquatic systems such as streams (Heino et al., 2003; Baattrup-Pedersen et al., 2002; Schäfer et al., 2007) and canals (Willby et al., 2001).

Regional scale environmental factors likely set the context for local conditions (see for instance Raatikainen et al. (2007) and Schäfer et al. (2007)), consequently influencing the vegetation composition in a ditch (Figure 1). This should be taken into account when identifying and determining management goals and measures to restore or maintain plant diversity. For instance, ditches in areas that receive mineral-rich deep groundwater (regulating P availability for plants (Lamers et al., 2002)) can have a higher potential to contain species rich communities compared to ditches receiving nutrient rich local groundwater from neighbouring hydrological units/polders (Wassen et al., 1990). In contrast to relatively nutrient poor sandy soils, peaty soils can release large amounts of nutrients and humic acids into aquatic systems due to peat mineralization (Rip et al., 2007). In this situation the continuous high input of substances from the surrounding soil type may limit the possibilities for maintaining plant diversity in drainage ditches regardless of for example propagule availability in the sediment.

A local ditch is always part of a large network of interconnected ditches in the polder. This connectivity may facilitate the distribution of plant propagules through the network by wind-driven hydrochory which can be an important process for colonisation by plants (Sarneel, 2010). Hence, a large and well-connected ditch network may enhance the recolonisation of dredged parts, although the presence of for instance *Elodea nuttallii* in surrounding ditches may also lead to fast development of a monoculture rather than recovery of a diverse vegetation. Therefore, whether connectivity has a positive or negative effect on ecosystem recovery and diversity largely depends on the species present in the system and the dominant ecological interactions (Scheffer et al., 2006). For instance, isolation of several aquatic systems, each having an unique community structure and species composition may lead to a higher biodiversity on a regional scale (Williams et al., 2004). This implies that for the recovery of ditch

vegetation after maintenance, the presence or absence of *Elodea* sp. or duckweeds and the water nutrient levels in surrounding ditches largely determine whether connectivity has a positive or negative effect. To facilitate recolonisation after maintenance activities not all ditches in a ditch network should be dredged or mown in a single year. This way undisturbed ditches are always present, serving as a source from which propagules can colonize the ditches in which maintenance was performed. This way heterogeneity is maintained across a hydrological unit by means of patchiness in degree and timing of disturbance.

Spatial heterogeneity in nutrient availability within or between hydrological units can also facilitate plant diversity as the three vegetation types were found at different phosphorus levels in water and sediment. Sediment phosphorus levels differed between the diverse submerged vegetation (found at values approximately between 200-500 mg P/kg) and monocultures by *Elodea* sp. (500-1000 mg P/kg) and free-floating plants (1000-1600 mg P/kg). Additionally, free-floating plant dominance was especially related to higher P levels in water (0.4-0.7 mg P/l) compared to the submerged vegetation types (0.1-0.2 mg P/l). Even though nutrient levels clearly differed, total biomass was comparable between the three vegetation types with *Elodea* sp. dominated vegetation showing relatively low total biomass compared to other studies. The comparable total biomass might be caused by a non-limiting availability of nutrients in all vegetation types causing high biomass production until light limitation occurs (Scheffer et al., 1993), resulting in comparable standing stocks in all ditches. Higher nutrient concentrations may also be used for increased P storage in plant tissue by for instance *Elodea nuttallii* (Garbey et al., 2004). This may result in higher P uptake, without an increase in total biomass. Disturbances due to maintenance may further limit the standing biomass of for instance *Elodea sp* as was shown in streams by Di Nino et al. (2005). Although standing biomass was comparable between the three vegetation types, the turnover rate of biomass might still be higher for vegetation types occurring at higher nutrient levels, thus resulting in differences in total produced biomass during a complete growing season. Since both monocultures have negative consequences for the ecological water quality, P levels in sediment (and in water for free-floating plant dominance) should be lowered to levels at which the diverse, submerged vegetation occurred. However, considering the predicted decrease in water P levels of just 3% in 2015 with the existing measures (PBL, 2008) and the expected increase in dominance of *Elodea* sp. and free-floating plants due to climatic warming (Netten et al., 2011), additional measures are likely needed to prevent the occurrence of monocultures.

 An important additional limitation for the recovery of a diverse submerged vegetation might be the composition of the propagule bank (Figure 1) which in a way reflects the history of the system. The propagule bank in the sediment of ditches dominated by free-floating plants mainly consists of propagules from these free-floating plants. Continuous dominance by free-floating plants results in build-up of a stock of free-floating plant propagules that survive severe conditions as they are located on the sediment. These propagules may outcompete propagules from submerged plants as fast growth of free-floating plant propagules early in the growing season results in low light availability, limiting germination and subsequent development of submerged plants. As a result fewer propagules are produced by these submerged species, further favouring free-floating plant dominance. Boedeltje et al. (2005) for instance found an impoverished submerged plant propagule bank in a canal with nutrient rich sediments containing large amounts of free-floating plant propagules from which free-floating plant dominance developed frequently. The reproduction strategy of free-floating plants, producing large amounts of propagules that germinate fast at the start of the growing season, likely acts as a stabilizing factor keeping the system in the state of free-floating plant dominance. Therefore, considering the alternative stable states theory (Scheffer, 1998), the extensive yearly buildup of a propagule bank can be considered a positive feedback, keeping the ditch in the free-floating plant dominated state (Scheffer et al., 2003). Removal of the nutrient rich top layer of the sediment can break this feedback resulting in disappearance of the free-floating plant dominance (Boedeltje et al. 2005). Removal of nutrient rich sediment in drainage ditches might likewise result in decreased free-floating plant development, possibly creating favourable conditions for colonization by submerged plants from surrounding ditches.

 A prerequisite for this colonization though might be that the ditch is well connected to a network of surrounding ditches in which a vital source population of submerged species is present, combined with low densities of free-floating plant propagules. In many drainage ditches the recolonisation might be slow though, due to the impoverished vegetation of surrounding drainage ditches (Janse and Van Puijenbroek, 1998). By creating heterogeneity in environmental conditions and consequently vegetation

composition within the hydrological unit a vital source of submerged plant species can likely be maintained. Enlarging the propagule bank by introducing submerged plant propagules might be a promising additional measure to accelerate submerged vegetation recovery, as it was already successfully applied in other aquatic systems (Hilt et al., 2006).

This thesis shows that disturbance of the sediment when maintenance is performed likely will cause increased germination of propagules from free-floating plants. Applying alternative maintenance methods that minimize sediment disturbance or removal of the propagule rich top layer of the sediment may therefore decrease the risk of prolonged free-floating plant dominance due to the propagule bank.

Elodea sp. is known for its disturbance tolerance and fast regrowth after cutting (Vernon and Hamilton, 2011). Therefore mowing (Figure 1) will likely be an additional factor influencing the occurrence of *Elodea* sp. dominance besides increased sediment nutrient levels. Contrastingly this thesis shows that the growth and survival of Shining and Grass-wrack pondweed are negatively impacted by cutting and regrowth may not occur at all if too much biomass is removed. Although no direct comparison was made between Pondweeds and *Elodea* sp. it seems likely that *Elodea* sp. will outcompete other more sensitive species such as Pondweeds in a frequently disturbed, eutrophic system. Lowering sediment P levels therefore likely need to be combined with changes in mowing method and frequency. Baattrup-Pedersen et al. (2003) for instance showed that species diversity was higher in streams that were subject to a lower mowing frequency. Creating zones along the ditch bank that are mown less frequent in addition to lowering sediment P levels likely is a promising measure to investigate. This way, heterogeneity in disturbance level within ditches (for instance yearly mowing in the central part of the ditch and less frequent in a zone close to the bank) will likely create variation in conditions and consequently higher species diversity.

At the highest spatial scale considered in this thesis, climatic warming will likely reduce the positive effects of the mentioned measures and conditions that support development of a diverse vegetation. Milder winters likely stimulate fast and early development of free-floating and evergreen submerged plants due to the characteristics of their overwintering organs. Additionally, on organic soils climatic warming may lead to increased phosphorus availability, as was also found for lakes (Mooij et al., 2005). Altogether these effects might increase the risk of a shift from a diverse vegetation to a monoculture of free-floating plants or for instance *Elodea* sp. (Scheffer et al., 2003). To counteract these effects of climatic warming an extensive effort is likely needed to stimulate the development of diverse submerged vegetation. A combination of measures might be effective containing further reduction of nutrient inputs, changing maintenance methods, creating habitat heterogeneity and stimulating recolonisation by annual submerged plants.
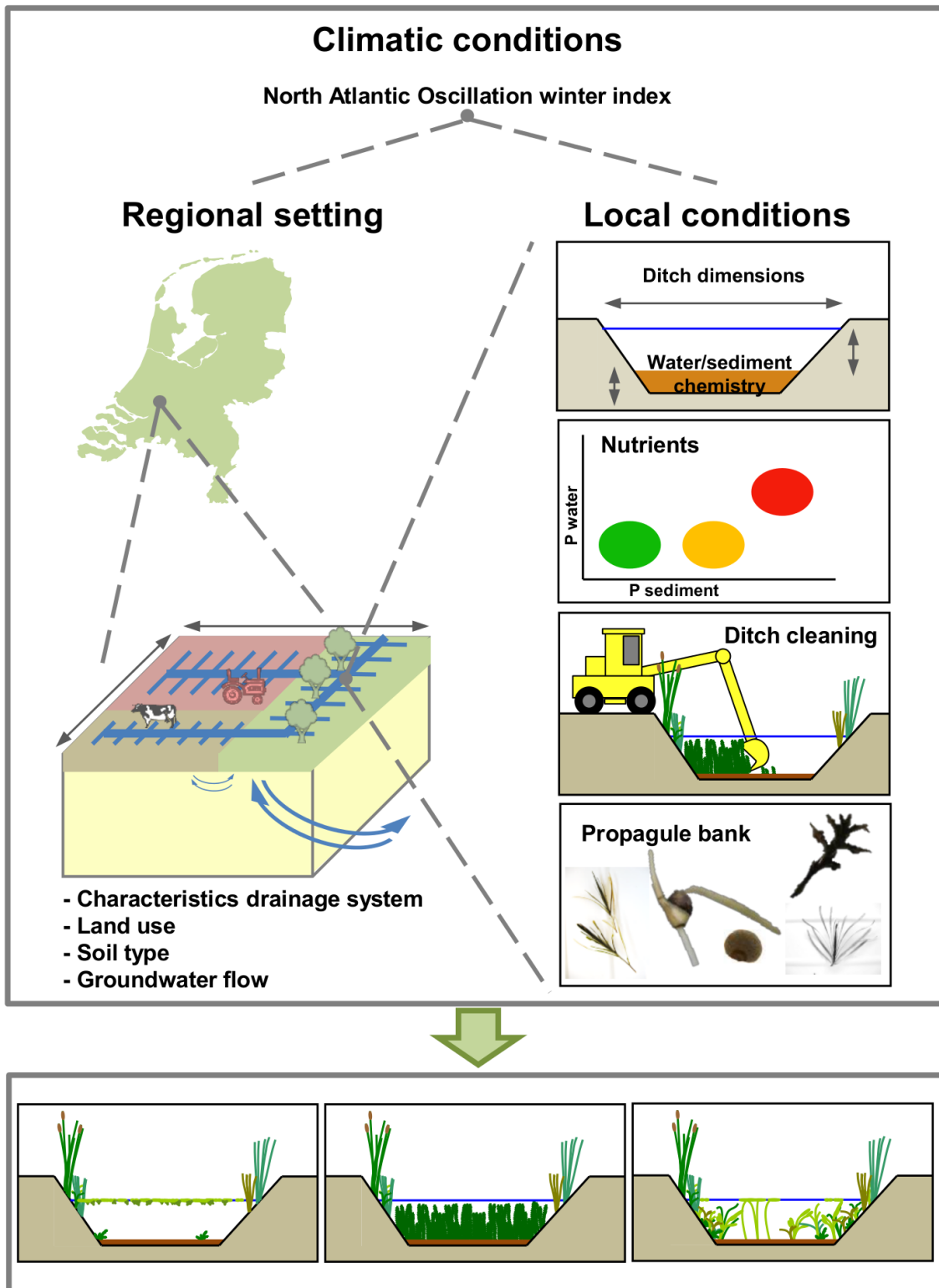
Figure 1. Schematic representation of the studied environmental factors and related differences in vegetation composition. Regional characteristics set the context for local conditions, while the combined effect of regional and local factors ultimately determines community composition in an individual ditch.

7.2 A polder scale vision on water quality management: redistributing functions and ecological goals

Drainage ditches are mostly studied as individual ecological entities (see for instance Portielje and Roijackers (1995), Twisk et al. (2003) and Milsom et al. (2004)). Although it is commonly recognized that an individual drainage ditch is part of a hydrological network in the context of quantitative water management, little attention has been paid to the influence of the ditch network on the ecological functioning of a single ditch. However, this thesis shows that factors within a ditch and at the level of the surrounding ditch network (hydrological unit or polder) are both important for the ecological functioning of a drainage ditch. Therefore, future management of drainage ditches can be more effective when based on an integrated view on the optimal design and management of the total polder. Consequently, heterogeneity in environmental conditions can be achieved on different spatial scales which facilitates diversity in plant community compositions.

When determining the optimal design of a polder, redistribution of all desired functions within or between polders can be considered (Figure 2). This will subsequently result in reassigning ecological targets to the ditches within a polder. The distribution of functions within and between polders is often historically determined, which can result in water from ditches with a low ecological quality being transported into ditches with high ecological targets. Agricultural land may for instance cause high outputs of nutrients, which may be transported to surrounding ditches that should develop a higher ecological quality (Figure 2.A). The achievable ecological water quality in an area with a nature function will therefore likely be limited if agricultural land use is situated close to this area and discharges high nutrient loads into the nature reserve (see for instance Rip et al. (2007)). In this situation, redistribution or isolation of functions will likely be an effective measure to increase water quality in ditches with high ecological goals. Functions may for instance be clustered across multiple polders, thereby separating functions that negatively influence each other. Within a single polder, areas with an ecological function can be located 'upstream' from agricultural areas or can be separated from the agricultural area by creating a recreational area acting as a buffer zone (Figure 2.B). This buffer zone can serve as a sink for dissolved materials like nutrients (Carpenter and Lodge, 1986).

Additionally, functions might at present be located in an area with suboptimal conditions. Nature reserves may for instance be located in intensively drained parts of the polder while agricultural land is located in wetter parts of a polder that may inundate periodically. By redistributing functions (agriculture in drier, arable areas, nature in wetter areas) the desired conditions for each function may be maintained more easily, lowering water management costs and possibly increasing ecological potential in areas with a nature function. Low-lying, non-agricultural areas may additionally be used as temporary water storage in case of a water surplus.

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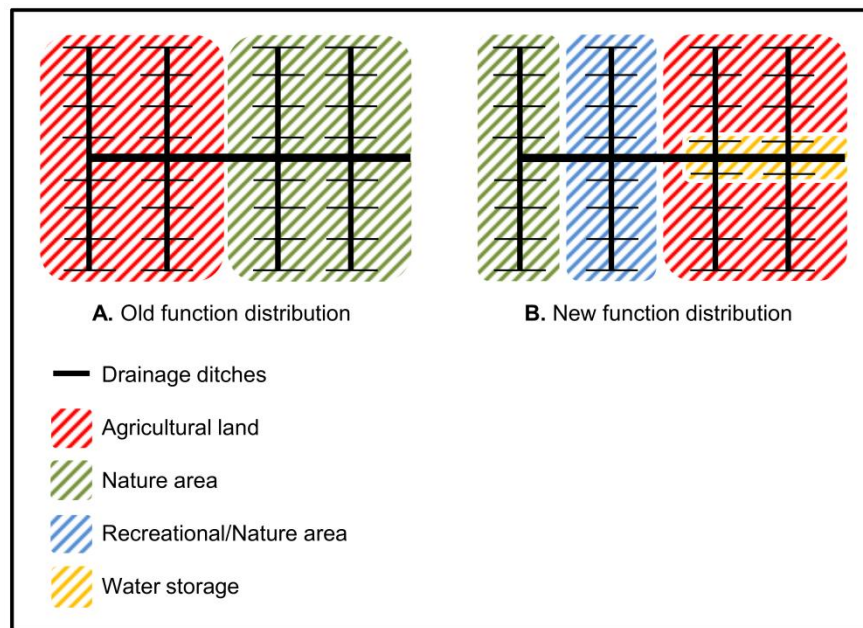
Figure 2. Schematic example of redistribution of functions in a polder which can increase the ecological quality of ditches with higher ecological targets.

After (re-)assigning functions to ditches within a polder, habitat heterogeneity can be enhanced by creating differentiation in ecological targets, design of ditches and maintenance strategies (diversity in method and frequency). Assigning different ecological targets to (parts of) ditches and ditch networks is the starting point for differentiated dimensioning and maintenance of ditches. Parts of ditches may for instance be used for development of early successional vegetation with Charophytes while late successional vegetation with helophytes are appointed to other parts (Nijboer, 2000). Based on these ecological targets part of the ditches in a polder may for instance be constructed narrower and deeper with less bank vegetation, while others are constructed broader and shallower with a large riparian zone. These differential designs then require different maintenance strategies. Broader dimensioned ditches with larger riparian zones may be mown at a very low frequency as shallow ditch banks may function as water storage. Narrower and deeper ditches may be mown more frequent to maintain early successional vegetation with Charophytes and to maintain their drainage function. Variation in these aspects within an individual ditch and across ditches in a polder network will likely result in diversity of habitat conditions, strengthening diversity in biota across ditches as was already observed by Verdonschot et al. (2011). Although this requires a radical change in the way we think about drainage ditch management from primarily efficiency oriented towards more ecological effects oriented, it will likely be an important prerequisite to maintain and restore an important ecosystem in the cultural landscape, the ditch!

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Summary

Drainage ditches can be found in many countries across the world and are important elements of the Dutch landscape. Although manmade they accommodate a wide variety of plant and animal species and, therefore, contribute largely to the biodiversity of the agricultural landscape. Due to their comparable ecological characteristics they might even serve as a surrogate for disappeared cut-off channels of river floodplains. However, due to disturbances such as eutrophication and frequent vegetation removal many ditches now show a monoculture of free-floating plants or of fast-growing submerged species like Elodea sp. rather than a diverse submerged vegetation. These monocultures deteriorate conditions for aquatic fauna, resulting in an overall loss of biodiversity. To maintain or restore a diverse vegetation, knowledge on driving forces behind the occurrence of different vegetation compositions is needed. Therefore this thesis focuses on identifying conditions and mechanisms that determine macrophyte community composition and functioning in drainage ditches in the Netherlands, with focus on effects of nutrient state, maintenance and seed bank properties.

To determine which environmental factors, operating at different spatial scales, relate to differences in macrophyte community composition, a field dataset from 67 ditches was analysed containing data on species and biomass composition and the environmental setting. In Chapter 2 the contribution was quantified of local and regional environmental factors in explaining patterns in species and biomass composition. Multiple factors at different spatial scales were related to the macrophyte communities, the most important being nutrient availability, occurrence of seepage, dimensions of the ditch and of the surrounding hydrological unit and soil type. The rather low explained variance per variable likely indicates a typical characteristic of macrophyte communities in drainage ditches: multiple factors affect their functioning without one being dominant. Local and regional factors contributed approximately two third and one third respectively to the total explained variance for both biomass and species composition data. The relations found with regional factors are likely explained by the strong connectivity between drainage ditches and the surroundings, causing intensive exchange of substances and biota.

Nutrients were regarded a dominant factor for the occurrence of different vegetation types in drainage ditches. Therefore, in Chapter 3 the most important nutrient fractions and levels were determined at which three vegetation types (monocultures of *Elodea* sp. or free-floating plants and diverse submerged vegetation) were observed in Dutch drainage ditches. The three vegetation types occurred in rather distinctive ranges of nutrient concentrations with total P in water and sediment being most important. Higher levels of sediment P distinguished the occurrence of monocultures (by *Elodea* sp. and free-floating plants) from the diverse submerged vegetation, while higher P levels in water distinguished free-floating plant dominated systems from ditches with a submerged vegetation (*Elodea* monoculture or other submerged plants). Remarkably, although nutrient levels clearly differed, no differences in total biomass were found between the three vegetation types. This was mainly caused by the, compared to other aquatic systems, relatively low total biomass of *Elodea* sp. dominated ditches, possibly resulting from increased P storage in *Elodea* sp. plant tissue, rather than increased productivity. Additionally, the small dimensions of most drainage ditches may have limited space for increased biomass development of free-floating plants (only growing at the water surface) and *Elodea* sp. despite higher nutrient availability.

Maintenance activities like mowing may endanger completion of the life-cycle or survival of macrophytes. In Chapter 4 the effect of cutting on survival and growth was determined for two Pondweed species by applying different cutting treatments under indoor experimental conditions. For both species short term negative effects of cutting on biomass production and survival were observed. *Potamogeton lucens* seemed to be a more tolerant species as strong effects were only visible when biomass was cut at the sediment–water interface. On the other hand, *Potamogeton compressus* seemed to be more vulnerable because every treatment (cutting halfway, at three quarters down the water column and at the sediment water interface) resulted in significantly lower below-ground and green shoot biomass production. Long term effects of cutting on *P. lucens* might occur through decreased development of the rhizome network while for *P. compressus* long term effects on

reproduction might be expected as flowering decreased when cut at the sediment–water interface and turion formation only occurred in the uncut controls. The decreased biomass production by *P. compressus* may lead to a competitive disadvantage in the field as fast-growing, disturbance tolerant species such as *Elodea nuttallii* (Planch.) St. John may outcompete the species. Creating patchiness in mowing height and frequency or applying a mowing regime that leads to reduced biomass development while species still survive might create opportunities to both maintain the water transporting function of the drainage system while preserving the species in the ditches.

Many ditches in the Netherlands nowadays contain a monoculture of free-floating plants and restoring suitable site conditions for submerged plants might create opportunities for re-establishment from propagules. The potential of the sediment propagule bank to initiate recovery under suitable conditions was studied in Chapter 5 by performing a germination experiment with sediments from ditches with a submerged vegetation and a monoculture of free-floating plants. Compared to sediments from ditches with submerged vegetation, sediments from free-floating plant–dominated ditches produced significantly lower numbers of individuals and species of submerged and emergent plants, while numbers of individuals and species of free-floating plants were higher. These results suggest that sediments from free-floating plant dominated ditches have lower potential to recover a diverse plant community. This probably results from positive feedback mechanisms caused by the vegetation present, maintaining the free-floating plant–dominated state. Sediment disturbance seems to strongly favour the germination of free-floating plant propagules, especially from free-floating plant dominated ditch sediments. Ditch maintenance activities such as mowing and dredging, therefore, will likely favour persistence of the free-floating plant dominated state. To shift from dominance by free-floating plants to a more diverse plant community, alternative maintenance methods should be considered that cause less sediment disturbance together with measures that promote (re-)colonization such as temporary drawdown or re-introduction of species.

At the highest spatial scale considered in this thesis climatic conditions influence many of the regional and local conditions. In Chapter 6 the effect of climatic variation on the cover of free-floating and submerged macrophytes was studied by relating the North Atlantic Oscillation (NAO) winter index to macrophyte cover in ditches in the Netherlands over the past 26 years. Mild winters were related to higher coverage of free-floating and evergreen submerged plants (like *Elodea nuttallii*) while cold winters coincided with higher coverage of annual submerged plants in the next growing season. On organic soils this effect of milder winters on free-floating plant development was significantly stronger, likely due to increased nutrient availability. These results suggest that milder winters may cause free-floating and evergreen submerged plants to outcompete annual submerged plants which may lead to a loss of diverse submerged vegetation. Lowering nutrient availability is likely one of the measures that will limit the negative effects of climatic warming.

In Chapter 7 (Synthesis) it is discussed that, similar to cut-off channels, heterogeneity in environmental conditions is an important characteristic in drainage ditches to maintain plant diversity. The environmental factors discussed in this thesis may all add to creating heterogeneity in conditions and consequently differences in vegetation composition. A schematic overview of the found relations is presented. To restore and maintain a diverse vegetation a combination of measures is likely needed, that influences multiple factors related to vegetation functioning, thereby also counteracting the negative effects of climatic warming on the development of a diverse vegetation. Finally, the use of a polder scale vision on water quality management is discussed arguing that future management of drainage ditches can be more effective when based on an integrated view on the optimal design and management of the total polder. This may then result in spatial redistribution of functions and ecological targets within and across polders/hydrological units to exploit the ecological potential. Subsequently, habitat heterogeneity can be achieved by creating differentiation in design and maintenance of drainage ditches.

Samenvatting

Sloten zijn overal ter wereld te vinden en vormen een belangrijk onderdeel van het Nederlandse landschap. Ondanks dat het door de mens gemaakte, kunstmatige wateren zijn, kunnen ze een grote diversiteit aan flora en fauna bevatten. Hierdoor dragen ze in belangrijke mate bij aan de biodiversiteit van het agrarisch landschap. Doordat sloten in ecologisch opzicht sterk lijken op afgesloten nevengeulen in rivieruiterwaarden zouden sloten zelfs een vervanger kunnen zijn voor de nevengeulen die op veel plaatsen zijn verdwenen. Verstoringen als eutrofiering en frequent vegetatie verwijderen hebben er echter voor gezorgd dat veel sloten momenteel een monocultuur bevatten van bijvoorbeeld kroos of Smalle waterpest (*Elodea nuttallii*). Deze monoculturen zorgen voor verslechterde leefomstandigheden voor waterdieren (vissen, amfibieën en ongewervelde dieren) waardoor de totale biodiversiteit van de sloot achteruit gaat. Om achteruitgang van de ecologische kwaliteit te voorkomen of terug te dringen is kennis nodig over de factoren die verantwoordelijk zijn voor het voorkomen van verschillende typen vegetatie. Het onderzoek in dit proefschrift richt zich daarom op het identificeren van condities en mechanismen die de samenstelling en het functioneren van watervegetaties in Nederlandse sloten bepalen, waarbij meer specifiek gekeken is naar de effecten van voedselrijkdom, onderhoud en de aanwezige overlevingsorganen.

Om te bepalen welke milieufactoren (op zowel lokale als regionale schaal) gerelateerd zijn aan verschillen in vegetatiesamenstelling is een dataset van 67 sloten geanalyseerd. De dataset bevat gegevens over soortensamenstelling, biomassa en milieucondities. In hoofdstuk 2 is de bijdrage gekwantificeerd van lokale en regionale factoren aan het verklaren van verschillen in biomassa en soortensamenstelling. Meerdere factoren van verschillende ruimtelijke schaalniveaus bleken gerelateerd aan verschillen in vegetatiesamenstelling. De belangrijkste factoren waren beschikbaarheid van voedingsstoffen (nutriënten), aanvoer van kwel, dimensies van de sloot en de hydrologische eenheid (polder) en het bodemtype. De lage verklarende waarde van de individuele variabelen indiceert waarschijnlijk een typische eigenschap van sloten; meerdere factoren zijn van invloed op het ecologisch functioneren zonder dat één factor dominant is. Lokale en regionale variabelen droegen respectievelijk twee derde en een derde bij aan de verklaarde variantie voor zowel biomassa als soortensamenstelling. De bijdrage van regionale variabelen wordt waarschijnlijk veroorzaakt door de sterke mate van verbondenheid tussen de sloot en zijn omgeving waardoor er sterke uitwisseling van stoffen en organismen plaatsvindt.

Eén van de hypothesen was dat nutriënten een dominante factor zijn voor het voorkomen van verschillende vegetatietypen in sloten. Daarom zijn in hoofdstuk 3 de belangrijkste nutriëntenfracties en het bereik van concentraties bepaald waarbij drie vegetatietypen voorkomen (monoculturen van kroos of waterpest (*Elodea* sp.) en een diverse ondergedoken vegetatie). De drie vegetatietypen zijn bij redelijk onderscheidende bereiken van voedingsstoffen aangetroffen, waarbij fosfaat in water en sediment de meest onderscheidende fracties zijn. Hogere P concentraties in het sediment onderscheiden monoculturen (van kroos en waterpest) van de diverse ondergedoken vegetatie. Met name hogere P concentraties in het water onderscheiden monoculturen met kroos van de twee ondergedoken vegetatietypen. Opvallend is dat er geen verschillen gevonden zijn in totale biomassa tussen de vegetatietypen, terwijl dit wel verwacht kon worden omdat verschillen in voedselrijkdom vaak tot verschillen in productiviteit leiden. De geringe verschillen in totale biomassa worden met name veroorzaakt door de, in vergelijking met andere aquatische systemen, relatief lage biomassa in Waterpest gedomineerde sloten. Dit geringe verschil kan veroorzaakt worden doordat Waterpest in staat is om bij hogere fosfor beschikbaarheid meer fosfor in weefsel op te slaan zonder een verhoogde productie van biomassa. Daarnaast remmen de kleine dimensies van sloten (geringe breedte en diepte) mogelijk de productie van biomassa van kroos en Waterpest ondanks een hogere voedselrijkdom. Maaien van watervegetaties kan het volbrengen van de levenscyclus en de overleving van soorten in gevaar brengen. In hoofdstuk 4 is daarom het effect van knippen bepaald op twee soorten Fonteinkruiden (*Potamogeton*) door verschillende knipbehandelingen toe te passen onder gecontroleerde omstandigheden. Zowel de productie van biomassa als de overleving werden bij beide soorten negatief beïnvloed. Glanzig fonteinkruid (*Potamogeton lucens*) lijkt een meer tolerante soort aangezien negatieve effecten alleen zichtbaar waren wanneer de planten op het sediment werden afgeknipt. Bij Plat fonteinkruid (*Potamogeton compressus*) had iedere knipbehandeling (halverwege de waterkolom afknippen, op driekwart of op het sediment) een negatief effect op de onder- en

bovengrondse productie van biomassa. Lange termijn effecten kunnen bij Glanzig fonteinkruid optreden door een verminderde ontwikkeling van het wortelstelsel. Voor Plat fonteinkruid kunnen de lange termijn effecten bestaan uit een verminderde reproductie aangezien knippen zorgde voor een veel lager aantal bloemen en overwinteringsknoppen. De lagere biomassa productie van Plat fonteinkruid leidt er mogelijk in het veld toe dat snel groeiende, verstoringstolerante soorten zoals Waterpest eerder de competitie winnen, waardoor Plat fonteinkruid verdwijnt. Door binnen een sloot variatie in maairegime toe te passen (bijvoorbeeld ruimtelijke variatie in frequentie en hoogte van afmaaien) kunnen mogelijk zowel de waterafvoer als de overleving van verstoringsgevoelige soorten zoals Plat fonteinkruid gewaarborgd worden.

Veel Nederlandse sloten worden gedomineerd door kroos en herstel van de geschikte milieucondities voor ondergedoken vegetatie kan ertoe leiden dat herkolonisatie plaatsvindt vanuit de voorraad overlevingsorganen in het sediment. In hoofdstuk 5 is de potentie van de overlevingsorganen in het sediment om vegetatieherstel te initiëren bestudeerd onder gunstige groeicondities. Hiertoe is een kiemingsexperiment uitgevoerd met sedimenten uit sloten met een ondergedoken vegetatie en sloten gedomineerd door kroos. Vergeleken met sediment uit sloten met een ondergedoken vegetatie kiemde er uit het sediment van kroos gedomineerde sloten significant minder individuen en soorten van ondergedoken en emergente planten. Daarnaast was het aantal individuen en soorten van kroos (*Lemnaceae*) juist hoger. Deze resultaten laten zien dat sedimenten in kroos gedomineerde sloten een lagere potentie hebben om herstel van ondergedoken vegetatie te initiëren, waarschijnlijk mede als gevolg van positieve terugkoppelingsmechanismen van de aanwezige vegetatie die de kroos gedomineerde toestand in stand houden. Verstoring van het sediment heeft een sterk positieve invloed op de kieming van overlevingsorganen van kroos, vooral uit sedimenten van kroos gedomineerde sloten. Activiteiten als maaien en baggeren hebben daarom waarschijnlijk een positief effect op de instandhouding van kroosdominantie. Om een omslag van kroosdominantie naar een ondergedoken vegetatie te veroorzaken moeten alternatieve onderhoudsmethoden overwogen worden die minder verstoring van het sediment veroorzaken, mogelijk gecombineerd met maatregelen die de kolonisatie bevorderen zoals tijdelijke droogval en herintroductie van soorten.

Op het hoogste ruimtelijke schaalniveau beïnvloeden klimatologische omstandigheden veel van de besproken regionale en lokale factoren. In Hoofdstuk 6 is daarom met behulp van de North Atlantic Oscillation (NAO) winter index geanalyseerd wat de relatie is tussen klimatologische variaties en de bedekking van kroos en ondergedoken waterplanten in Nederlandse sloten in de afgelopen 26 jaar. Zachte winters waren gerelateerd aan hogere bedekkingen van kroos en groen blijvende ondergedoken waterplanten (zoals Smalle waterpest) in het daarop volgende groeiseizoen. Strenge winters aan hogere bedekkingen van eenjarige ondergedoken waterplanten welke alleen overwinteren middels winterknoppen, knollen en wortelstokken. Op organische bodems hadden zachte winters een significant groter effect op de bedekking van kroos, waarschijnlijk als gevolg van de hogere beschikbaarheid van nutriënten. Deze resultaten laten zien dat zachtere winters ervoor kunnen zorgen dat kroos en groen blijvende ondergedoken waterplanten de competitie winnen van eenjarige ondergedoken waterplanten, wat mogelijk kan leiden tot een verlies van diverse ondergedoken vegetatie. Verlagen van de nutriëntenbelasting kan één van de maatregelen zijn om de negatieve effecten van klimaatopwarming te beperken.

In hoofdstuk 7 (Synthese) wordt aangekaart dat verscheidenheid (heterogeniteit) in milieucondities een belangrijke karakteristiek is om na te streven in sloten om zodoende de plantendiversiteit te behouden, analoog aan de heterogeniteit in condities in afgesloten nevengeulen. De besproken milieufactoren in dit proefschrift kunnen allen bijdragen aan het creëren van die heterogene condities en als gevolg daarvan verschillen in vegetatiesamenstelling. Een schematisch overzicht toont de gevonden relaties tussen milieucondities en vegetatiesamenstelling. Om een diverse vegetatie te herstellen en behouden is waarschijnlijk een combinatie van maatregelen nodig die ingrijpen op verschillende beïnvloedende factoren om zodoende ook de negatieve effecten van klimaatopwarming op de ontwikkeling van diverse vegetaties tegen te gaan. Als laatste wordt een alternatieve visie op waterkwaliteitsbeheer in polders gepresenteerd. Gesteld wordt dat het toekomstig beheer van de Nederlandse sloten effectiever kan zijn wanneer het gebaseerd is op een geïntegreerde visie op de inrichting en het beheer van de gehele polder. Dit kan leiden tot een ruimtelijke herverdeling van functies en ecologische doelen binnen en

tussen polders om zo de ecologische potentie van gebieden optimaal te benutten. Vervolgens kan de heterogeniteit in omstandigheden vergroot worden door differentiatie aan te brengen in het ontwerp en beheer van individuele sloten.

Acknowledgements

Curriculum Vitae

Johannes Petrus (Jeroen) van Zuidam graduated in 2004 for his MSc in Environmental Sciences at Utrecht University with specialization hydro-ecology. From 2004-2006 he worked at the water board of Delfland as a policy advisor in ecology and water quality. In 2007 he started his PhD study on the ecological functioning of drainage ditches at the Aquatic Ecology and Water Quality Management Group of Wageningen University. During his PhD he contributed to a book (to be published in 2013) containing the current knowledge on the ecological functioning and management of drainage ditches. The aim of the book is to make all current knowledge (including the acquired knowledge in the PLONS project) more easily accessible to water managers in the Netherlands. At present he works as a Postdoc at the Ecology and Biodiversity Group at Utrecht University. He studies the colonization of open water by wetland plants (floating mat formation) in newly created ponds in the Volgermeer polder as part of the Peatcap project, initiated by the Centre for Wetland Ecology.

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o   Teaching assistant for the course Introduction Marine and Estuarine Ecology

Oral Presentations
o   *Vegetation in drainage ditches: A biomass based typology*. Aquatic Sciences: Global Changes from the Center to the Edge, ASLO/NABS, 6-11 June 2010, Santa Fe, New Mexico
o   *Influence of nutrient state and maintenance (mowing and dredging) on ditch vegetations*. SENSE/EPCEM PhD Symposium, 10 October 2008, Wageningen
o   *Ditches: an upgrade for the rural landscape?* Symposium Werkgroep Ecologisch Waterbeheer, Subgroep Sloten, 9 June 2008, Utrecht

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