Storage Effects

The relationship between the hydrological dynamic of small infield pools and plant functional groups

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Introduction

Temporary pools and ephemeral wetlands within intensively treated agricultural landscapes are important features influencing species distribution as well as the hydrology of the area. They are called ‘kettle holes’ in Europe (Kalettka and Rudat 2006), ‘potholes’ in North America (Mitsch and Gosselink 1993) and ‘sloughs’ in Canada (Woo and Rowsell 1993). Their origin is often not always clear. Edvardson and Okland (2006) grouped small eutrophic pools into three classes: a) naturally originated, b) constructed, and c) pools as results of agricultural farming practises.

Naturally small infield pools emerged either from dead-ice sinkholes (Frielinghaus and Vahrson 1998) or from post glacial ground water rising (Kalettka 1996). They are often larger in volume and the bottom is covered with a thick peat layer. They are at least temporarily groundwater connected. Artificial infield pools in the moraine landscape are mostly marl holes (Kalettka 1996), dug to excavate the calcium rich marl for fertilization of the surrounding fields. These pools are less than 1000 years old. They are situated on hilltops or at hillsides with no groundwater connection. Because of the young age of marl holes the water permeability of the pool basement is relatively high compared to kettle holes. New small infield pools can arise in depression by intensive treatment of the agricultural landscape. Heavy agricultural engines compact the soil. Continuously ploughing in the same depth leads to a plowsole with lateral run off into depressions with delayed water infiltration into the soil. Ploughing with surrounding the wet depressions raises edges around the wet area. With time a new temporally small infield pool will evolve. These pools are mainly tail water influenced (Frielinghaus and Vahrson 1998). They have a high probability of flooded spring seasons and of dry summer periods.

Nowadays the term vernal pool becomes more important in describing temporally small water bodies mainly situated in Mediterranean semi arid landscapes. According to Burne and Griffin (2005) vernal pools are all wetlands that are biologically active in spring with a high risk of drying up over the dry season in the year. The hydroperiods of vernal pool are very variable within a single pool over time as well as among pools in the same time period. De Meester et al. (2005) defined temporary pools in general as small water bodies with an open surface area between 1m² and 5ha. Their mean water depth is less than 8m. They occur in the landscape with a factor of 100 compared to bigger lakes. They vary strongly according to their hydrology, morphology, origin, water chemistry, connection to other aquatic systems, and their distribution within the landscapes (Oertli et al. 2005). Temporary pools are very stable in their feature (see Collinson et al. 1995). Dry periods lead to a rapid oxidation of organic matter resulting in a very slow sediment filling by organic sediments. On the other hand, intensive agricultural treatments on the catchment area lead to sediment loading in small infield pools by the factor 5 in the last century compared to the mean sediment loading 600 years ago (Frielinghaus and Vahrson 1998). This high sediment accumulation compared with higher nutrient input changes the pool environment (Davies et al. 2004).

To avoid terminologically disagreements the term “small infield pool” will be used in the following studies. By definition small infield pools are all water bodies within an agriculturally treated open landscape. Hence, pools in forest areas are not included in this study. The catchment area of small infield pools is small with no connection to a runoff ditch. As Burne and Griffin (2005) and Oertli et al. (2005) already mentioned small infield pools are very variable in form, size, mean water depth, and hydro periods.

Small infield pools act as groundwater recharge or discharge. They collect runoff water from the surrounding catchment area. According to Lissey (1971) the catchment area of moraine kettle holes can be independent of the topography. The water runoff into small infield pools can contain surface runoff or lateral flow on hidden soil layers. But also, the catchment area can even vary over time (Chorley 1978).

These wetlands are regarded as important landscape features that provide habitats for numerous species (Mitsch and Gosselink 2000). They act as island biotopes (Hall et al. 2004, Kumke et al. 2007) in a surrounding sea-like agricultural landscape. The knowledge of their functioning in the agricultural treated landscape is poorly investigated (Kalettka 1996). The large variability of small infield pools in morphology, hydrological and water chemical dynamic was not studied until the early nineties of the last century (Schneeweiß 1996).

Studies in hydrology and ecology of rivers and riparian flood plains as well as groundwater influenced wetlands exist more often than studies in small pool hydrology (Abell 2002, Biggs et al. 2005, De Meester et al. 2005). The high variability in soil conditions and geo-hydrological circumstances sets strong limits of the application of mechanistic hydrological models to a high number of small infield pools. Therefore, such models are not widely available (Pyke 2004). Often, studies on the hydrology of small infield pools recognised only a very small set of pools (see Cherkauer and Zager 1989, Ferone and Devito 2004, Mouser et al. 2005).

Woo and Rowsell (1993) have analysed one pothole in Canada to describe all important factors influencing the pool water budget. They used 2 years of investigation to describe the variability of the pool. Hence, it is well studied but a transformation to other pools is not given. Nath and Bolte (1998) developed a water budged simulation model. This model requires daily weather data and lots of pool related data. The verification of the model was done on two pools. The data requirements of the model lead the model to be not applicable for a great number of small infield pools. Ferone and Devito (2004) investigated for two years two contrary pool-peatland complexes in Canada and showed different environmental influencing the water budget. Mouser et al. (2005) investigated the hydrology of one kettle hole for one year, comparing the hydrological processes to the density of carnivorous plant species.

The protection of kettle holes with their species inventory appears prevalent in the mind of public and scientific view in the last two decades with an exponential growth in the last 10 years (Persson and Wittgren 2003, Cereghino et al. 2008). In North East Germany small infield pools have a widely distribution with up to 40 per km^2 on an area of 38000km^2 with a total number between 150'000 and 300'000 (Klafs and Lippert 2000). But, more than 50% of the pools are lost during the last century in North East Germany (Klafs and Lippert 2000). This number is comparable with the wetland loss in the United States. Johnston (1994) postulated that over 53% of the Nation's 900000km^2 of wetlands were destroyed in the last two centuries. According to Edvardsen and Okland (2006b) the same decreasing of pool number and area is seen in Japan (Shimoda 1997a), Denmark (Moller and Rordam 1985) and United Kingdom (Wood et al. 2003).

Nowadays, small infield pools are protected by law in North East Germany. But, only recently, there have been substantial steps been taken to reduce wetland losses. They are still decreasing in number and area (Mouser et al 2005). A protection of pools requires knowledge of the long term hydrology.

Sturtevant (1998) postulated that investigation of species populations should include the environmental conditions of the last years. But, most biological studies of small infield pools include only short periods of observations of the pools hydrologic conditions (Pyke 2004). Research dealing with the spatial and temporal variability of their environmental characteristics is very rare (Pyke 2004, Kalettka and Rudat 2006).

Also, the interaction between environmental conditions and habitat functions (Gibbs 2000) as well as the influence of pool connectivity for meta-communities (Hanski and Gilpin 1991, Semlitsch 1998) is rarely studied.

The hydrological regime of small infield pools in North East Germany changed dramatically due to melioration activities which increased in 1970's (Kalettka 1996). This impact caused a great loss of small infield pools and wetland habitats in North East Germany (Kalettka 1996).

Some researches about small infield pools in Germany were done in the past starting with Röpke(1929), followed by Janke and Janke (1970), Klafs et al. (1973), Fischer (1983), Wegener (1983), Sternberg (1986), Jeschke (1987), Hamel (1988) and Bolbrinker (1988).

Most biological studies within small infield pools include only sporadic short observations of the pool hydrologic condition and many studies are only limited to proxies (correlation to one easily visible and as static established abiotic parameter) (Pyke 2004). Only a small part of publications deal with the interaction of the abiotic environment and the biotic species pool (see Wood et al. 2003).

Pyke (2004) developed a model to describe the hydrology of vernal pools in response to climatic time series. The model has two major components; a water balance model and a time series analysis. The model has the great advantage of modelling lots of vernal pools within the same meteorological impact under recognising typically pool attributes important for the water budget and distinguishing several pools. It recognises soil attributes vegetation cover and pool geometry. For evaluating all pools in the same climatic region, the investigation effort is too high. But the solution, getting hydrological time series for many pools by evaluating only pool environment typically characteristics and meteorological time series is a great advantage in getting an overview of the variability of pool hydrology within a single area as well as comparing the hydrology of small infield pools of different climatic regions.

Kalettka and Rudat (2006) investigated over 100 kettle holes in a time period of 10 years. They described these pools in a hydromorphic way and explained the hydrology considering the vegetation type. But the hydrological regimes were detected from a 10 years study with 4 water depth measurements per year. The physical relationship between climatic conditions and water level fluctuations were missing. Therefore, this study required a great long term investigation effort for each recognised kettle hole and can't be used to characterise other small infield pools.

Johnson at al. (2004) monitored the hydrological character of a prairie wetland in the United States for more than 10 years. They concluded that dry and wet periods were influenced by weather extremes either drought or wet weather conditions respectively.

In contrast to lakes, swamps and reeds, the variability of water levels in small infield pools may create strong shifts in habitat quality for wetland plants and macrophytes, i.e. submerged plants. Specifically, longer periods of drying up should drastically alter the habitat conditions for wetland or submerged plants. Such species may only persist in a landscape of pools if they are able to track the spatiotemporal shifts in water levels or sustain long periods of withering by delaying population decline until water levels rise again (Kleyer et al. 2007). Therefore, the quantification of the variability of pool water levels in relation to climate and soils is a prerequisite for the understanding of the habitat functions of infield pools. Changes in the environmental conditions can change the species composition (Sturtevant 1998). Rapid changes in community structure may be relatively easy to quantify while on the long term they may be more difficult to predict (Sturtevant 1998). The species community is a reaction of the environmental conditions (Grace and Wetzel 1981, Van der Valk 1981). But, the actual monitored species inventory is a reaction of the environment of the last years, not only of the present environmental conditions (Gleason 1927, Grace and Wetzel 1981, Sturtevant 1998).

Nowadays, the research focuses on three main topics. As real kettle holes are post glacial relics they allow finding associations between climate change and environmental and ecological changes seen in the sediment accumulation (McLachlan and Brubaker 1995, Bunting et al. 1996, Bunting and Warner 1999, Sanchez et al. 1999, Anderson et al. 2000, Birks et al. 2000, Kremenetski et al. 2003, Sawada et al. 2003, Zhao et al. 2006).

A second research branch resides in the conservation of small infield pools to protect their species pool. Here, the work focuses on invertebrate and amphibian research (Semlitsch et al. 1996, Skelly 1996, Skelly et al. 1999, Babbitt et al. 2003, Solimini et al. 2005), vegetation structure, (Vitt and Slack 1975, Van der Valk 1981, Reinikainen et al. 1984, Gopal 1986, Bolbrinker 1988, Blindow 1992, Kazmierczak et al. 1995, Galatowitsch and Van der Valk 1996, Sturtevant 1998, Fernandez-Alaez et al. 1999, Riis and Hawes 2002, Magee and Kentula 2005, Edvardsen and Okland 2006b) and species composition as well as species interaction between predator pressure and species occurrence (Woodward 1983, Skelly 1996).

A third research interest is seen in the "Island Ecology theory" of small infield pools and their suitability as habitats for meta-populations. Due to the strong differences in habitat suitability of small infield pools to their surrounding environment (agricultural species diversity poor landscape) they act as species rich islands in a species poor sea-like landscape. Hence, the connectivity of small infield pools for meta-communities appears more in the front of research interest (Cottenie and De Meester 2003, Williams et al. 2004).

Most of the water and riparian plants are widely distributed (Santamaria 2002). Even rare and endemic plant species have a high distribution range (Santamaria 2002). Their habitats occur on a wide range of geographical patterns. But, aquatic plant species show only small taxonomic differentiations compared to terrestrial plant groups (Hutchinson 1975). According to Santamaria (2002) the limited impact of allopatric speciation among populations occurring in separate geographic areas, and of adaptive radiation following long-distance dispersal events seems to have contributed to the maintenance of few species with broad ranges. On a narrow level of observation it might be composed that widespread species are groups of siblings (Santamaria 2002). Genetic variation within populations tends to be low (Laushman 1993, Hofstra et al. 1995). Often aquatic individuals are clonal offsprings from the same mother plant (De Meester et al. 2002, Combroux and Bornette 2004, Riis and Sand-Jensen 2006). Their short time moving distance is quiet narrow according to geographical barriers.

But on the other hand, genetic strong differentiations among populations are common (Laushman 1993). Dispersal of aquatic plant species over long distances may occur mainly via birds (Charalambidou and Santamaria 2002, Clausen et al. 2002, De Meester et al. 2002, Green et al. 2002, Mueller and van der Valk 2002, Santamaria and Klaassen 2002, Sanchez et al. 2006) and is mentioned already by Darwin (1859).

The plant species inventory of wetlands is mainly prognosticated by the eutrophication level, base richness and water level gradients (Wheeler and Proctor 2000). Only a few consider population- or community level processes (Van der Valk 1981, Poiani and Johnson 1993, Ellison and Bedford 1995). A small number of studies dealt with the small infield pool species composition (see Srivastava et al. 1995, Shimoda 1997a, Vestergaard and Sand-Jensen 2000, Heegaard et al. 2001, Edvardsen and Okland 2006a) or species richness of such habitats (see Williams et al. 2004, Edvardsen and Okland 2006b).

Also, the response of species to changes in the habitat quality of small infield pools is poorly studied (Willby et al. 2000, Pyke 2004).

Plant species existing in a very dynamic habitat have to be adapted to changing environmental conditions. The habitat quality can change from almost dry ground over the whole vegetation period to flooded areas for several years. Therefore, the nutrient concentration and oxygen availability differ strongly annual as well as among years. Agricultural impact from the surrounding landscape effects the nutrient concentration in the water bodies in a strong way. Therefore, plant species need special traits or trait groups to survive in such environment.

To understand the variability of plant species in small infield pools and to protect it in the view of climate change these plant trait groups have to be investigated.

There are many studies of aquatic and riparian plants in temporary pools. But mainly, the studies concentrated on describing the current diversity in plant communities (Blindow 1992, Kazmierczak et al. 1995, Luthardt and Dreger 1996, Barbour et al. 2005, Molina 2005, Pignatti and Pignatti 2005, Edvardsen and Okland 2006a, Della Bella et al. 2008).

The causes for the occurrence or absence of wetland species in small infield pools are rarely discussed. Mainly, the studies considered either only a small sample of plant species or a small sample of hydroperiods under glasshouse conditions. Van der Valk (2005) states that water depth tolerance are the primary determinant of distribution of emergent species. Kennedy et al. (2003) investigated of 5 riparian plant species the growth response to water level variation and competition. The plant species showed different responses in plant height, leaf size, tiller production or morphological structures to different environmental conditions. Kercher and Zedler (2004) investigated 17 wetland species according to four different hydrological regimes. For most of their species they found a higher shoot-root mass ratio, less biomass accumulation, shorter plant height and less flowering individuals for flooded habitats. Flood tolerance due to rapid early growth for plant species was suggested but not tested. Miller and Zedler (2003) investigated two wetland plants on their response of two different hydroperiods and water depth. They concluded that two plant traits are responsible for the dominance of the invasive plant species *Phalaris arundinacea* due to the species *Spartina pectimata* in wetlands.

Grouping plants species from a community into plant assemblages was established by Du Rietz (1931). But the concept of grouping plant species according to their environmental preferences was already established in the nineteen's century (van der Maarel 1980). Du Rietz defined his major vegetation types for Swedish peat vegetation (Du Rietz 1949). Du Rietz's vegetation types were defined by floristic presence and absence data which were not based on environmental conditions (Du Rietz 1954). But, they could be related to ombotrophic and minerotrophic habitats. The classification system has been extended later in recognising also differences in hydro chemical and topographical description of wetlands (Wheeler and Proctor 2000).

The background behind the grouping of plant species into plant types was to reduce the number of units that led to a descriptive characterisation of the plant kingdom. Plant functional groups (PFGs) can fill the gap between high species distribution modelling effort and descriptive species occurrences (Smith et al. 1997). They also provide a broad sensitivity of species changes to perturbations

(Smith et al. 1997). Functional grouping is also of growing relevance in studies of the potential impacts of global climate change (Woodward and Cramer 1996, Diaz and Cabido 1997).

Many traits of the early subscription of plant functional groups were easily observable traits (Boutin and Keddy 1993). With more knowledge of plant competition in the environment the recognised traits became more complex and harder to measure. Plant species are defined by their trait specification. But, environmental conditions constrain plant traits in a certain limit whereas biotic internal forces separate species by their traits (Weiher et al. 1998). Hence, plant traits, trait attributes or their combinations (syndromes) responding to the environment and thereby to its changes by human impact or climate change are of more interest than traits or syndromes responsible for the uniqueness of each plant species as they allow to predict plant occurrences.

The wetland vegetation types as described by Wheeler and Proctor (2000) are based on their responses on environmental characteristics. Plant species grouping into vegetation types according to their response on environmental factors can be seen as functional classifications of species. These vegetation types are more like modules defined by Paine (1980). Species within a vegetation type do have per definition a similar response to a certain environment. But this response lacks explanation which limits the value of these vegetation types. Species need to be grouped much closer to find similarities in plant traits within this group which can explain the response of this group to environmental conditions.

On the base of the two requirements for finding PFGs (similar in traits and similar response to environmental condition) three strategies to identify the plant functional groups with their response to the environment are established. PFGs can be generated by a subjective, deductive or data-defined approach (Gitay and Noble 1997). While the first two approaches are more common in global environmental change modelling the last is preferred at local and regional modelling scales.

The first strategy uses a theoretical approach and groups all plant species with a similar life strategy into one functional group. These resulting groups can be tested in field experiments. Hutchinson (1975) classified wetland species into morphological plant life strategies. Menges and Waller (1983) were one of the first who studied the traits which were responsible for plant species to survive in temporary flooded forest flood plains. The advance is the strategy concept by

Grime (1977). Kautsky (1988) applied a similar concept testing four functional plant groups on macrophytes in the Baltic Sea.

The second approach of finding plant functional groups is to create plant species assemblages according to environmental responses and search for similarities in traits of plant species within each assemblage. This method works in an opposite way than the first method. Species are grouped according to similarities in their response to the environment. Similarities in their traits have to be found. Fernandez et al. (1999) investigated two temporary Mediterranean pools in Spain. They grouped the recorded species according to a hydrological gradient and divided the species into 4 groups. They discussed the species diversity but not the traits within each group as well as in the pools. Magee and Kentula (2005) investigated 43 wetland site with 2208 1m² plots. Present vegetation data were taken within a nearly two month summer period in 1993. The hydrological regime was described by annual mean water level and annual mean fluctuation of a three year time series of water level measurements in each wetland with a frequency of 2 weeks. Compared to the different hydrological regimes in the plots 31 species could be grouped into nine assemblages.

The third method is the data defined objective approach. The hierarchical order of either response or trait similarities as a pre-investigation is not required in that method.

Till now, data defined objective approaches in classifying aquatic macrophytes in plant functional groups are poorly applied (Willby et al. 2000). These species are mostly grouped according to morphological traits like growth form (Du Rietz 1931) and life form (Raunkiaer et al. 1934) similar to terrestrial plant species grouping (Kautsky 1988, Rorslett 1989, Murphy et al. 1990, Boutin and Keddy 1993, Garcia-Mora et al. 1999, Tabacchi and Tabacchi 2001, Bouchard et al. 2007).

We found only three studies using a data defined approach for this task (Willby et al. 2000, Xiong et al. 2001, Nygaard and Ejrnaes 2004). Willby et al. clustered 120 aquatic macrophytes in 20 plant functional groups. Xiong et al. grouped the response of single traits over the gradient of litter and silt accumulation. Nygaard and Ejrnaes clustered hierarchical 250 wetland species according to environmental responses and applied a classification tree to identify clusters of co-occurring species which could be separated by their functional attributes. The resulted 4 PFGs were tested in a greenhouse experiment but couldn't be proofed.

However, the state of the art pool conservation and pool ecology investigation is manifested in long-term monitoring (Cereghino et al. 2008). Pool characteristics and pool species responses are required for an effective pool management. Pools should act as early warning system for changes in other aquatic systems (Cereghino et al. 2008). Till now modelling the species responses to pool environment as well as simulating pool environment due to climate change and farming practices impacts are rarely tasks of pool studies.

Understanding the variability of pool hydrology can only be gathered by long-time water level time series either measured or simulated. The measuring effort of long-time series is unreasonable for the great number of pools. The simulating approach has the big advantage of implementing future climate scenarios to predict changes in pool environments. Therefore, in this study we simulate the hydrology of pools by using a time series modelling similar to Pyke (2004). With the aid of the models, hydrological changes due to climatic changes in the past as well as in the future can be estimated and coupled to the potential species composition of small infield pools. Here, we are mainly interested in the water level statistics 'drying up frequency' (P) and 'mean high spring water level' (SHW) of the small infield pools, as they are essential for ecological analyses. P gives an indication of how often a certain species has to adapt from an aquatic to a terrestrial environment, while SHW is an expression of the water depth during the germination or mating period in small infield pools. Both factors together indicate valuable ecological functions such as habitat suitability for plant species.

Second, even with this approach the measurement effort for a wide range of pools is too high. Therefore, I developed statistical transfer functions to regionalise our simulation results. We used relationships between short-term measurements out of a single hydrological year and simulated long-term water level time series. With this method we could describe the hydrological characterisation for a large set of pools in the same meso-scalic climatic area of which only limited data were available. The lack of recognising a great amount of small infield pools with their unique hydrological description could be closed. This allowed us to quantify the proportion of infield pools with strong shifts between aquatic and terrestrial conditions on the landscape scale.

Third, we used a modified fourth-corner method (Lehsten et al. in press) in a data based approach to form plant functional groups of wetland species based on their response to habitat dynamics within small infield pools. We derived a novel method which allowed us to group a large number of species with a large number of investigated plant traits non-subjectively. A single trait analysis of all traits of the non woody vascular wetland plant species was applied to calculate a hierarchy of trait attributes ranges (trait classes) for plant species to survive in small infield pools. The hierarchy displays the importance of certain trait specifications over the different pool environmental conditions.

In the context of warmer and drier summer and a longer vegetation period in North Germany already present in the recorded climatic data and expected for the study area by the climate research (Christensen et al. 2007) we could use the results to predict which plant functional groups have a high risk to disappear and which PFGs can become dominant in the future in small infield pools.

Part I: Hydrology of small infield pools

Chapter 2:

Simulation of water level fluctuations in small infield pools using a time series model

Running title: 'Simulation of water level fluctuation'

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Abstract

Small infield pools, also known as kettle holes, are widespread in Europe and North America. They act as important island habitats for amphibian and wetland species within an intensively treated, homogeneous agricultural landscape. However, the properties that make them attractive for several wetland species are largely unknown. Even though they are protected by law in some countries, changes in the environment affecting the hydrological regime and species composition are often ignored. To gain knowledge of how small infield pools function and the way that they are affected by climatic change will require a model that can be applied to many small infield pools regardless of their origin, morphology and interaction with the surrounding groundwater system. In this paper, we use a time series model developed for groundwater modelling and show that the requirements for modelling the hydrology of small infield pools can be met by using climatic time series data, such as evapotranspiration, precipitation and water level observations, of two year duration. Our results show that it is possible to simulate the water level dynamics for a large number of small infield pools, which would be relevant for many organisations taking an interest in such pools. Our simulations result in time series of 50 year lengths, which show a decrease in the minimum water levels over time and an increase in the yearly water level fluctuations in all pools. These trends are a result of rising temperatures in the study area of around one degree in the last 50 years. Such results lead to the hypothesis that small infield pools will dry up more frequently, and for longer periods. With the prognosis that climate change will result in warmer and dryer summers in Europe in the future, the physical properties and species composition of small infield pools will also change. The species that are presently recorded can be seen as a result of conditions of the last decade's climate. Hence, conservation strategies for small infield pools should include the effects of climatic changes.

Keywords: small infield pools, ponds, time series model, hydrology

Introduction

In North East Germany small infield pools are widely distributed, occurring with densities of up to 40 per km^2 over an area of 38000km^2, which results in a total number between 150,000 and 300,000 pools (Klafs and Lippert 2000). The origin of many small infield pools is not always clear. Edvardson and Okland (2006) group small eutrophic pools into three classes: those with a natural origin resulting from special geological conditions, those originating mostly from agricultural activities, or those constructed.

More than 50% of the kettle holes were lost during the last century in North East Germany (Klafs and Lippert 2000). This number is comparable to the wetland loss in the United States (Dahl 1990, Johnston 1994), Japan (Shimoda 1997a), Denmark (Moller and Rordam 1985) and the United Kingdom (Wood et al. 2003). Despite national protection and private conservation effort of wetlands, these features are still decreasing in number and area (Mouser et al 2005).

Small infield pools can either infiltrate into the surrounding groundwater system, or be fed by groundwater seepage (or both). They can collect surface runoff from the surrounding catchment area. According to Lissey (1971) the catchment area of moraine kettle holes can be independent of the topography, because of lateral flow over impermeable soil layers. The catchment area can even vary over time (Chorley 1978). Mechanistic models describing the hydrology of small infield pools are not widely available (Pyke 2004). The high variability in soil conditions and geo-hydrological circumstances sets strong limits to the application of mechanistic hydrological models on a greater number of kettle holes. In the past, studies on the hydrology of small infield pools recognised only a very small set of pools (see Cherkauer and Zager 1989, Ferone and Devito 2004, Mouser et al. 2005).

The knowledge about the functioning of small infield pools in the agricultural landscape is very fragmentary (Kalettka 1996). Especially the interaction between environmental conditions and habitat functions (Gibbs 2000) and the large variability of small infield pool types defined in morphology, hydrology and water chemistry was not investigated until the early nineteen nineties (Schneeweiß 1996).

Storage effects

Most biological studies of small infield pools include only short periods of observations of the pools hydrologic conditions (Pyke 2004). Research dealing with the spatial and temporal variability of their environmental characteristics is very rare (Pyke 2004, Kalettka and Rudat 2006).

Studies in hydrology and ecology of rivers and riparian flood plains as well as groundwater influenced wetlands are more common than studies in small pool hydrology (Abell 2002, Biggs et al. 2005, De Meester et al. 2005).

We found only one study in which a hydrological model was developed and applied to several small infield pools (Pyke 2004). Inputs for the model are climatic time series and pool environmental characteristics. It has two major components, a water balance model and a statistical analysis of the resulting water level series. Pyke developed the model for vernal pools in California.

In our study we will analyse the hydrology of 17 small infield pools using statistics that describe the water level dynamics comparable to the methods used by Pyke (2004). Here we use the PIRFICT time series model available in the computer program Menyanthes (Von Asmuth et al. 2004) for simulating water level series over a longer period. Compared to PHYDO, the hydrological model used by Pyke, the PIRFICT model has the advantage that it needs only a limited number of input parameters. While PHYDO requires data on the basin morphology, soil characteristics, and vegetation cover, our time series model requires meteorological and water level data only and we will demonstrate that an observation period of two years is sufficient to model the dynamics of small infield pools regardless of their origin and bed material. The water level dynamics are a function of the physical properties of the site as well as climatic effects (Larson 1995, Moorhead 2003). Physical properties of small infield pools such as soil and basement permeability, groundwater flow and pool size are unique for each pool. The hydrology of small infield pools is mainly driven by precipitation and temperature (Poiani and Johnson 1991). However, evapotranspiration (which is a function of temperature) is a better parameter for pool water loss than temperature. Therefore, a time series model for modelling the water level fluctuations in small infield pools requires only two input series, precipitation and evapotranspiration. Physical pool properties like catchment area, basement level and soil permeability are expressed in a simple response function which is estimated by the model itself.

With the aid of the model, hydrological changes due to climatic changes in the past as well as in the future can be estimated and coupled to the potential species composition of small infield pools. Here we are mainly interested in the water level statistics drying up frequency (P) and average spring high water level (SHW) of the kettle holes, as these results are needed for an ecological analysis. P gives an indication of how fast a certain species has to adapt from an aquatic to a terrestrial environment, while SHW is an expression of the water depth during the germination and mating period in small infield pools. Both factors indicate valuable ecological functions such as habitat suitability for plant species. For the study we choose a morphologically very inhomogeneous area within a terminal moraine split by a glacial outburst.

Methods

The research area

The basis for the choice of the research area were the geological map of Mecklenburg Western Pomeranian (LUNG 2005) and the map of the number of infield pools per area (pool density) by Klafs and Lippert (2000). The hydrological characteristics of the pools in the area should vary in a wide range in both average spring high water level as well as drying up frequency. Therefore, the area chosen needed to be inhomogeneous in topography as well as in sediment layers. But such areas do not exhibit a high pool density (Kalettka 1996, Klafs and Lippert 2000, Lung 2005). Our final choice was an area central of Mecklenburg Western Pomeranian (see figureA1-1), which forms a good compromise between morphological diversity and pool density.

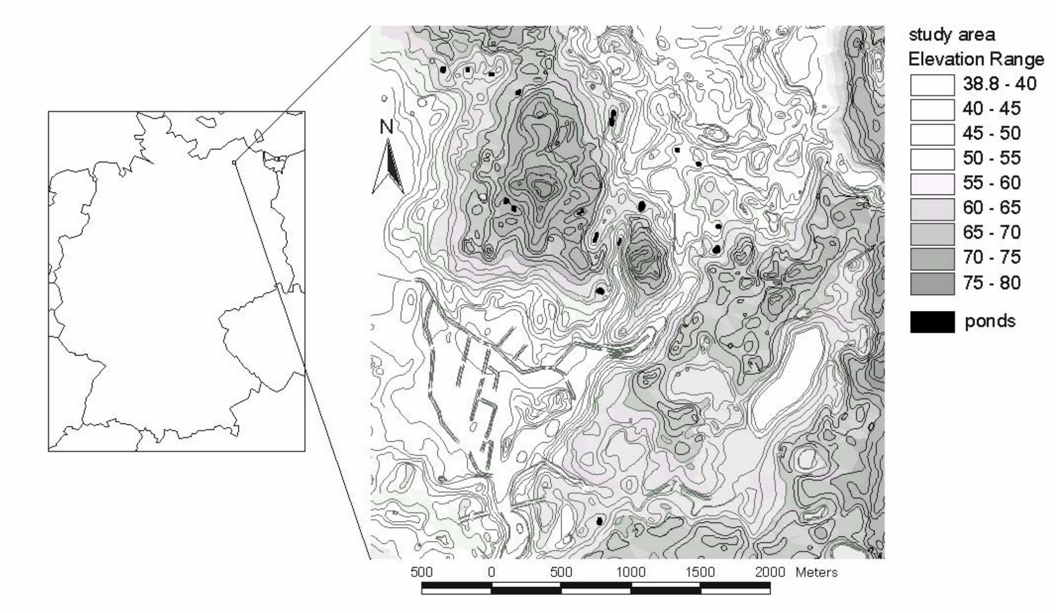

Figure A1-1: Map of the study area. An outburst channel divides the area into northern and southern parts. The small infield pools are marked in black. Parts of the channel drain into the Breesen Lake in the South West of the study area. Two pools are lying in the southern part of the study area dominated by sandy sediments. Three pools lie in the depression, four on top of the marl hill in the North and 8 pools surround the marl hill area.

The study area is 12km² including 46 pools of which 17 were investigated. During the glacial period, a glacial outburst from the Pomeranian Staffel of the Weichsel period intersects the area in a North-Western and a South-Eastern part. Relics of the outburst are fine sandy depressions speckled with lakes, pools and meadows of different sizes. The glacier edge outskirt of the Pomeranian Moraine crosses the area in west-east direction. The southern part is a sandure region in which mainly larger kettle holes with peat accumulation are found. It is partly covered by sediments of the terminal Moraine. The Northern area is dominated by clay and silt lenses underlain by sandy materials with mainly rain water filled pools on hill slopes or on the tops of hills. According to the groundwater map of the study area (LUNG, 1987), most of the pools in the sandy channel are groundwater fed. Small infield pools in depressions in both parts of the region may have originated from local farm practise. The maximal height difference of the study area is about 40 meter per km^2.

Several interglacial periods have resulted in large sedimentations in the broad border between the glacial formations terminal moraine and sandure. Therefore, sediment layers are heterogeneous and formed independently from each other. The kettle holes size varies between $100m^2$ and 6ha. Because of the differences in geomorphology and pool size in the study area, the hydrological dynamics are also expected to vary considerably.

In the west the area is bordered by the shallow ‘Breesen Lake’, which has an average depth of 1m and an area of about $2km^2$ of open water. Now forested former heath-lands represent the Southern border. The heath-land extends to the east to a small forest belt on the terminal moraine ridge, which borders the area in the east and north to the Breesen Lake.

Data collection

We randomly chose 17 kettle holes and recorded the water level in the years 2002 and 2003 on a daily basis, using automatic data logging probes (PDLA70, ecoTech, Bonn, Germany (eco-Tech 2002)). They had to be removed from the measurements stations over wintertime because of high damage risk by frost. Therefore, our measurement periods are only between April and November. The instruments measured the total pressure above the sensor. To obtain the absolute water level, the depth profiles were recorded twice in the year 2002 and once in April 2003. The air pressure was recorded in the middle of the study area. The air pressure decreases with altitude at a rate of approximately 1.2 mm water column per meter, which was taken into account when calculating the correct water levels in the pools.

Storage effects

In 2003 a meteorological station was installed in the region, and the parameters precipitation, temperature, air pressure, wind velocity, and wind direction were logged every 6 hours. These parameters were used to calculate the potential evapotranspiration by applying the Pan evaporation method described in the free download “Crop evapotranspiration - Guidelines for computing crop water requirements – FAO Irrigation and drainage paper 56”(Allen et al. 1998). A comparison between the evapotranspiration and precipitation series in study area and those of surrounding meteorological stations maintained by the DWD (German Weather Service) was performed. The meteorological data from the station in Schwerin, 60km from the study area proved to fit well with our observations (see Box 01). Therefore, we applied the time series of evapotranspiration and precipitation of the nearest weather station Schwerin (DWD 1996-2004). Except for a short period of missing data at the end of the Second World War, observations are available on a continuous and daily basis since 1900. Using this data, we simulated water level fluctuations in all pools over a period of 54 years, and estimated trends in the meteorological series over this time period. These results allowed us to relate the data collected in this study in 2002 and 2003 to the hydrological and meteorological circumstances over a longer time period.

Time series analysis

From a system identification or signal analysis point of view (e.g. Ljung 1999), water level fluctuations can be seen as a reflection of the dynamics of the inputs into the hydrological system (in this case precipitation and evaporation). The transformation of the input into the output (the water level) is described by the transfer function. Mathematically, a transfer function can consist of either physical-deterministic or empirically derived relationships (Von Asmuth and Knotters, 2004). In an empirical time series model, the complex deterministic functioning of the system is simplified and represented by a single transfer or impulse response function (IR function).

We modelled the water level fluctuations of the small infield pools with the PIRFICT time series model. For this purpose we used the program Menyanthes by von Asmuth, Maas and Knotters (2004). An advantage of the PIRFICT model as compared to other time series modelling methods is that it can handle input series at any (even irregular) frequency, and the time steps of the output series are not coupled to that of the input series. Furthermore, the PIRFICT model uses response functions with a distinct hydrological basis, which simplifies the modelling process and reduces the amount of knowledge and labour required for applying it (Von Asmuth et al., 2002).

In the PIRFICT time series model, the Pearson type III distribution function (PIII df) describes the response of the water level to precipitation. The physical basis of the PIII df is that it describes the response of a series of coupled linear reservoirs. Mathematically, the PIII df is given by:

$$\Theta(t) = A * \left(\frac{\alpha^n t^{n-1} e^{-\alpha t}}{\Gamma(n)}\right) \qquad \text{(A1-1)}$$

in which A, α, and n are parameters that are estimated by the model, while $\Gamma(n)$ is the so-called gamma function.

The response to evapotranspiration is regarded to be the same as that for precipitation (but negative), except for a reduction factor that allows for an average reduction of the potential evaporation (Von Asmuth et al., 2008). The evapotranspiration factor includes the so called crop factor or effect of differences in vegetation cover, but also a decrease of the evapotranspiration due to soil water shortages. The difference between the simulated and observed time series results in a new series, called the 'residual series'. The residual series is modelled separately with a noise model, which removes autocorrelation (i.e. dependencies between observations) from the data. For statistical reasons, application of a noise model is a prerequisite in case of auto-correlated data. All in all the model contains five different parameters, three for the precipitation series (A, α and n), one for the evaporation and one for the noise model, that are estimated from the data. Important parameters that describe the calibration results of the model are the EVP (Explained Variance Percentage), which indicates the success of the calibration, the Root Mean Squared Error, the Root Mean Squared Innovation and Akaike's Information Criterion (AIC).

The time series model is calibrated on the available water level observations. The input or explanatory series are the precipitation and the potential evaporation of a free water surface. Precipitation data and data for calculating potential evaporation data according to Allen et al. (1998) are gained from the station Schwerin pursued by the German Weather Service.

Storage effects

For each of the small infield pools a model was generated. The models were calibrated on the available water level observations in each hydrological year (2002 and 2003) separately, and on the combined series of two year length. Consequently, these models were used to simulate the water level fluctuations in the pools over the last 50 years.

Results

Water levels

In the study area, the average precipitation is 620mm per year for the last 100 years. The average potential evaporation is 730mm per year. In the hydrological year 01.10.2001 – 30.09.2002 the precipitation was 810mm, which is 31% above the long term average. The potential evaporation rate was only slightly higher (740mm), so in this year there was a precipitation surplus. In the following hydrological year the precipitation was slightly less than an average, whereas the potential evaporation was 7% higher. Therefore in this year, the precipitation deficit was larger than average. Compared to the last 100 years, both hydrological years can be classified as climatologically extremes when judged by the difference between precipitation and evaporation. The first year tends to be wet and nearly reaches the 95% percentile caused by the high precipitation rate. The second year is very dry and reaches the 25% percentile.

In 2002, the difference between the minimum and maximum water level (fluctuation) in each pool ranged from 8 to 44 cm. The maximum levels ranged up to 2,06m above the bottom of the pool. In 2003, however, the fluctuations ranged from 26cm to 132 cm, which is three times the value of 2002. The maximum water levels, on the contrary, decreased and ranged between 31cm and 1,82m in 2003. Hence, weather conditions do not cause only water level changes over a short period, but also large differences in average water levels and fluctuations from year to year. However, the pools do not show all the same relative difference in level and fluctuation from 2002 to 2003. In some pools, the fluctuation in the hydrological years 2002 and 2003 was almost equal, whereas in others, the fluctuation in 2003 is even five times that of 2002. Please note that the fluctuations in the surrounding groundwater levels will probably be higher, as several pools ran dry in the observation period (and normally the groundwater level rises above the pool level in wet periods because of the smaller storage coefficient). A summary of water levels and their fluctuations of the pools are given in table A1-1.

Table A1-1: Minimum, maximum and fluctuation of the water level in all pools in the hydrological years 2002 and 2003. The meteorological differences between both years are clearly visible in the hydrological behaviour of the pools. The levels given are levels above the bottom of the pool. A value of 0cm as a minimum level indicates that the pool has run dry.

water level 2002	min [cm]	max [cm]	max-min [cm]	water level 2003	min [cm]	max [cm]	max-min [cm]
Pool04	80	104	24	Pool 04	35	70	36
Pool05	96	111	15	Pool05	29	56	27
Pool06	65	73	8	Pool06	19	49	29
Pool07	53	63	10	Pool07	0	38	38
Pool08	130	140	10	Pool08	75	101	27
Pool13	83	100	17	Pool13	0	70	70
Pool14	137	155	18	Pool14	14	94	80
Pool16	140	156	16	Pool16	66	133	67
Pool17	56	66	10	Pool17	17	44	26
Pool18	74	100	26	Pool18	0	56	56
Pool19	47	55	8	Pool19	0	32	32
Pool32	162	206	44	Pool32	50	182	132
Pool34	53	28	25	Pool34	0	25	25
Pool35	34	56	22	Pool35	0	31	31
Pool37	61	85	24	Pool37	20	51	31
Pool40	116	134	18	Pool40	63	90	27
Pool46	136	150	14	Pool46	33	95	62
Min	34	28	8	Min	0	25	25
Max	162	206	44	Max	75	182	132

Time Series Models

Model results for 2002:

Table A1-2: Calibration statistics and model parameters with standard deviation for all pools using the available data of 2002. EVP is the Explained Variance Percentage, Dbase the local drainage base, parameters 1, 2 and 3 are the parameters of the PIII df, parameter 4 is the evaporation factor and 5 the decay of the noise model.

			Precipitation						Evaporation		Noise	
Pool	EVP	Dbase [m]	P 1 (M0)	Std	P 2	Std	P 3	Std	P 4	Std	Decay	Std
Pool 04	71.9	117.0	135500	1E+06	0.0000	0.0003	1.20	0.05	1.0	0.08	14	8
Pool 05	97.4	0.8	240	7.5	0.0120	0.0005	1.52	0.02	0.9	0.02	21	19
Pool 06	70.7	0.6	752	340	0.0014	0.0005	1.03	0.04	0.8	0.05	15	8
Pool 07	87.2	0.7	950	250	0.0017	0.0003	1.22	0.03	0.8	0.04	22	15
Pool 08	86.5	1.4	35	3.9	0.0582	0.0097	1.77	0.19	1.4	0.09	23	18
Pool 13	96	491.0	342100	3E+06	0.0000	0.0002	1.28	0.02	1.3	0.05	21	15
Pool 14	98.8	1.8	334	20	0.0092	0.0006	1.54	0.04	1.7	0.08	14	11
Pool 16	92.4	349.0	166200	3E+06	0.0002	0.0020	1.63	0.03	1.5	0.13	21	15
Pool 17	85.2	0.6	134	12	0.0086	0.0011	1.07	0.03	0.7	0.03	18	15
Pool 18	92.4	616.0	367500	3E+06	0.0001	0.0005	1.51	0.01	1.4	0.08	26	17
Pool 19	89.8	38.3	40870	59000	0.0001	0.0002	1.24	0.03	1.1	0.05	18	12
Pool 32	85.9	-0.6	6927	920	0.0016	0.0002	1.47	0.04	0.6	0.04	15	5
Pool 34	90.4	0.0	1181	540	0.0051	0.0021	1.37	0.03	0.8	0.06	38	24
Pool 35	89.4	-2.7	19250	13000	0.0002	0.0001	1.09	0.02	0.6	0.02	14	10
Pool 37	88.8	134.0	178800	1E+06	0.0000	0.0001	1.20	0.03	1.0	0.04	21	17
Pool 40	92.2	72.5	34860	7E+05	0.0001	0.0010	1.05	0.02	1.5	0.11	23	14
Pool 46	98.9	23.7	6561	2200	0.0008	0.0002	1.50	0.01	2.1	0.13	22	17
Min	70.7	-2.68	35		0.0000		1.03		0.62		14	
Max	98.9	616	367500		0.0582		1.77		2.11		38	

Per pool, we used 7 parameters and the standard deviations of 5 of them to describe the model results (see table A1-2). These were the 5 model parameters previously described, the EVP (explained variance percentage), and the local drainage base. For the models calibrated on the 2002 data the EVP values were mostly acceptable. According to Von Asmuth (2004) an EVP of less than 70% indicates that there are important data or processes missing in the model. Although one model (70.7%) almost reaches this limit, none are really below. However, the drainage levels are much too high for more than 50% of the models. Drainage levels of less than 1m above the pool bottom could be acceptable, though they can still be influenced by poor parameter estimates. While for 10 out of the 17 pools the estimated drainage resistance M0 is much too high, for one (pool 08) it is probably too small. Additionally, most of the standard deviations are mainly in the order of the parameter values. Nearly 50% of the standard deviations of parameter 2 are in the order of the estimated value itself. Finally, also the noise parameters of all models show standard deviations that are nearly as high as the value itself. Judging from these results, we conclude that time series analysis on data over less than one year may not result in useful models. The fact that this period was also extremely wet may have influenced the results negatively also.

Model results for 2003

Like 2002, the model results for the single year 2003 were also poor. In table A1-3, the same parameters are given as in table A1-2. Since the weather conditions of this year were completely different from the year before, the same modelling procedure gave very different results.

Table A1-3: Calibration statistics and model parameters for all pools using the available data of 2003.

			Precipitation						Evaporation		Noise	
Pool	EVP	Dbase [m]	P 1 (M0)	Std	P 2	Std	P 3	Std	P 4	Std	Decay	Std
Pool 04	99	0.71	305.6	79	0.014	0.002	1.615	0.06	0.54	0.07	23.6	26.4
Pool 05	99.3	6.14	2511	1800	0.001	0.000	1.308	0.05	1.65	0.47	24.0	30.2
Pool 06	94.5	-25.40	30050	16000	0.000	0.000	1.334	0.10	0.37	0.05	22.3	19.0
Pool 07	94.4	0.10	468.2	1800	0.004	0.010	1.381	0.11	0.53	0.41	24.5	28.2
Pool 08	86.7	1.03	206.1	100	0.007	0.004	1.518	0.27	0.68	0.31	35.7	10.4
Pool 13	99.8	0.58	381	21	0.009	0.000	1.383	0.03	0.83	0.04	22.4	25.2
Pool 14	98.7	-1.37	1686	67	0.009	0.000	1.812	0.04	0.19	0.01	21.6	10.9
Pool 16	99.9	0.61	1039	48	0.004	0.000	1.447	0.02	0.55	0.02	22.6	19.2
Pool 17	98.3	-46.00	74190	19000	0.000	0.000	1.451	0.05	0.45	0.04	22.5	31.2

			Precipitation						Evaporation		Noise	
Pool	EVP	Dbase [m]	P 1 (M0)	Std	P 2	Std	P 3	Std	P 4	Std	Decay	Std
Pool 18	99.4	-29.10	31040	9900	0.001	0.000	1.537	0.05	0.36	0.03	22.7	30.0
Pool 19	98.5	-0.19	1492	2500	0.002	0.003	1.240	0.06	0.60	0.11	24.8	41.3
Pool 32	99.1	-0.89	2070	140	0.009	0.001	1.810	0.05	0.30	0.02	41.1	11.9
Pool 34	95	-4.02	2232	2000	0.006	0.005	1.578	0.17	-0.03	0.21	30.0	35.4
Pool 35	98.8	-18.10	31320	5800	0.001	0.000	1.591	0.05	0.50	0.05	23.1	68.4
Pool 37	98.9	0.69	4.561	18	0.012	0.003	1.044	0.09	30.63	120	23.9	22.1
Pool 40	98.2	-0.54	1281	5300	0.005	0.015	1.688	0.22	0.36	0.48	24.1	39.3
Pool 46	99.8	1.27	183.7	19	0.012	0.001	1.456	0.05	1.32	0.12	23.0	32.9
Min	86.7	-46	4.561		0.0003		1.044		-0.03		21.59	
Max	99.9	6.14	74190		0.0137		1.812		30.63		41.07	

The model results for 2003 show better explained variances (EVP) than those of the preceding year. Only three models yielded drainage levels that are more than 1m above the pool bottom. However, there are four models which have drainage levels of more than 18m below the pool bottom. For such small infield pools with a relatively short distance to each other, such differences in drainage level are not plausible. The estimated drainage resistance (parameter M0) is too high for 4 models (compared to 2002: 10 models) and in one model too small. Nevertheless, the standard deviation of the drainage resistance is in the magnitude of the parameter value itself for 9 models. Parameter 2 is approximately 10 times higher than in 2002. However, large standard deviations occur in 2003 also, as in 2002. The evapotranspiration factor is not plausible for 4 models. For 6 models the standard deviation of the evapotranspiration factor is too high. Although the models of 2003 (dry conditions) fit the observed water level fluctuations much better than in 2002 (wet conditions), the models may be acceptable for 5 pools only.

Model results for the combined data of 2002 and 2003

In the previous sections, the results of models calibrated on series of water level observations over a period of 7 months did not prove satisfactory, neither for very wet nor for relatively dry conditions. Here, we combined the data into one time series. The results are listed in table A1-4.

Table A1-4: Calibration statistics and model parameters for all pools using the combined data of 2002 and 2003.

			Precipitation						Evaporation		Noise	
Pool	EVP	Dbase [m]	P 1 (M0)	Std	P 2	Std	P 3	Std	P 4	Std	decay	Std
Pool04	95.3	0.90	145	3	0.022	0.0008	1.72	0.04	0.81	0.01	11	6
Pool05	96.5	0.75	261	9	0.011	0.0007	1.48	0.03	0.79	0.01	24	10
Pool06	94.1	0.26	391	39	0.006	0.0007	1.16	0.02	0.49	0.01	22	9
Pool07	94.5	0.33	224	23	0.008	0.0011	1.26	0.03	0.51	0.01	22	10
Pool08	92	-0.05	911	67	0.003	0.0002	1.25	0.03	0.26	0.01	67	29
Pool13	98.7	0.65	281	6	0.011	0.0005	1.33	0.02	0.94	0.01	19	8
Pool14	94.7	0.80	470	10	0.015	0.0011	2.10	0.09	0.66	0.02	56	17
Pool16	99.3	0.62	1116	24	0.004	0.0001	1.37	0.01	0.57	0.01	26	9
Pool17	93.7	0.37	389	42	0.004	0.0003	1.07	0.02	0.62	0.01	18	10
Pool18	96.4	0.43	514	39	0.008	0.0008	1.26	0.02	0.63	0.01	21	8
Pool19	94.9	0.45	464	45	0.008	0.0008	1.32	0.02	0.63	0.01	21	11
Pool32	98.8	-1.61	2858	68	0.004	0.0001	1.46	0.02	0.38	0.01	53	13
Pool34	93.1	-0.20	1082	120	0.007	0.0005	1.43	0.02	0.68	0.01	29	12
Pool35	91.4	-0.97	1041	87	0.004	0.0002	1.12	0.02	0.32	0.01	25	12
Pool37	93.2	-0.75	1089	65	0.006	0.0002	1.57	0.04	0.38	0.01	47	12
Pool40	87.1	0.97	297	11	0.013	0.0009	1.42	0.04	0.77	0.01	35	13
Pool46	96.9	0.71	687	35	0.011	0.0006	1.85	0.03	0.58	0.01	42	12
Min	87.1	-1.61	145		0.00		1.07		0.26		11	
Max	99.3	0.969	2858		0.02		2.10		0.94		67	

Using the daily water level measurements of both years (2002 and 2003), the models of the 17 infield pools show a much better performance than if the data of only one year is used. The explained variances of two models are better than those of the individual years (one even rises from 86.5 (2002) and 86.7 (2003) to 92%). For three models the explained variance is lower. For all other models the explained variances lie between those of the single year models. The level of the drainage base is less than 1m above the pool bottom for all models, which is acceptable, and does not fall more than 2m below the pool bottom.

Simulations

Using the resulting models, the water level fluctuations of all 17 kettle holes were simulated on a daily basis over a period of 54 years between 1950 and 2004 (see table A1-5).

Table A1-5: Estimated water level statistics for all pools, based on model simulations over a period of 54 years. The statistics given are the mean maximum water level (MAX), the mean spring high water level (SHW), the mean water level

(MMW), the mean minimum water level (MIN), and the mean yearly fluctuation. These statistics describe the situation in an average year, and do not contain information about the existing inter annual variability in the water level dynamics. As such, however, they do show the average differences between several small infield pools.

[m]	Mean max water level	Mean spring high water level	Mean mean water level	Mean min water level	Mean fluctuation
Pool	MAX	SHW	MMW	MIN	MAX-MIN
Pool04	1.08	1.06	0.87	0.63	0.44
Pool05	0.92	0.90	0.70	0.47	0.46
Pool06	0.65	0.60	0.48	0.30	0.35
Pool07	0.57	0.53	0.44	0.32	0.25
Pool08	1.11	1.02	0.96	0.82	0.29
Pool13	0.81	0.78	0.51	0.18	0.63
Pool14	1.21	1.18	0.87	0.51	0.70
Pool16	1.28	1.22	1.03	0.77	0.51
Pool17	0.62	0.58	0.47	0.31	0.31
Pool18	0.85	0.79	0.54	0.21	0.64
Pool19	0.81	0.76	0.55	0.27	0.54
Pool32	1.25	1.05	0.77	0.29	0.96
Pool34	0.39	0.31	-0.10	-0.61	1.00
Pool35	0.28	0.16	0.03	-0.21	0.49
Pool37	0.45	0.30	0.14	-0.17	0.63
Pool40	1.24	1.20	0.93	0.59	0.65
Pool46	1.28	1.23	0.94	0.59	0.69

The mean water levels in all pools range from minus 0.1m to 1m above the bottom of the pool. The mean fluctuations of the water level lie between 25cm and 1m. The mean spring high water levels over the last 54 years vary between 16cm and 1.2m depth. Therefore, the water level dynamics in the pools can be regarded as very different. The fluctuation seems to be independent from the mean water level.

From the simulated water level series drying up frequencies were calculated (table A1-6). The drying up frequency of a pool indicates how often the water level drops below the pool bottom for more than 90 days in a row, divided by the number of years for which data is available. Because several (plant) species cannot migrate easily with the water level, it can also be of importance when a pool partially dries up. In order to account for this effect, in the following we distinguish three depth zones in each pool according to the mean spring high water level. First is the littoral zone in which the mean spring high water level is less than 10cm, second the intermediate zone where it is between 10cm and less than 50cm, and third the deeper zone where the spring high water level is at least 50cm. We used the mean spring high water level for this zone definition instead of the mean water level, as the growth period for vegetation in central Europe starts in spring. As a consequence, the water level in spring is more important than the mean water level, which is normally reached in the beginning of July.

Table A1-6: The yearly drying up frequency P with which the water level drops below the pool bottom, in a certain depth zone, for a period of more than 90 days in a row. When the deeper zone was absent in a pool, this is indicated with “n.n.”.

Pool	P(SHW<=10cm)	P(10<SHW<=50cm)	P(SHW>50cm)
Pool04	0.98	0.02	0.00
Pool05	0.98	0.15	0.00
Pool06	0.85	0.02	0.00
Pool07	0.80	0.00	0.00
Pool08	0.57	0.02	0.00
Pool13	0.98	0.44	0.02
Pool14	0.98	0.61	0.00
Pool16	0.83	0.35	0.00
Pool17	0.83	0.00	0.00
Pool18	0.96	0.41	0.02
Pool19	0.94	0.28	0.02
Pool32	0.76	0.56	0.26
Pool34	0.98	0.89	n.n.
Pool35	0.93	0.59	n.n.
Pool37	0.98	0.48	n.n.
Pool40	0.96	0.52	0.00
Pool46	1.00	0.35	0.00

The drying up frequencies for the pools as a whole varies between almost zero and 0.89. Since 1950, 10 of 17 simulated pools went never dry for a period longer than three months. Their mean water level was between 48cm and 1m and their spring high water level between 53 cm and 1.25m. The pool with the highest drying up frequency has a negative mean water level of minus 10cm but an average spring high water level of 31cm.

Except for one pool, the frequency of dry periods in the littoral zone is always above 0.75. The intermediate zone has drying up frequencies between almost zero and 0.9. The deeper zone exists in 14 of the modelled small infield pools with a drying up frequencies of 0.26 at maximum.

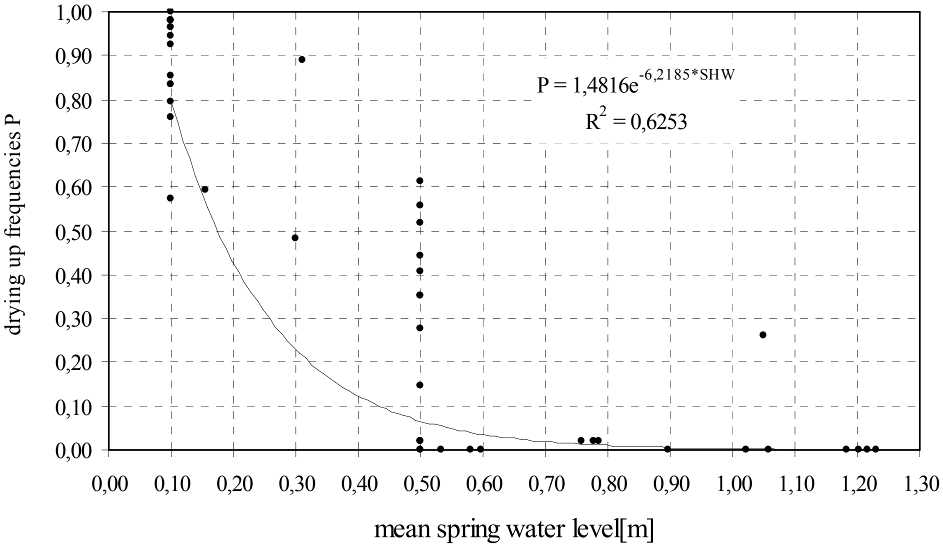

Figure A1-2: Average spring high water level (SHW) compared to the drying up frequency of 17 small infield pools divided in up to three zones (littoral, intermediate and deeper zone). The trend function is a power function with a correlation coefficient of 0.6.

A comparison of the drying up frequency with the average spring high water level of the different pools and pool zones (see figure A1-2) shows that there is a general correlation between both. A higher average spring high water level is associated with a lower drying up frequency. The correlation is visible but not strong. Hence, other factors influence this relationship as well, for example the functioning and interaction with the surrounding groundwater system.

In order to detect changes in the dynamics of the pools due to climate changes over the last 50 years, a trend analysis was performed. The maximum water levels proved to differ strongly between the years. Differences in maximum water level of the same pool range between 26cm and 2.5m over the simulated period. Trends in the maximum level, however, are not recognisable (see figure A1-3). The mean water level might decrease slightly over the last years, but if present at all, this decrease is very weak.

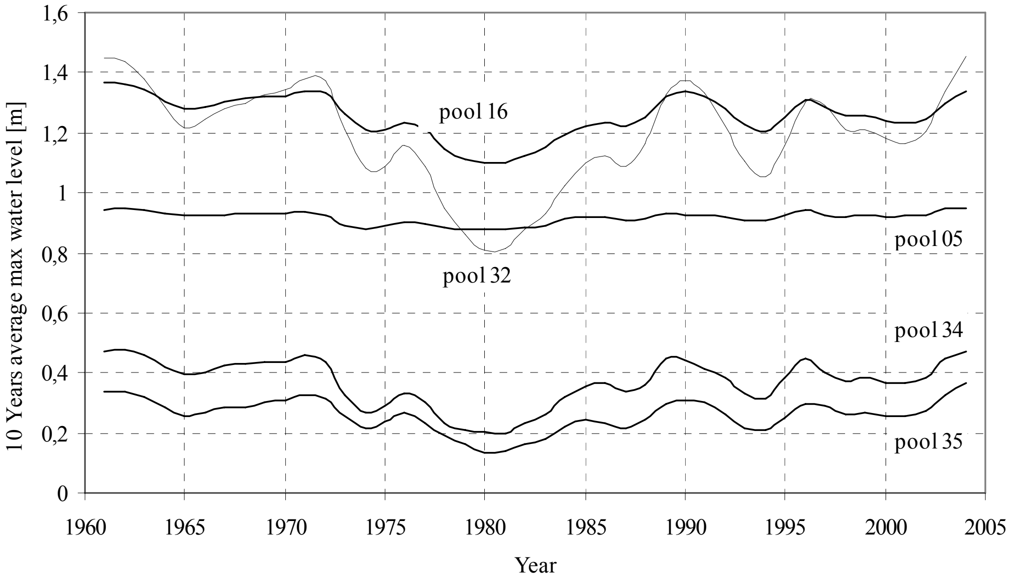

Figure A1-3: Selection of pools and their moving average of the maximum water level (window of 10 years). There are no trends detectable. Of all pools the maximum water level of pool 32 reacts most sensitive to weather variations whereas the maximum water level of pool 05 is most stable over time.

In contrast to the maximum levels, the minimum water level series as well as the water level fluctuations do show linear trends. Whereas the minimum water level decreases with time (table A1-8, figure A1-5) the fluctuation increases (table A1-7, figure A1-4).

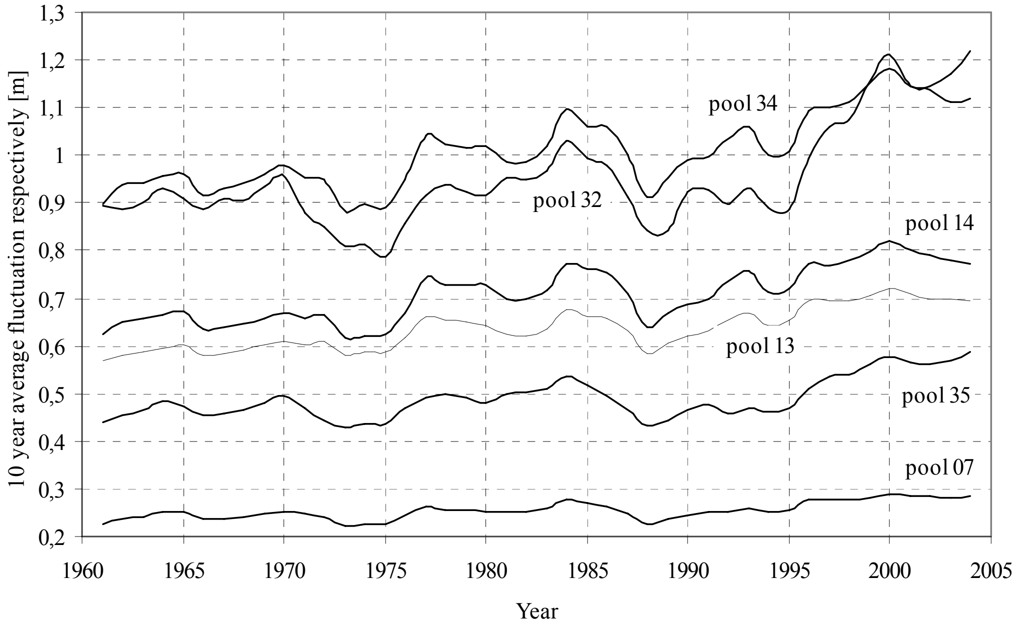

Figure A1-4: Selection of pools with their moving average of the fluctuation in the water levels (window of 10 years).

Table A1-7: Moving average of the fluctuation in the water levels between 1950 and 2004 (window of 10 years). MIN: minimum fluctuation [m], MAX: maximum fluctuation [m]. Difference: MAX-MIN. The last two columns show the correlation coefficient between year and fluctuation and the linear trend function.

Pool number	MIN	MAX	Difference	Factor r^2	Function
32	0,79	1,22	0,43	0,45	Tfluc = 0,0056year - 10,161
34	0,88	1,18	0,30	0,65	Tfluc = 0,0049year - 8,7667
46	0,59	0,82	0,23	0,57	Tfluc = 0,0033year - 5,9459
14	0,62	0,82	0,20	0,66	Tfluc = 0,0036year - 6,5046
16	0,44	0,62	0,18	0,62	Tfluc = 0,0028year - 5,1221
18	0,57	0,74	0,17	0,61	Tfluc = 0,0028year - 4,9824
40	0,58	0,74	0,16	0,70	Tfluc = 0,003year - 5,2988
35	0,43	0,59	0,16	0,43	Tfluc = 0,0021year - 3,7484
13	0,57	0,72	0,15	0,74	Tfluc = 0,0029year + 0,5415
19	0,48	0,63	0,15	0,62	Tfluc = 0,0024year - 4,3084
8	0,25	0,37	0,12	0,32	Tfluc = 0,0013year - 2,3473
5	0,41	0,52	0,11	0,70	Tfluc = 0,0021year - 3,7488
4	0,40	0,50	0,10	0,73	Tfluc = 0,0019year - 3,3612
6	0,31	0,41	0,10	0,55	Tfluc = 0,0015year - 2,6568
17	0,28	0,36	0,09	0,66	Tfluc = 0,0015year - 2,5999
7	0,22	0,29	0,07	0,53	Tfluc = 0,001year - 1,8105
37	0,50	0,79	0,29	0,18	Tfluc = -0,0024year + 5,3896

Storage effects

The fluctuations range from 22cm to 1.22m. The differences in fluctuation within a pool range from 7cm to 43cm. The linear trends show an increase in fluctuation over time. The correlation coefficients are always higher than 0.3 except for one pool. According to the trend, the fluctuation increases at a rate of 10cm to 60cm per 100 years. There is only one small infield pool that does not show an increase in the fluctuation.

The minimum water levels that occurred in the simulated period range from -82cm to 91cm. In the same pool, the differences in minimum water level ranged from 8cm to 39 cm. Due only to climatologic differences, a decreasing trend in the minimum water level is visible (table A1-8, figure A1-5). In 50 years the minimum water level shows a decrease between 11cm and 71cm.

Table A1-8: Moving average of the minimum water levels between 1950 and 2004 (window of 10 years). MIN: minimum value [m], MAX: maximum value [m]. Difference: MAX-MIN. The last two columns show the correlation coefficient between year and minimum water level and the linear trend function.

Pool number	MIN	MAX	Difference	r^2 Factor	Function
34	-0,82	-0,43	0,39	0,37	Tmin = -0,0053year + 9,8756
16	0,60	0,91	0,31	0,31	Tmin = -0,0038year + 8,3714
46	0,45	0,70	0,24	0,32	Tmin=-0,0031year + 6,7831
14	0,39	0,62	0,22	0,45	Tmin = -0,0032year + 6,9048
18	0,10	0,31	0,21	0,45	Tmin = -0,0029year + 5,9302
40	0,50	0,68	0,18	0,60	Tmin = -0,0029year + 6,3177
19	0,18	0,36	0,18	0,43	Tmin = -0,0025year + 5,1881
13	0,09	0,26	0,18	0,57	Tmin = -0,0028year + 0,2557
5	0,40	0,53	0,13	0,51	Tmin = -0,002year + 4,4402
6	0,23	0,36	0,13	0,38	Tmin = -0,0016year + 3,5455
17	0,25	0,37	0,13	0,39	Tmin = -0,0017year + 3,6756
4	0,58	0,69	0,11	0,70	Tmin = -0,0019year + 4,3728
7	0,27	0,36	0,08	0,42	Tmin = -0,0011year + 2,4702
35	-0,36	-0,10	0,26	0,23	Tmin = -0,0025year + 4,733
32	-0,14	0,55	0,69	0,22	Tmin = -0,0071year + 14,257
8	0,68	0,89	0,20	0,16	Tmin = -0,0017year + 4,076
37	-0,30	-0,09	0,21	0,11	Tmin = 0,0016year - 3,3045

Four pools do not show linear trends in the minimum water level during this period. They will not be considered here, but it should be mentioned that these four have the same elevation and surround the marl hill in the north-eastern part of the study area. So they may have been influenced by the same local groundwater table, draining into the Breesen Lake.

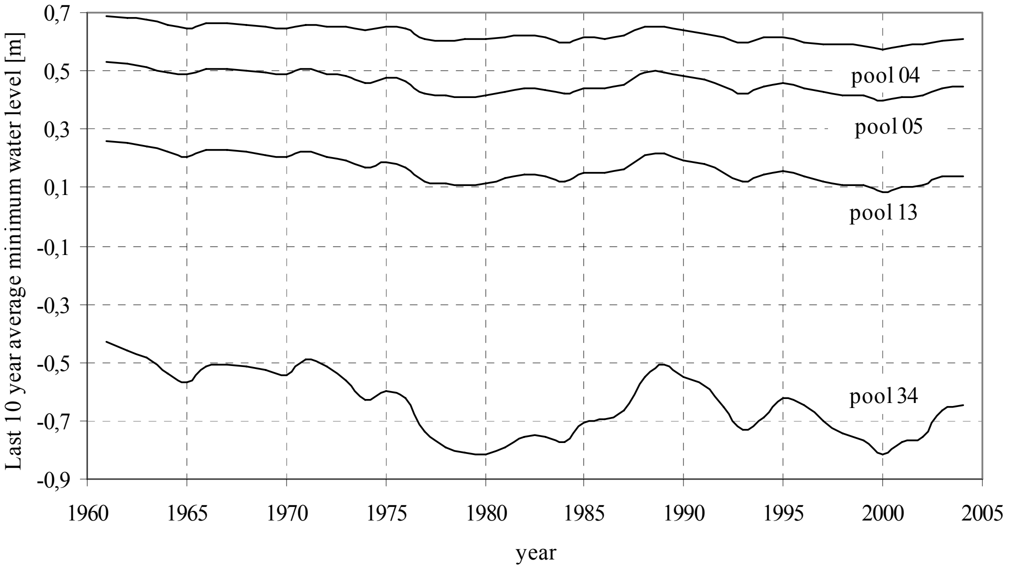

Figure A1-5: Selection of pools with their moving average of the minimum water levels (window of 10 years).

As the results show that there is no trend in yearly high water level, but a decrease in low water level with time. We examined the reasons for driving the pool high water level as well as the pool low water level. In Box 02 we show that there are changes in climatic conditions in the study area detectable. In the last 60 years the temperature rose of 1°C in average. As mentioned before, the temperature is strongly correlated with the evaporation rate. The precipitation rate shows a large variation between years. But there is no trend in rising or lowering precipitation rate. Because of the trend in temperature rising we compared the low water level with the yearly evaporation rate. Except for the four pools with no decreasing low water level all other pools correlate well with the yearly evaporation rate. The best fit is seen in the correlation of the yearly low water level with the yearly evaporation rate with a time delay of half a year (see table A1-9). Low water levels occur in general at the beginning of the hydrological years (i.e. on the first of October in Central Europe). The half year delay originates from the fact that the annual evaporation sum between the first of April of the previous year and the thirtieth of March of actual year correlates best with the low water level of the actual year.

Table A1-9: Correlation square factors between yearly low water level and annual evaporation rate with different time delays. A time delay of 0 years indicates the evaporation rate of the forgoing last 365 days.

time delay in years	0	0.25	**0.5**	0.75	1	1.25	1.5
pool 04	0,02	-0,41	**-0,79**	-0,79	-0,77	-0,48	-0,10
pool 05	-0,03	-0,45	**-0,76**	-0,75	-0,72	-0,45	-0,08
pool 06	0,02	-0,30	**-0,61**	-0,59	-0,55	-0,45	-0,18
pool 07	0,01	-0,34	**-0,66**	-0,64	-0,60	-0,43	-0,13
pool 08	0,04	-0,15	**-0,34**	-0,34	-0,30	-0,45	-0,33
pool 13	-0,04	-0,46	**-0,80**	-0,79	-0,76	-0,48	-0,10
pool 14	-0,03	-0,45	**-0,74**	-0,72	-0,69	-0,44	-0,08
pool 16	0,01	-0,26	**-0,49**	-0,48	-0,44	-0,52	-0,35
pool 17	0,02	-0,30	**-0,60**	-0,59	-0,55	-0,50	-0,25
pool 18	0,00	-0,38	**-0,70**	-0,68	-0,64	-0,46	-0,13
pool 19	0,00	-0,38	**-0,69**	-0,67	-0,63	-0,45	-0,13
pool 32	0,02	-0,20	**-0,39**	-0,38	-0,35	-0,49	-0,35
pool 34	0,00	-0,36	**-0,64**	-0,62	-0,58	-0,49	-0,20
pool 35	0,04	-0,19	**-0,43**	-0,42	-0,38	-0,46	-0,29
pool 37	0,07	0,12	**0,09**	0,05	0,02	0,06	-0,14
pool 40	-0,03	-0,44	**-0,78**	-0,77	-0,74	-0,47	-0,09
pool 46	0,00	-0,38	**-0,65**	-0,62	-0,59	-0,47	-0,17

The rise of the pool water level over the winter period is driven mostly by the precipitation rate (as evaporation in winter is minimal). Therefore, we compared the yearly precipitation rate with the high water level occurring in spring time. The high water levels of the pools correlate well with the yearly precipitation rate with a time delay of one year (see table A1-10).

Table A1-10: Correlation square factors between yearly high water level and annual precipitation rate with different time delays. A time delay of 0 years indicates the precipitation rate of the forgoing last 365 days.

time delay in years	0	0.25	0.5	0.75	**1**	1,25	1,5	1,75
pool04	0,31	0,54	0,69	0,67	**0,72**	0,48	0,23	0,04
pool05	0,27	0,54	0,74	0,80	**0,88**	0,66	0,42	0,16
pool06	0,37	0,61	0,75	0,78	**0,85**	0,67	0,46	0,22
pool 07	0,38	0,63	0,76	0,76	**0,83**	0,62	0,39	0,14
pool08	0,26	0,51	0,67	0,72	**0,79**	0,76	0,63	0,49
pool13	0,27	0,54	0,74	0,80	**0,87**	0,66	0,41	0,16
pool14	0,24	0,51	0,73	0,82	**0,87**	0,66	0,40	0,13
pool16	0,17	0,43	0,63	0,76	**0,86**	0,82	0,68	0,49

time delay in years	0	0.25	0.5	0.75	1	1,25	1,5	1,75
pool 17	0,28	0,54	0,71	0,78	0,88	0,75	0,57	0,36
pool 18	0,33	0,59	0,74	0,78	0,87	0,66	0,43	0,18
pool 19	0,32	0,58	0,74	0,79	0,88	0,68	0,45	0,19
pool 32	0,20	0,45	0,64	0,74	0,83	0,80	0,67	0,50
pool 34	0,25	0,51	0,71	0,82	0,91	0,76	0,55	0,29
pool 35	0,32	0,57	0,72	0,75	0,83	0,73	0,58	0,40
pool 37	0,12	0,12	0,06	-0,02	0,103	0,06	-0,03	0,00
pool 40	0,32	0,58	0,73	0,75	0,82	0,58	0,33	0,10
pool 46	0,27	0,53	0,74	0,83	0,89	0,71	0,47	0,19

Discussion

In our study we showed that a series of daily water level observations over a period of two years, and accompanying evaporation and precipitation data, suffice to model the dynamics of small infield pools. With the resulting models a long series of water level fluctuations could be simulated for each pool. The simulation results could be used to explain the hydrological variability between the pools, as well as the hydrological variability among years. Furthermore, we could show that the trend in rising yearly temperature and the resulting rising yearly evaporation rate is responsible for the decrease of the low water levels. This means that the habitat conditions of small infield pools will be altered, or are already being altered, due to climatic changes. Small infield pools are important features in the agricultural landscape and are essential for both plant and animal species (Gibbs 1993). These species communities are very sensitive to disturbances and hydrological changes. Their presence is a result not only of the present environmental conditions (Grace and Wetzel 1981, Van der Valk 1981), but also of the environmental conditions over the last years (Gleason 1927, Grace and Wetzel 1981, Sturtevant 1998). Therefore, small infield pools should be managed as dynamic systems rather than as static systems (Mitsch and Gosselink 1993).

However, most ecological research in small infield pools results in the description of the current environmental conditions rather than their dynamic behaviour. Often, the link between the dynamics in the species pool and the environmental dynamics is not even mentioned (Luthardt and Dreger 1996, Schneeweiß 1996).

Although some research work on the hydrology of small infield pools is done, it remains difficult to model their water level dynamics as a function of abiotic parameters like the catchment area, the bed material, the origin and genesis of the pools. As mentioned before, often the catchment area is independent from the topography (Lissey 1971), and it can be very hard to identify its exact extent. As a result, deterministic hydrological models of small infield pools (for which detailed information about the catchment area as well as other geohydrological parameters is needed) often lack the accuracy that is needed for ecological applications. Kalettka (1996) postulates that kettle holes in glacier channels have the highest probability of being water-filled perennially, as he supposes them to be most influenced by groundwater (Ferone and Devito 2004). Schindler (1996) verified the hypothesis that lateral inflow of groundwater from the surrounding catchment area is an important factor for the water balance in kettle holes. Differences in the dynamics of the surrounding groundwater system as well as differences in the drainage resistance of the pool bottom layer can explain the weak correlation between spring high water level and drying up frequency.

Johnson et al. (2004) described the influence of extreme weather conditions on changes in the water level. Weather extremes (either dry or wet) can respectively cause droughts or high water levels in wetlands (Moorhead 2003, Johnson et al. 2004, Dempster et al. 2006). This is in fact logical and exactly what we found, too. Schmidt (1996) found that the water level shows a lagged response to precipitation and evaporation events. Even though this lag was smaller in our study (one year for precipitation and 0.5 years for evaporation, compared to two year in Schmidt's study), it could explain why also in our study time series of less than two years did not produce good models.

The hypothesis that higher temperature and resulting higher evaporation rates may have a greater impact on pool hydrology than changes in precipitation (Poiani et al. 1995) could be confirmed by our measurements over the two climatic extreme years as well as with the simulation results.

The two extreme years in weather conditions, used for the time series analysis, show nearly the full range of water level fluctuations. Because of the effects of extreme weather conditions, we suggest that the measurement campaign in further studies on pool water level dynamics should be carried out over a period of three years or longer.

Another model which has been used to model small infield pools is PHYDO by Pyke (2004). Compared to PHYDO, time series models can be used for all pools regardless of their geohydrological setting and interactions with the surrounding groundwater system. PHYDO can only be used for hydrologically isolated vernal pools. PHYDO calculates water volume, water surface area, water temperature, and water depth. A time series model confines the calculation only to the parameter that was measured. In our case it was the water level, which is most important for ecological studies in central Europe. Evaporation and precipitation series are necessary as input for both models. Additionally, PHYDO also needs the catchment area size, information about the soil (up to two layers can be defined with their thickness, storage coefficient), the vegetation cover of the catchment area, and simplified pool size in form of two axes.

Evaporation of the pool will be calculated for PHYDO as twice the evaporation of a well watered grass surface. For the catchment area PHYDO applies a seasonal growth function based on FAO 56 guidelines (Allen *et al.* 1998) and modified the basic evaporation. Menyanthes uses PAN evaporation and will correct it with a factor estimated during modelling time. This modified PAN evaporation will be applied for the catchment area as well as for the pool surface. Using PAN transpiration with a correction factor simplifies the data input. Compared to the catchment area small infield pools have an untended small surface. This procedure used in Menyanthes is more expedient. Often the crop management is not even known from past years.

The water level measurements were taken between April the first and end of November for both hydrological years. Therefore, the impact of snow (Woo and Rowsell 1993, Poiani et al. 1996) and the resulting strong changes in water run off (Poiani et al. 1995) were not recognised in the time series analysis. During the study period there was little snow fall in the area and in the melting season most of the snow accumulation had already disappeared by evaporation. Therefore, the models might underestimate spring high water levels (Poiani et al. 1995) while overestimating winter water levels. This can result in underestimated average mean water level but should not influence the drying up frequencies.

Taking this fact into account and recognising a general warming of the area of around 1°C for the last 60 years (see Box 02) with resulting less snow periods, the effect of a decrease in the mean pool water level over time should be stronger than calculated.

If it were possible to take into account the actual evapotranspiration rate (which incorporates the actual vegetation structure and soil water shortages), and the increased duration of the growth period due to increased temperatures within the infield pools, the negative trend in minimum water level would became even stronger than our estimates. During the winter period, evaporation is low because of the low temperature and inactivity of the vegetation. Therefore, in the winter season the water level in small infield pools will be driven mainly by precipitation. Hence, if the precipitation does not show any trend over time, neither should the maximum water level.

Intensive agricultural treatments on the catchment area with high fertilizer applications resulted in pollution and nutrient enrichments of pool sediments and water bodies. Ripl et al. (1996) estimated the nitrate and phosphorus loss in agricultural catchment areas feeding the pools as 20kg per ha per year. This and melioration activities in the early Eighties in North East Germany (Kalettka 1996) fosters fast growing and tall wetland plant species with higher transpiration rates (Lenssen et al. 1999, Pauliukonis and Schneider 2001) and higher sediment deposition rates (Pokorny and Hauser 2002). Melioration (i.e. improved drainage) leads to a decrease in mean and high water levels resulting in smaller open water areas in wetlands.

A decrease in water levels leads to increased decomposition of the accumulated organic matter in the pool and surrounding soils, which in turn results in an increase of the nutrient availability (Keddy et al. 2000). This is already seen by the strong increase of *Salix* species and *Solanum dulcamara* in small infield pools of the study region since the last 30 years (pers. comment Neubauer 2002).

Linear time series models do not consider water loss due to surface overflow, which was also not observed in the field. However, Kalettka and Rudat (2006) described kettle holes with a spring overflow leading to an increase in the water surface area up to a multiple of the pool surface. In that case, a threshold non-linear time series model should be applied to the data (e.g. Von Asmuth & Knotters, in prep.)

Keddy (1991) emphasised that differences in the length of flooding periods in wetlands creates strong gradients in the nutrient availability. Such hydrological gradients may affect soil conditions, germination abilities of plant species and biotic interactions (Austin 1990, Coops and Van der Velde 1995, Lessen et al 1999). This heterogeneity of hydroperiods may influence the species richness along flooding gradients at most sites (Vivian-Smith 1997, Pollock et al 1998).

In our study, climate changes may drive the vegetation structure into a succession process which will alter the habitat quality in a drastic way. So, the currently observed plant species can partly be seen as relics of former habitat conditions.

Modelling and simulation results suggest that a simple time series model (as available in Menyanthes), with no more than precipitation and evaporation time series of the meteorological meso climatic zone as input parameters, produce sufficient water level time series to estimate trends in water level changes due to climate changes. Average hydrological parameters from the water level time series can be used to describe the small infield pools in response to ecological or hydrological questions.

The results of the simulations are in agreement with the findings of other authors, that small infield pools with there recent high nutrient level (Pokorny & Hauser 2002) and with higher temperatures have a high risk of longer dry seasons (Poiani et al. 1995) and higher litter accumulation (Lenssen et al. 1999). Such changes will affect the vegetation structure, and will lead to changes in the species composition from aquatic and wetland plant species to wetland and terrestrial plant species.

Chapter 3:

Climate

Box 01: Correlation of local measured weather data to meso scalic weather data

For modelling the water table time series of the small infield pools, the precipitation and evapotranspiration of the area are of interest. The potential evapotranspiration was calculated according to the FAO guideline for evapotranspiration paper 56 (Allen et al. 1998). These calculations include temperature, humidity, wind velocity, and radiation of both stations. Therefore, investigations of correlations of these parameters between the stations were not done.

The weather station Schwerin is located ca. 60km to the west of the study area. Therefore, west rain fronts reaching the DWD station Schwerin will arrive at the study area with a time delay. Hence, it is useful to evaluate the cumulative time series of the precipitation (see figure B01-1) of the stations rather than daily precipitation time series. The summed precipitation time series of both stations are correlated with $r^2=0.98$. The cumulative precipitation of Reimershagen is slightly lower than that of Schwerin. Reasons are the westward location of Schwerin to Reimershagen. The program Menyanthes (Von Asmuth et al. 2004) calculates precipitation with a Pearson III distribution function. With this function time delays and higher values can be corrected. Hence, the precipitation time series from Schwerin can be used in the program Menyanthes and will be reduced and time corrected by this program with nondynamical factors. Because of problems in data logging of the precipitation measurement, the investigated time series have only 40 values. We reduced the precipitation time series of Schwerin in the same way.

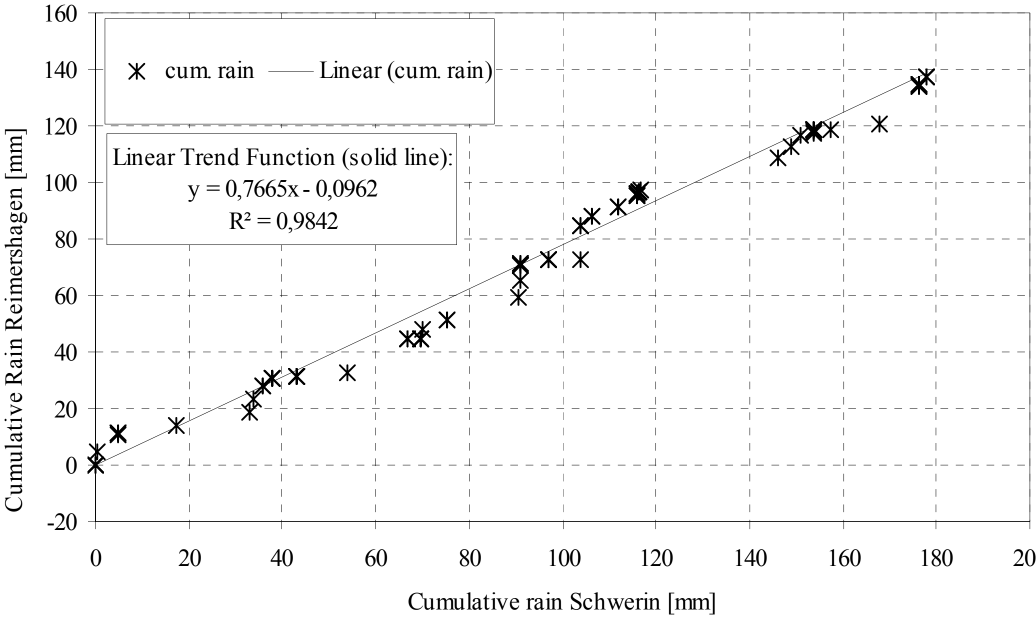

Figure B01-1: Cumulative precipitation time series in Schwerin and Reimershagen. The linear correlation between the cumulative precipitations of both stations has a good fit with an r^2 of 0.98.

Except for the radiation, all parameters were measured which are needed to calculate the potential evaporation rate in Reimershagen as well as in Schwerin. A comparison of daily evapotranspiration rates shows a strong linear dependency between both stations (figure B01-2). The correlation coefficient is 0.95. The distance of 60km in westwards direction does not have great influences on daily evaporation rates. The slope of the trend function is one, whereas the fixed value is -0.05. This indicates a mean error between Schwerin and Reimershagen of 1%.

If the cumulative evaporation rates of both stations will be compared (figure B01-3) the linear correlation factor is 1. This indicates a strong correlation between the two evapotranspiration rates. The slope is 1 and the fixed value is -0.24 which indicates an error of 1% in average.

Because of the good correlation between evapotranspiration in Schwerin to Reimershagen, the weather data in Schwerin could be used to calculate the potential evapotranspiration rate with respect to the FAO guideline paper 56 (Allen et al. 1998).

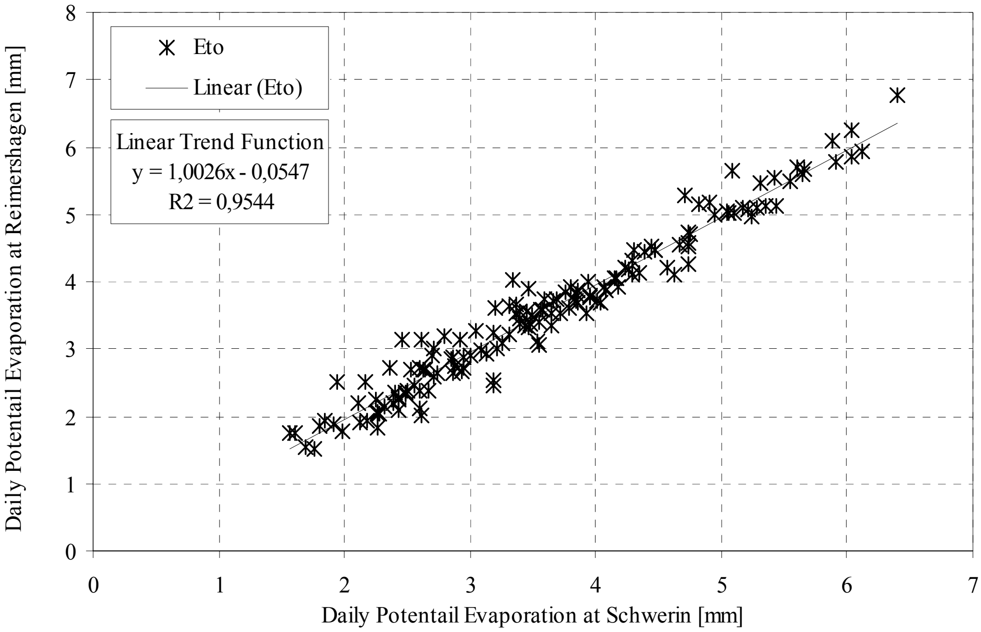

Figure B01-2: Daily evapotranspiration rates in 2003 of the station Schwerin compared to the same time series calculated by weather data measured in Reimershagen. The correlation of both time series is $r^2=0.95$.

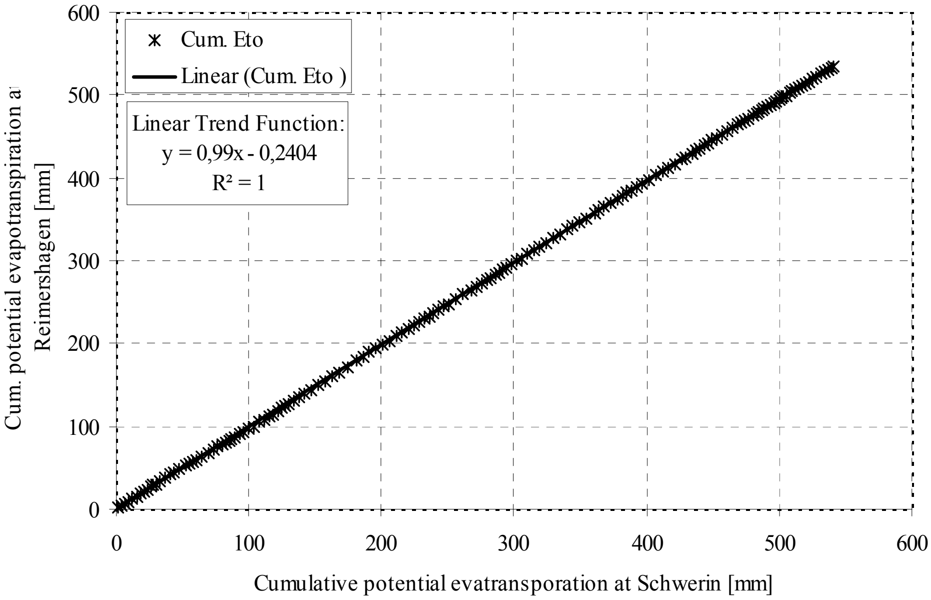

Figure B01-3: Comparison of the cumulative potential evapotranspiration rates of the two stations Schwerin and Reimershagen. ET_0 Schwerin is identical with ET_0 Reimershagen with an error of 1% on average. The correlation factor of 1 shows the very high correlation between both time series and the validity to use the weather data of Schwerin for the location Reimershagen.

Storage effects

The good fit of precipitation time series and the very good fit of the evapotranspiration time series between the two locations Reimershagen und Schwerin enabled us to apply the weather data time series from Schwerin to model the water table time series of small infield pools near Reimershagen.

Box 02: Trends in temperature and precipitation of the time series observed by the DWD station Schwerin

The evaporation is a function of the temperature. Therefore, rising temperature, as expected in many climate scenarios, will raise evaporation rates. Secondly higher temperature can also extend the vegetation period, leading to higher transpiration rates. We investigated almost 60 years of data time series of daily maximum temperature observed at the DWD station Schwerin (DWD 1996-2004). Because of a time gap of 5 years during the Second World War we did not had a longer continuous time series. The mean of the daily maximum temperatures of the last ten years was calculated. These windows were plotted with a weekly time step (figure B02-1). Between the year 1947 and 2004 a mean temperature increase of nearly one degree occurred. The graph shows clearly the rising trend of the temperature since the last 60 years.

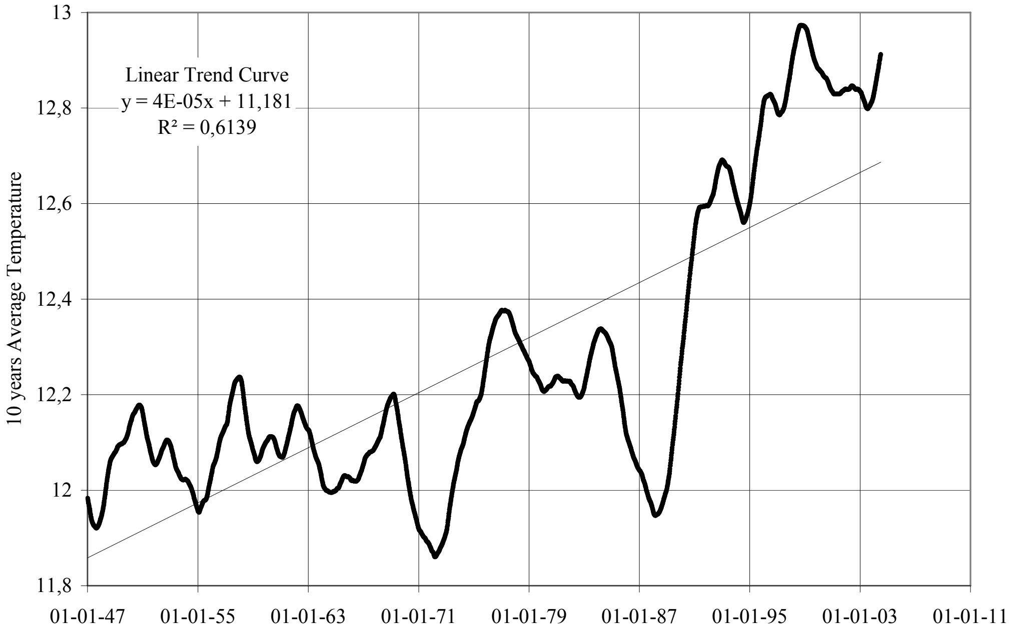

Figure B02-1: Yearly average temperature in a sliding window of 10 years. A strong rising in average temperature is obviously especially since the early ninetieth of the last century. Already a linear trend curve shows this rising trend in average maximum temperature.

The water budget gain of a small infield pool is directly related to the precipitation. Therefore, we investigated the daily precipitation time series of the DWD weather station Schwerin as well (DWD 1996-2004). The yearly precipitation rate was plotted in a ten year moving window (figure B02-2). No obviously trend in precipitation could be found between 1950 and 2004. But the 10 years average yearly precipitation rate varies within the time period between 570mm per year and 680mm per year. This is a difference of 12 percent. Precipitation influences fluctuation in water level among the years while evaporation as a result of changing temperature within a year may responsible for fluctuation within the years.

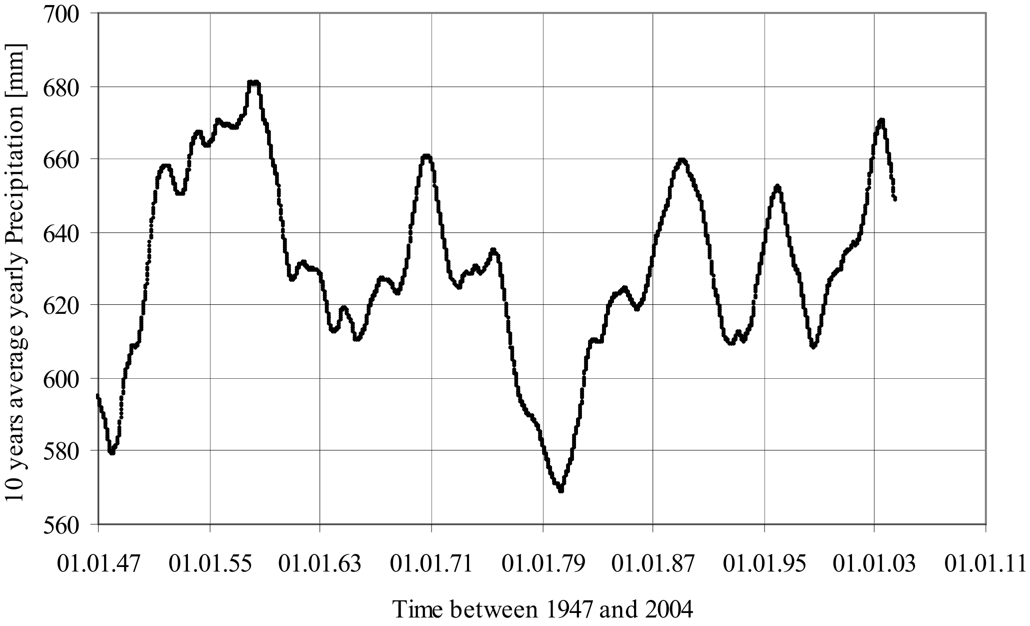

Figure B02-2: The yearly precipitation rate within a moving window of ten years between 1947 and 2004. Since the last 60 years there is no trend in changing precipitation rate. But there are great differences in precipitation rate among the years.

Chapter 4:

The relationship of short period measurement parameters to long time hydrological characterisation of small infield pools in northern Germany

Running title: 'Regionalisation of hydrological parameters'

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Abstract

Small infield pools are one of the few remaining semi-natural landscape elements in agriculturally-dominated pleistocene landscapes such as in northern Germany or Poland. Though their species composition has been frequently studied in the past, very few attempts have been made to investigate their hydrological regime. It has however been demonstrated that the hydrological parameters of mean high spring water level and drying up frequency are key elements determining the suitability of pools for plant species. These parameters are therefore required to understand and predict the species composition of small infield pools. For their estimation, long term climate data can be used in conjunction with short term measurements of water levels at a high temporal resolution. However, these measurements are very expensive to perform and can normally only be done on a limited number of pools. Here, we present a method to infer the spring water level and drying up frequency for a large number of pools using water level data with a high temporal resolution for a limited number of pools within the area and data with a much coarser temporal resolution (e.g. monthly, manually collected) for additional pools. This can be used to analyse the current species composition and estimate the species composition in a changing climate for a much higher number of pools, given the same amount of available resources.

Furthermore, the results show the affiliations of the small infield pools to their origin (kettle holes, marl or constructed holes, and pools in agriculturally-treated depressions due to anthropogenic soil compaction).

Keywords: small infield pools, ponds, hydrological characterisation, bed materials and origin

Introduction

Small infield pools are widely distributed in Pleistocene moraine landscapes (Edvardsen and Okland 2006), and are important features both as habitats for wetland species and as water bodies influencing the regional hydrology. They are also called vernal pools (Burne and Griffin 2005).

Small infield pools can act as groundwater recharge or discharge. They collect runoff water from the surrounding catchment area. According to (Lissey 1971) the catchment area of moraine pools can be independent of the topography. The water runoff into small infield pools can contain surface runoff, or interflow on hidden soil layer surfaces. Additionally, the groundwater table and the infield water recharge may temporarily interact independently from the topography of the catchment area (Chorley 1978). The hydroperiods are very variable within a single pool over time as well as among pools in the same time period (Burne and Griffin 2005). This high variability in pool water recharge sets strong limits to apply mechanistic hydrological models on a greater number of pools. Resulting, mechanistic models describing the hydrology of pools are not widely available (Pyke 2004).

In contrast to lakes, swamps and reeds, the variability of water levels in small infield pools may create strong shifts in habitat quality for wetland plants and macrophytes, i.e. submerged plants. Specifically, longer periods of dry conditions should drastically alter the habitat conditions for wetland or submerged plants. Such species may only persist in a landscape of pools if they are able to track the spatiotemporal shifts in water levels or sustain long periods of withering by delaying population decline until water levels rise again (Kleyer et al. 2007). Therefore, the quantification of the variability of pool water levels in relation to climate and soils is a prerequisite for the understanding of the habitat functions of infield pools. Changes in the environmental conditions can change the species composition (Sturtevant 1998). Hence, a protection of pools requires knowledge of the long term hydrology.

However, despite national protection and private conservation effort of wetlands, these features are still decreasing in number and area (Mouser et al. 2005). And, only a few studies deal with the hydrology of small infield pools (see Rosenberry and Winter 1997, Winter and Rosenberry 1998, Mansell et al. 2000, Conly and Van der Kamp 2001, Richardson et al. 2001, Brooks and Hayashi 2002, Conly et al. 2004, Bauder 2005, Grant 2005, Van der Valk 2005, Dempster et al. 2006).

This motivated us to analyse the long-term hydrology of a larger set of infield pools. In principle, water levels and drying up frequencies could be recorded by automatic devices that provide a continuous logging of water levels in all pools. However, such measurements are costly if performed for a large number of pools and often are not available for longer time scales. Therefore, in this study, we used hydrological simulations of long-term water level variation based on short-term continuous logging of water levels for a small number of infield pools (Lehsten et al. 2008). A statistical transfer function then regionalised the relationship between short-term measurements and long-term water level variation for a larger number of small infield pools. This allowed us to quantify the proportion of infield pools with strong shifts between aquatic and terrestrial conditions on the landscape scale.

Neither modelling nor regionalisation of long-term hydrological regimes of infield pools has been extensively been tackled before.

There are several modelling approaches for small infield pools, for example those of Cherkauer and Zager (1989), Woo and Rowsell (1993), Nath and Bolte (1998), Ferone and Devito (2004), or Mouser et al. 2005. But none of the models can be applied to a broad number of pools.

Also, there are several studies dealing with long term observation of pools, such as Kalettka and Rudat (2006) and Johnson et al. (2004). But either they miss the hydrological characterisation of the pools or the pool number is minimized.

Most advantage is seen in the two time series models for vernal pools by Pyke (2004) as well as for small infield pools in general by Lehsten et al. (2008 in process). With such models long water table time series can be produced to calculate hydrological parameters for describing many pools in a hydrological way. An observed water level time series for each pool and meteorological parameters time series with certain lengths for the study area are required for both models. Hence, further developments are required to describe the hydrology of all pools within a meso scalic weather region.

The hydrology of small infield pools is very variable among neighbouring pools, within a hydrological year as well as among years. To compare the water depth of small infield pools an average hydrological depth parameter can be used. Hydrologically, the average mean water level appears to be more useful. But it is reached during the end of June or the beginning of July, when most of the riparian and water plant species are already established. Therefore, the mean spring high water (SHW) level is of higher ecological relevance to the occurrence of species in the pools. This parameter SHW gives an impression of the pools depth during germination and mating time of most pool related species. To compare the water level fluctuation between pools and among years the frequency of dry conditions of site is of relevance. We considered the water level dependence on time length, as most species can survive short dry periods, especially if the dry periods are followed closely after the reproduction period. Hence, a pool is defined to be dry if it dries up for more than 1.5 month in the vegetation period. With the minimum water level expected at the beginning of October which is also seen as the end of the vegetation period, it indicates that the dry period of the hydrological year needs to be at least three month long. This second parameter P indicates the dynamic of water table changes among years. Hence, both parameters can characterise hydrology of a pool and its suitability for certain species.

The hydrological parameters mean spring high water level (SHW) and drying up frequency (P) of small infield pools can be calculated using long time series of water level fluctuation. With a shorter water level time series of one hydrological year, the explicit measured data describes the in situ hydrology of the pools. As mentioned before, such short time observation are more commonly used than modelling techniques in most study cases. Hence, there is a need to develop transfer functions from short explicit measured time series to general information of the pool hydrology. Our aim in this study is the presentation of such a transfer function from explicitly measured values to general information of the average spring water level and the drying up frequency.

With the resulting transfer functions the hydrological characterisation of all small infield pools can be described. This regionalisation of the transfer functions is an advantage for all studies dealing with small infield pools, e.g. biologists, ecologists, nature conservation organisations, water management organisations and so on.

Methods

The study area

The study area is situated in North East Germany (53°40'N and 12°10'E) (see figure A2-1) and covers a size of 12 km². Small infield pools have a wide distribution in this region, with up to 40 pools per km² of an area of 38000 km², and a total number between 150,000 and 300,000 pools (Klafs and Lippert 2000). A pre-investigation with help of the geological map of a broader area (LUNG, 2005) comparing several potential study sites was conducted to ensure that the hydrological characteristics of the pools vary considerably and that the amount of pools per area is high enough to (I) allow to sample several of them over a short time period and (II) to ensure that there are no considerable differences in precipitation between them.

During glaciations, an outburst had taken place in the study area. Today, the relicts of the outburst consist of a sandy channel speckled with lakes, small infield pools and meadows. The channel still serves as groundwater flow channel (LUNG, 1987). The glacier edge outskirt of the Pomeranian Moraine crosses the area in east west direction. The southern part consists of a sandure region with relics of the moraine edges, where large peat accumulating infield pools can be found. These large (more than 5 ha) infield pools are believed to be dead-ice sinkholes.

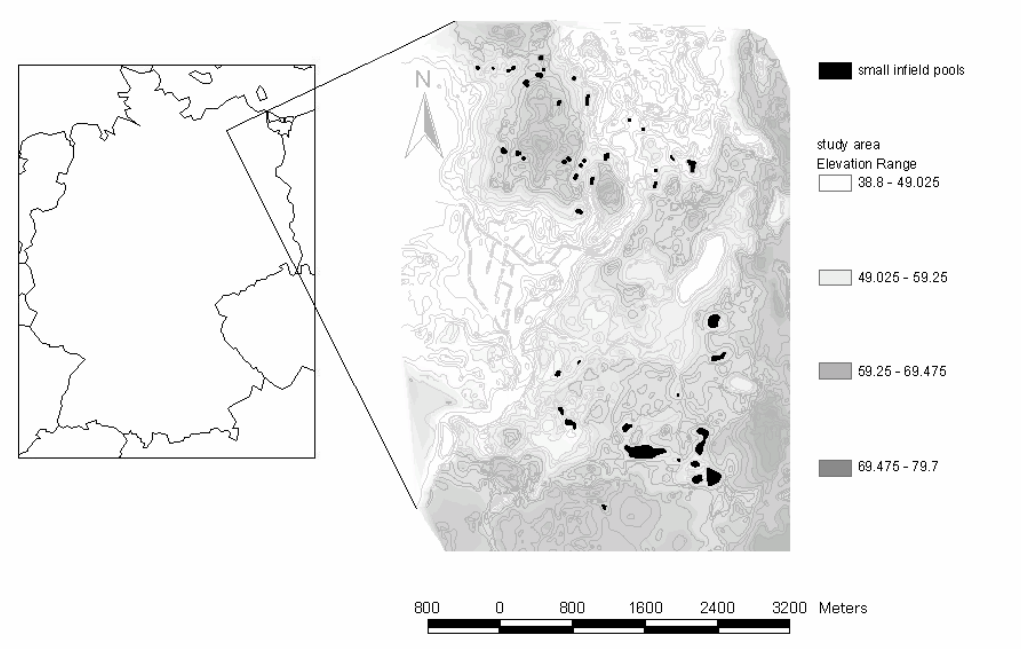


Figure A2-1: Map of the study area in North-East Germany. The infield pools are black marked.

The northern area is dominated by clay and silt lenses underlain by sandy materials. The terrain height difference per square km (terrain energy) is up to 40m. Pools in that part of the area which has no connection to the glacial outburst tend to be rain water filled, while pools within the glacial outburst have a high probability of being influenced by groundwater. Pools in depression zones of the both zone are expect being temporally tail water influenced.

At the edge between the terminal moraine and the sandure several sediment movements have taken place between periods of glacier melting. Therefore, sediment layers are very heterogeneous. The sizes of the 46 investigated pools vary between $100m^2$ and 5ha. Due to the high variation in morphology of the study area, of the different sizes of the small infield pools and their different location in the landscape we expected the hydrology of the pools also to vary considerably.

Storage effects

Measurements

Continuous meteorological data for the area are available since 1950 from the nearest weather station (Schwerin, 60km apart from the study area, DWD 1996-2004). A statistical analysis showed a strong correlation between meteorological recorded data (precipitation and evaporation) in the research area and the data from weather station in Schwerin. Hence, weather data from Schwerin were used for the simulation of water levels since 1950 (Lehsten et al. 2008).

For 17 randomly chosen infield pools (“A pools”) daily water table measurements were taken for two hydrological years (2002 and 2003) with automatically gauge logger called PDLA70 distributed by ecoTech, Bonn, Germany (eco-Tech 2002).

For another 29 small infield pools (“B pools”) the water levels were recorded manually every 4 weeks during the same time period as for the A-pools. The water level was measured as differences between the actual water table and an installed fix point. The absolute depths were determined with a depth profile or alternatively when the pools dried up.

Menyanthes

The automatically logged daily water levels of the 17 A-pools and the meteorological parameters precipitation and evaporation of the same time period were used to calculate the water level time series since 1950 with the model Menyanthes (Von Asmuth et al. 2004). The procedure is described in more detail in Lehsten et al. (2008). With this time series the drying up frequencies (P) and average spring water levels (SHW) for each A pool could be calculated.

Transfer function and regionalisation

To develop transfer functions for SHW and P these data had to be compared with characteristically measured data. The highest water level of a certain periods is an expression of the potential depth of the pool. The water level fluctuation of a certain period is an expression of how strong the hydrological system reacts to local conditions and meteorological impacts. Hence, for both hydrological parameters SHW and P, the maximum and minimum water levels of a hydrological year express these two parameters. The hydrological year 2003 was one of the driest years in the last century in North Germany (Lehsten et al., 2008), around 40% (17 of 46 pools) of the pools dried up. Hence, the amplitude of changing water level could not be measured as the lowest water level was below the pool bottom. Therefore, only the data from the year 2002 were used for the transfer functions.

Estimation of the spring water level transfer functions

All small infield pools (A- and B-pools) experienced similar weather conditions. Small infield pools with similar spring water level and similar fluctuation level over the recorded time period should have similar long term spring water level. Small infield pools with the same dynamic in water level changes are assumed to have the same hydrological behaviour in equal water depths, even if the absolute water depths are different. Therefore, we assumed it feasible to compare the water levels of the A-pools to the water levels of the B-pools.

If the fluctuations between pools are similar, we can assume a relationship between the long term average spring water level and the observed spring water level in 2002 (formula A2-1), which may be linear (formula A2-2).

$$SHW = f\left(SHW_t\right) \qquad \text{(A2-1)}$$

$$SHW = m_1 * \left(SHW_{2002}\right) + c \qquad \text{(A2-2)}$$

SHW is the long term spring water level of the last 50 years and SHW_{2002} is the spring water level measured in 2002. In an ideal case (no fluctuation at all) in equation (A2-2) the factor m1 would have the value 1and c would be zero.

If we assume the spring water levels in 2002 (SHW_{2002}) similar between pools, we can suppose a linear relationship between SHW and the recorded fluctuations, independent of SHW_{2002} (formula A2-3, A2-4).

$$SHW = f\left(fluctuation\right) \qquad \text{(A2-3)}$$

$$SHW = m_2 * \left(MAX_{2002} - MIN_{2002}\right) + c \qquad \text{(A2-4)}$$

SHW is the average spring water level of the last 50 years, MAX_{2002} and MIN_{2002} are the maximum and minimum measured water levels in 2002. Combining both functions the average spring water level can be seen as a function of the observed spring water level and the observed fluctuation of the year 2002:

$$SHW = m_1 * SHW_{2002} + m_2 * (MAX_{2002} - MIN_{2002}) + c \qquad \text{(A2-5)}$$

The parameters m_1, m_2 and c are fitting parameter which will be statistically optimised by a regression analysis.

Estimating the drying up frequency of the B pools

The pool drying up frequency (P) depends directly on the spring water level and the fluctuation of a pool. With respect to habitat suitability, the hydrological defined drying up frequency is not of interest. Rather, the infield pools should stay dry over a longer period, since most species can survive short dry periods. We consider a site to be dried up when water plants can not survive in a vegetative stage anymore. This usually happens if a dry period is longer than 1.5 months between beginning of April and end of September (own observations based on floristic records) or longer than 3 month for a whole hydrological year.

For ecological questions it is useful to divide each pool in zones according to the water depth differences between the pool banks to the centre. These ecological zones coincide with different spring water levels and drying up frequencies and consequently provide different habitats. Hence, each pool was separated into zones having a mean SHW of 10cm, between 10cm and 50cm or more than 50cm, if existent.

For pools with similar fluctuations (MAX-MIN) of a hydrological year the drying up frequencies (P) is lower on positions with higher maximum water level (MAX). Pools with similar maximum water levels of a certain hydrological year lead to higher drying up frequencies (P) in pools with higher fluctuations in the same hydrological year.

We assume, that P can be related to the minimum and maximum water level of year 2002 using formula A2-6.

$$P = 1 - \left(1 - \left(\frac{MAX_{2002}}{MAX_{2002} - MIN_{2002}} + 1 \right)^{-a} \right)^{b} \tag{A2-6}$$

MAX_{2002} and MIN_{2002} are the maximum and minimum water level measured in 2002. The two fitting parameter a, b will be estimated using the data from the A-pools. For the developing of formula A2-6 see Box 03.

Results

Spring water level and drying up frequencies of the 17 automatically logged A-pools

In general, pools with higher spring water level have a lower drying up frequency. The best fit of a trend function is shown in figure A2-2. The r^2 value of 0.48 indicates that the drying up frequency depends not only on the spring water level. There are other factors involved, too.

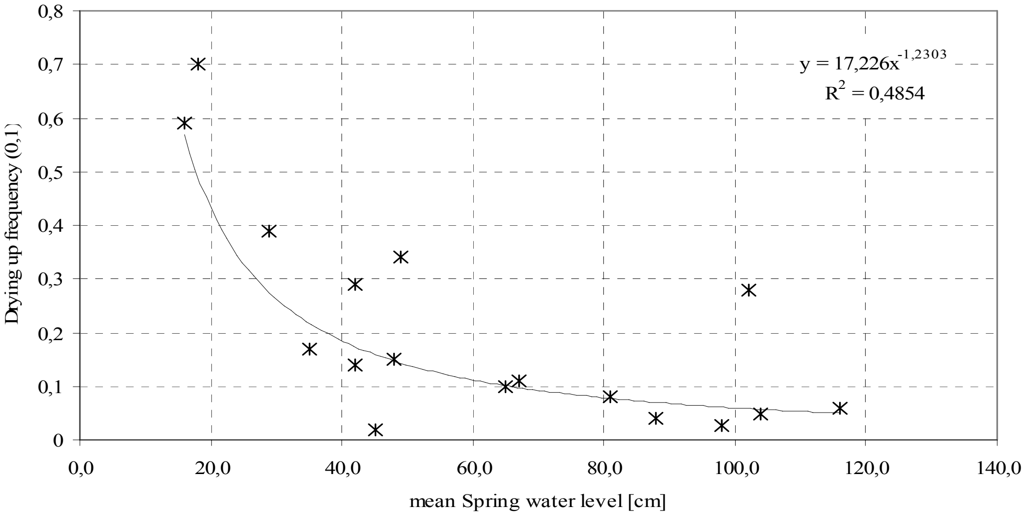


Figure A2-2: The average spring water level (SHW) and the drying up frequency (P) of the A-pools calculated of the simulated 54 years water level series. Note that there is a general trend of higher spring water level leading to lower drying up frequencies. However, the relationship is weak.

Correlation of the average spring water level of the A-pools and their spring water levels in 2002

Fitting the parameters of formula A2-5 (relationship between the spring water level and fluctuation of a single hydrological year to the mean spring high water level of the last 54 years) with a linear regression leads to the following function:

$$SHW = 0.78 * SHW_{2002} - 0.82(MAX_{2002} - MIN_{2002}) + 1.91cm \qquad \text{(A2-7)}$$

SHW, SHW_{2002}, MAX_{2002}, and MIN_{2002} are expressed in cm. The relationship between these parameters is shown in figure A2-3. The squared correlation is 0.93.

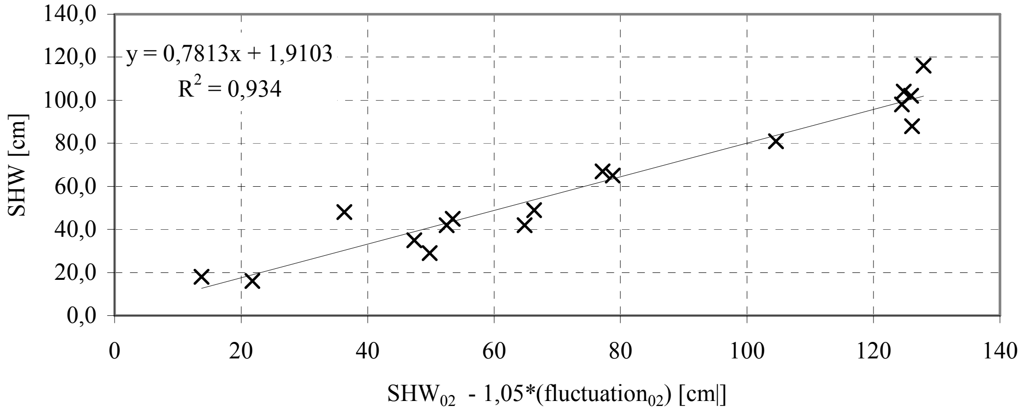


Figure A2-3: Linear correlation of the average spring water level and the fluctuation of the year 2002 (r^2=0.93) for A pools. The ranges of the average spring water levels are between 15cm and 1.3m.

The results of the transfer function to the B-pools are shown in figure A2-4. The x-axis is a term of the spring water level 2002 and the fluctuation in 2002 in the relation of the parameters m1 and m2. As seen in this figure, the average spring water levels tend to be lower than the measured spring water levels in 2002.

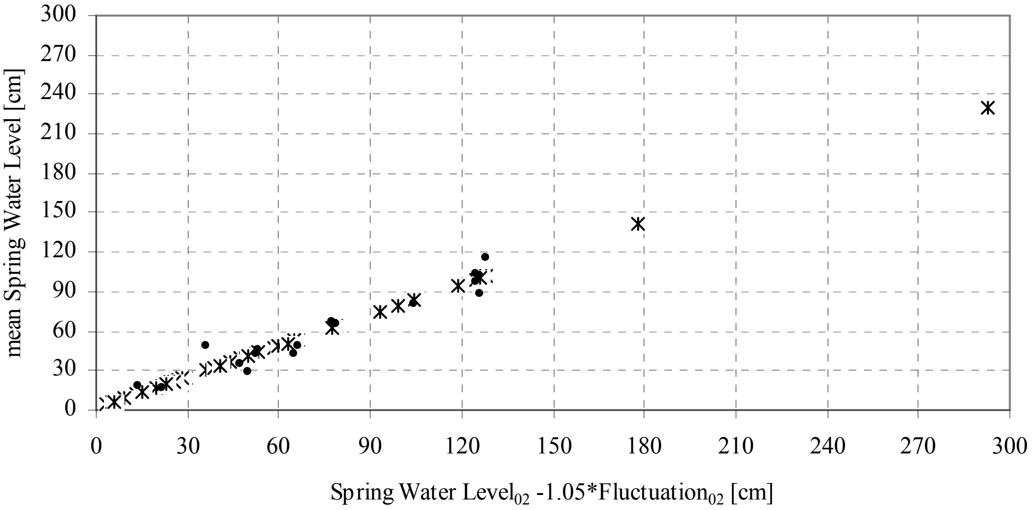


Figure A2-4: Short term recorded parameter SHW and fluctuation versus long term calculated SHW according to formula 15 of A-pools (dots) and B-pools (crosses).

Drying up frequency

The average drying up frequency P for 54 years coincides very well with the drying up frequency calculated from the minimum and maximum water levels measured in 2002. A linear trend function between long time calculated P and P calculated out of measurements taken in 2002 has a squared correlation of 0.98 (see figure A2-5).We estimated the parameters a, b of formula A2-6 with a regression. The two parameters for the formula A2-6 are estimated to a=2.317 and b=14.9657.

$$P = 1 - \left(1 - \left(\frac{MAX_{2002}}{MAX_{2002} - MIN_{2002}} + 1 \right)^{-2.317} \right)^{14.9657} \qquad \text{(A2-8)}$$

MAX_{2002} and MIN_{2002} are the maximum and minimum water levels in 2002 respectively.

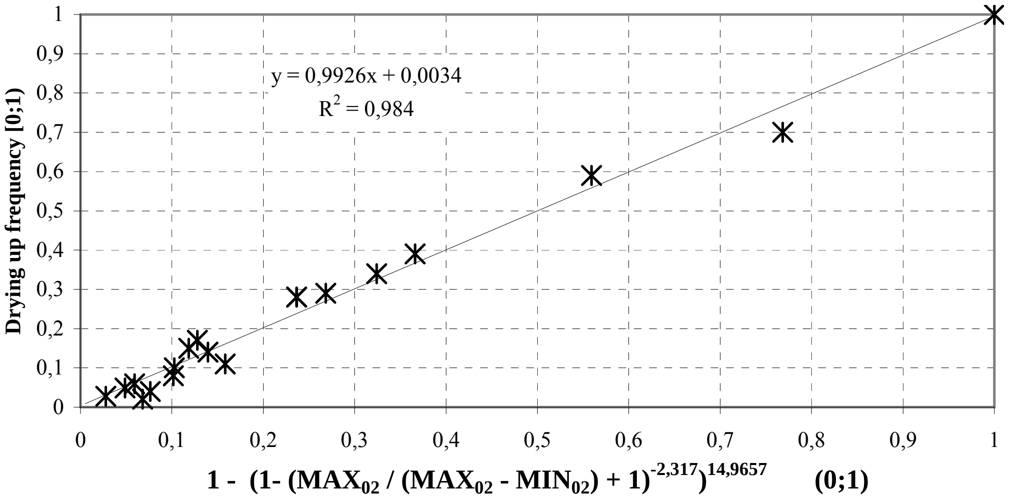


Figure A2-5: Regression of drying up frequency of the A-pools estimated by formula A2-6 as x-axis to the calculation by simulating the water levels of the last 54 years as y-axis. Note the good correlation between drying up frequency and maximum and minimum water level of the hydrological year 2002 (r^2= 0.98). The parameters a, b were calculated by a regression with a=2.317 and b=14.9657.

We applied equation A2-8 to the measurements of the B pool (see figure A2-6).

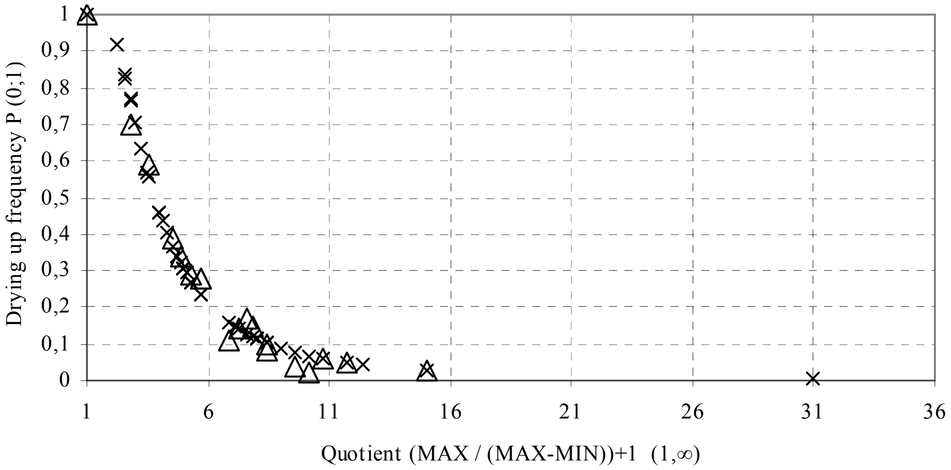


Figure A2-6: Calculation of the drying up frequency out of the quotient of maximum water level and fluctuation of the single year 2002 of all A and B pools (crosses). In addition, the calculated drying up frequencies of the 54 year water table time series of the A-pools are represented as triangles in the graph.

Hydrological characterisation and genesis of the pools

When applying the transfer functions to all pools, drying up frequency (P) increases when mean spring water level (SHW) decreases (figure A2-7). The relationship is similar to that simulated for the A pools (figure A2-2) (r^2=0.47).

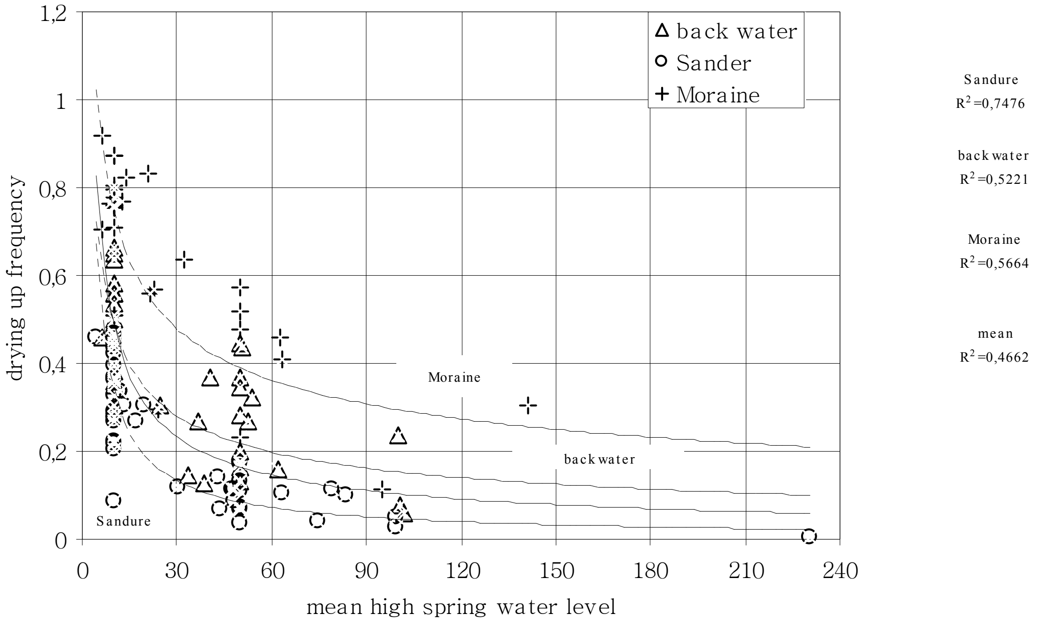


Fig. A2-7: Trends of the drying up frequency of pools and their zones in North East Germany to the mean high spring water level. The relationship of drying up frequency and average spring water level of all investigated pools is shown. Pools in the marl region are well distinguishable from ground water influenced and temporary ground water influenced pools.

If only pools sharing the same origin (groundwater influenced kettle holes in the sandure region, marl holes, or tail water influenced small infield pools in depression zones of the moraine area) are considered we got much better trends. Pools lying in marl sediments (crosses in figure A2-7) tend to have a very high drying up frequency. Pools in the sandure region (circles in figure A2-7) tend to have very low fluctuation. Tail water influenced pools are less in drying up frequencies than rain water filled pools but dry up more frequent than ground water influenced pools (triangles in figure A2-7).

If only the drying up frequency of the pools is considered 37 of all pools have a drying up frequency of less than 0.5. The other 9 pools tend to dry up more often than every second year. These 9 pools are all anthropogenically created marl holes in the moraine region. Pools with a drying up frequency of more than 0.7 might be considered as terrestrial rather than limnic. These are 6 marl holes with a spring water depth between 7cm and 22cm. Pools with a very low drying up frequency less than 0.2 can be seen as limnic system. These are 19 pools of which one is a rain filled pool and 5 are tail water filled. However, the rain water filled pool and the two tail water influenced pools are deep with a mean high spring water level of ca. 1m. To compare the pools in a better way, the bank zone of each pool is more of interest. As mentioned before, the bank zone of a pool is defined with a mean spring water level less than 10cm. Taking a drying up frequency of P=0.5 as a distinguishing attribute, 24 pools have a low drying up frequency. These are all groundwater influenced pools in the sandure region and in the channel and five pools in the intermediate zone. The marl holes and the other 9 pools in the intermediate zone have a drying up frequency of their bank zones of more than 0.5. For all marl holes their bank zones can be seen as terrestrial rather than as limnic with a drying up frequency of more than 0.7. Only marl holes have a higher probability of terrestrial behaving bank zones in this study area.

Discussion

Pools are widespread in moraine areas of the world. They are important features in the landscape and are essential for both plant and animal species (Gibbs 2000). These communities are highly sensitive to disturbance and hydrologic changes. Therefore, they must be managed as dynamic rather than static systems (Mitsch and Gosselink 1993).

In the view of the rapid decrease in number and area (Mouser et al. 2005) of pools, Klafs et al. (1973) could not explain why two neighbouring pools showed different dynamics in water table changes.

Kalettka (1996) postulates that kettle holes in glacier channels have the highest opportunity to be perennial water filled. Schindler (1996) verified the hypothesis that the lateral precipitation discharge of the catchment area is an important factor for the water balance in pools. Johnson et al. (2004) monitored the hydrological characteristics of a prairie wetland in the United States for more than 10 years. They concluded that dry and wet periods are influenced by weather extremes, either by drought or wet weather conditions respectively. Schmidt (1996) showed the results of another ten year water table sampling of 4 kettle holes in a study area comparable to that in this study. He found a time lag of the response of the water dynamic to precipitation effects of about two years.

These studies show that the demands of model precision and corresponding data requirements, the applicability to large number of different pools over long time scales, and the ability to generalise results are not easily met. However, our combination of modelling, simulating, deduction of transfer functions and regionalisation provide all the requirements needed to describe the hydrology of a great number of small infield pools in the same meso scalic climatic zone independently from their origin. Since most parts of North East Germany belong to the same meso scalic climatic zone, the transfer functions between short time measurements and hydrological characteristics can be applied to most of the pools when measuring the water table variation during a single hydrological year and when comparing it with the water table fluctuation of the simulated 17 pools of the same hydrological year.

The measured spring water level of the A-pools in 2002 are between 40cm and 1.40m, whereas the total range of 2002 measured spring water levels (including the B-pools) are between 15cm and 2.9m. The measured fluctuations in 2002 ranged between 10 and 61cm for A-pools and between 2cm and 45m for B-pools. That enables us to apply the transfer function for a larger number of pools and to characterise their hydrology with high efficiency.

The correlation of water fluctuation and water depth to drying up frequency confirms our expectations. This correlation requires only two parameters, a and b (for a further discussion of these parameters see Box 03 and 04).

The parameters of the transfer function for the mean spring high water level show that the measured spring water levels of the year 2002 are higher than the mean spring high water levels. The goodness of fit of the regression between the mean spring water level and the measurements in 2002 ($r^2=0.93$) is not as good as for the drying up frequency. Because of the slope of the regression function of m=0.78 and a fixed value of 1.9cm for pools with low fluctuation in general and a spring water level (which is constant because of the low fluctuation) of more than 10cm the mean spring high water level would be underestimated.

For pools with measured spring water depth of less than 10cm the estimated mean spring high water level tends to be comparable to the real mean spring high water level. Pools with 50cm measured spring water level can be underestimated by up to 10cm. For further investigations and interpretations, the errors in the average spring water level need to be taken into account. The correlation would have gained much better results if the shape of function between fluctuation and mean high spring water level would not be assumed as linear. But, with the given data it was not possible to find a better specified function. Also, the water level was measured from the bottom of the pool (top of the sediment layer). If we could used the mean spring high water level from the basement instead from top of the sediment layer the results of the transfer function would fit better with the calculated mean spring high water. Because of the high number of investigated pools and their position in the landscape it was impossible for the project to drill boreholes down to the basement. The basement distance to the pool bottom could have risen up to 10mm per year in the last 30 to 40 years according to Pokorny & Hauser (2002). This strong sediment deposition in the pools arises from the catchment area due to intensification of agricultural activities in the catchment area.

The combination of both independently calculated hydrological parameters of drying up frequency (P) and average spring water level (SHW) allows pools to be grouped according to their bed materials and morphology (see figure A2-07).

The 13 anthropogenic marl holes in the moraine region tend to have the highest drying up frequency compared to the other pools. The hydrologic regimes of pools in the moraine will be more sensitive to local scale disturbances, rather than larger scale disturbances (Ferone and Devito 2004). Their response to local rain fall events is much stronger. Runoff from rain water into the ground water does not affect them. Such water is lost for marl holes because of the vertical distance between ground water table and marl holes basement. Therefore, after the precipitation event and runoff these pools are only subject to water loss by either transpiration or due to the permeability of the pool basement.

The 14 temporary ground water influenced pools in depressions tend to have intermediate drying up frequencies according to marl holes or kettle holes. These pools will be fed either by temporary artesian groundwater and rain water if the ground water level is temporary higher, or the pools will be fed only by rain water if the ground water level drops down. A groundwater flow reversal can occur in dry periods (from the pool to the adjacent area) while a recharge to the pool occurs in wet periods in moraine areas (Ferone and Devito 2004). Another temporary influence on larger hidden water bodies is due to local impermeable sediment layer beneath these pools. Hence, they could be temporarily influenced by spring tail waters caused by the impermeable zone feeding the pools. While in dry periods the temporary hidden water body decreases to a minimum and the pools tend to feed it. Therefore, such pools can act like groundwater-influenced pools and sometimes as rainwater filled marl holes. If such pools are shallow with a mean spring high water level of less than 10cm they seem to be rather terrestrial than limnic. Such pools are typical vernal pools with flooded seasons in spring and dry conditions in summer and autumn. Longer evolved tail water pools in moraine depressions are deeper in spring water level. Therefore, their drying up frequency is in general lower, between 0.2 and 0.5.

In contrast, a continuous flow-through of ground water through the pools occurs in the 19 ground water influenced pools in the sandure region and the channel as detected by Ferone and Devito (2004) in pools in lowlands. They tend to have the lowest drying up frequency compared to the other two groups. Their response to precipitation impact is slower and depends not only on local and temporary scales, but also on larger and long time scale disturbances. The ground water layer acts as buffer zone and compensates precipitation and transpiration effects. Such pools can always be identified as limnic systems in the landscape.

Shallow groundwater exchange between pool and adjacent peat lands varied seasonally and differed between the moraine and lowland complex (Ferone and Devito 2004). That suggests that pools in the sandure region will be influenced by the surrounding groundwater level and larger scale weather conditions. But, pools in the terminal moraine will be influenced by the surrounding groundwater level only in high precipitation periods in the larger scale. Precipitation and evaporation are the most influencing parameters of the water level fluctuation over the year. Pools with no connection to the groundwater level will not be influenced by groundwater re- or discharge. Hence, these pools are most influenced by local and temporary weather conditions. Therefore, these pools have the highest fluctuation in water table over the year as well as within a decade (ibid).

We found similar hydrological behaving types of small infield pools as described by Ferone and Devito (2004) and could compare them with the types of origin described by Edvardsen and Okland (2006). Therefore, the developed procedure to transform hydrological short time measured parameters from pools to long time descriptions of these pools is the most efficient way to characterise a great number of small infield pools within the same meso scalic climatic area. This transfer functions are of great relevance in ecological studies, nature conversation, and in agricultural management dealing with the management and investigation of small infield pools. The results are validated due to the classification of the small infield pools into three types of ground water affected pools (Ferone and Devito 2004) as well as due to their origin (Edvardsen and Okland 2006). The resulting coincidence drying up frequency and mean spring high water level with the genesis of the pools can be seen as an indirect validation of our method.

Box 03: Derivation of the formula A2-6

If the quotient of maximum water level and fluctuation of a measured time period is an expression for the drying up frequencies the function for this expression (formula B03-1) needs to run between cero (never dries up) and one (yearly drying up periods). But in fact, theoretical it runs between cero and infinite. To get the quotient in the borders of cero and one, first the value one has to be added to the quotient to avoid values less than one (formula B03-2). Than, the reciprocal of that term has be calculated (formula B03-3) and a power function with an exponent greater than one has to be applied (formula B03-4).

We assume the drying up frequency to be

$$P =: f\left(\frac{MAX}{MAX - MIN}\right) \tag{B03-1}$$

MAX and MIN are the maximum and minimum values of the recognized time period. As higher the maximum and as lower the fluctuation as lower should be P. Therefore, with rising Quotient P should lower. Hence, the function should be written in a reciprocal way. But, to avoid values smaller than 1 (in reciprocal term greater than 1) the absolute value one has to be added first (equation B03-2).

$$P =: f\left(\left(\frac{MAX}{MAX - MIN}\right) + 1\right) \tag{B03-2}$$

MAX and MIN are the maximum and minimum values of the recognized time period. As higher the maximum and as lower the fluctuation as lower is P. Mentioned, it is still a negative correlation.

$$P =: f\left(\frac{1}{\left(\frac{MAX}{MAX - MIN}\right) + 1}\right) \tag{B03-3}$$

MAX and MIN are the maximum and minimum values of the recognized time period. Now, the quotient runs between the borders cero and one. With a rising quotient P will rises as well. The correlation has to be done only due to a power function with no absolute values (B03-4).

$$P =: f\left(\left(\frac{1}{\left(\frac{MAX}{MAX-MIN}\right)+1}\right)^{a}\right)$$

(B03-4)

MAX and MIN are the maximum and minimum values of the recognized time period. The exponent ‘a’ lowers the values of the function. To avoid values out of the limits ‘a’ runs between 1 and infinite”.

But it is not possible to fit the function m * P + n (m=1; n=0) with the function (1 / (MAX / (MAX – MIN) + 1))^{a}.

The actual function can never express a linear function. Therefore, the curvature has to be reduced. The parameter ‘a’ changes both parameters m, n in the same direction (rising a (a>=2) results in lowering m and n).

If the actual function would be subtracted from the value one, the new function would also be in the limits of cero and one. But, the term would give a negative correlation to the P values (B03-5).

$$P =: f\left(1-\left(\frac{1}{\frac{MAX}{MAX-MIN}+1}\right)^{a}\right)$$

(B03-5)

As mentioned before, a fitting of the P values can be done by a power function. Hence, a second fitting parameter has to be added (B03-6).

$$P =: f\left(\left(1-\left(\frac{1}{\frac{MAX}{MAX-MIN}+1})\right)^{a}\right)^{b}\right)$$

(B03-6)

Written in another way, the function will have following form:

$$P =: f\left((1-(\frac{MAX_{02}}{(MAX_{02}-MIN_{02}}+1)^{-a})^{b}\right)$$

(B03-7)

Because of the negative correlation and the condition P needs to run between cero and 1, the correlation function is a subtraction of formula B03-7 from the value one (B03-8).

$$m*P+n=1-(1-(\frac{MAX_{02}}{(MAX_{02}-MIN_{02}}+1)^{-a})^{b}$$

, m=:1 and n=:0. (B03-8)

As mentioned before, rising ‘a’ lowers both m and n whereas rising parameter ‘b’ rises m and lowers n. The function B03-8 is identical with the function (A2-6).

Box 04: Discussion of the parameter for formula A2-6

If the parameter 'a' rises, the value x^a lowers with x in the limits of cero and one and a>=1. The parameter x^a stands for the term $1/(max/fluctuation+1)^a$ where max is the maximum water level and the fluctuation is the water level difference within a time period. The first derivation is x^{a}'= $a*x^{(a-1)}$. Hence the slope of the partial function rises with rising a (a>=2). If the term will be extended to $1-(x^a)$ the value of the slope will rises with raising 'a' but with a negative sign. Hence, if the parameter 'a' rises the term under the b-th power rises. It will shift in the direction of the right boarder one. Therefore, the term $(1-x^a)^b$ and its slope value will rises with higher 'a'. But still, the slope is negative. Because, the end function is written with $P= 1- (1-x^a)^b$, the slope will turn into a positive direction again. Hence, with rising a, the slope of the end function will rises too.

With a rising slope in the function x^a, for x between cero and one and a>=2 a linear correlation trough the function will end in lowering of the absolute value n. That results in a rising absolute value n for a linear correlation for the function $1-(x^a)$. The same happens if it will be raise to a higher power 'b' with b>=2, $(1-x^a)^b$. Resulting, a linear correlation of the function $1-(1-x^a)^b$ ends with a lowering absolute value if the parameter 'a' rises.

A rising parameter b fits the function $y=(1-x^a)^b$ against the function $y=-m*x$, for $0<=x<=1$, m>=0 and a, b >=2. Hence, the negative slope of the function will become greater in value with rising 'b'. Therefore, the positive slope of the function $y=1-(1-x^a)^b$ rises too with rising 'b'. But with rising 'b' a linear correlation trough the function $y=1-(1-x^a)^b$ will result in a lowering absolute value n=1. Hence, such linear correlation trough the function $y=1-(1-x^a)^b$ will end in a rising absolute value n if 'b' rises.

For the fit of the function $m * P + n = 1-(1-x^a)^b$, with m=1; n=0 and $0<=x<=1$, both parameters 'a' and 'b' act in the same way to m. But, for the absolute value they act in an opposite way. Therefore, if such a correlation exists between the maximum water level and the fluctuation over a time period to the average drying up frequency than the parameters can be estimated with exact one solution.

Part II: Plant functional groups in small infield pools

Chapter 5:

Pre-investigations

Box 05: Diaspore analysis

With this analysis the plant species observation had to be verified. We could not relate species to certain zones of the pools but we could examine the full species pool.

To reduce the effort we examined 50% of the given pools via random sampling. Diaspore analyses are common for terrestrial plant species but are rarely done for wetland species and macrophytes. In general there are two soil layers which are involved in the investigation, the top layer of up to 5cm depth and a lower layer between 5 and 10cm depth. Sometimes there is a third layer involved.

We applied following method. We analysed soil samples out of 20 pools which were collected in March 2003. We let the diaspore emerge over spring and summer season of 2003. Because there were cool periods in winter 2002/2003 such frost period was not induced in the experiment. To get soil samples of the pools we used a riverside borer. We adjusted a movable plate of 10cm in diameter on the bore rod. With the plate we could realize different sample depth zones since the plate avoid deeper boring.

The soil samples were dispread on quartered square metre big trays which were covered with humus rich garden soil and well watered (figure B05-1). The experiment was covered with light permeable gauze to avoid seed input (figure B05-2).

Figure B05-1, B05-2: Soil samples on the experiment trays, covered by gauze.

Storage effects

The seedlings were identified and the numbers counted (figure B05-3). Unidentifiable seedlings were pricked out and labelled for further identifications (figure B05-4). To compare and identify the seedlings we sampled seeds in the field if possible or ordered them from gardening shops. The seeds were sowed out in comparable conditions and to the same time.

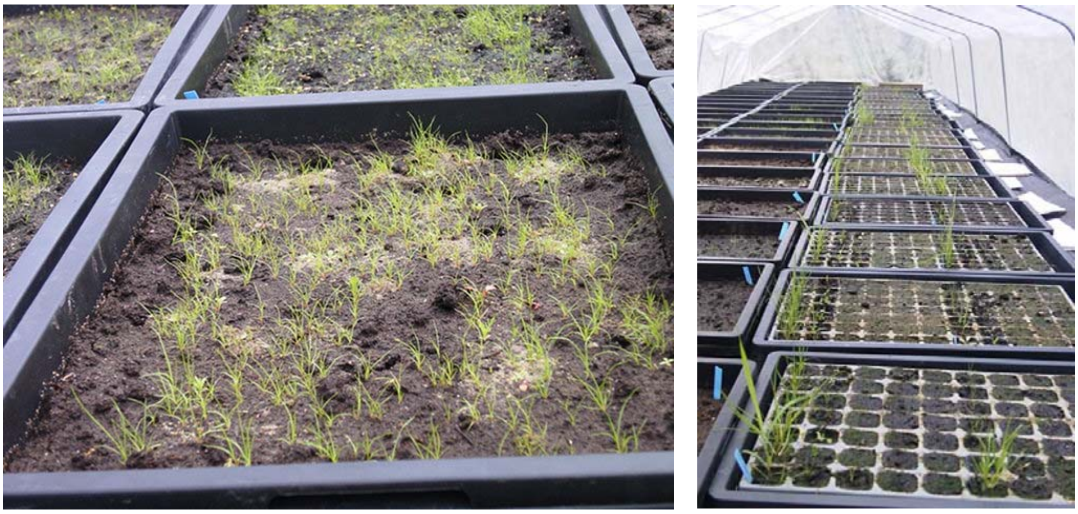


Figure B05-3, B05-4: Germination of seed, seedling prick out into extra trays.

With plant growth the individuals were separated into single plant pots (figure B05-5).

Figure B05-5: grown seedling in plant pots. Here are from the left site *Lycopus europaeus, Peucedanum palustre, and Galium palustre.*

After germination period stopped we let the soil probes completely dry up for 4 weeks until we watered them again (figure B05-6). Then, we repeated the experiment.

Figure B05-6: Dried up trays.

Results

Except for pygmy rushes (*Juncus Pygmeaus*) we could not examine other plant species which we did not observed in the field. Pygmy rushes are wide spread over farming fields as they germinate on each vegetation free soil area, preferred on sites with short rain flood events which the crop did not survived. Therefore, we did not include them in further investigations.

The seed number distribution between upper and lower sediment layer varies strongly. As expected in average the seed number proportion is lower in the lower sediment layer with 44 percent of all germinated individuals. But over the different pools the seed number proportions varies between 16 and 66 percent of germinated seeds. We could not found any relation of seed distribution between upper and lower sediment layer to mean high spring water level or drying up frequency. Pools with turf accumulation had higher amount of seed in the lower layer with 45 percent. Pools with no peat accumulation had in general lower seed proportion in the lower sediment layer with 35 percent of total seedling number. The result can be caused by several processes. Either it implies that seed dormancy is longer in pools with peat accumulation. Or sedimentary processes are much stronger in pools without peat accumulation which leads to more compressed sediment layers. This would result in different sediment ages in the deeper zones. In pools without peat the deeper sediment zone would be older than in peat accumulated pools resulting in higher amount of diaspora in peat accumulated pools. To identify the responsible processes further investigations are needed.

Box 06: Water chemistry of 47 small infield pools over a time of two years

The water chemistry was measured every 4 weeks between April the first and end of September in the year 2002. The measurements were not taken, if the pool couldn't reach due to high standing crop or if they went dry. We measured phosphorus, nitrate, ammonium, ph-values and water conductivity as well as water temperature. Because, in small infield pools water temperature is related to the actual air temperature and it needed a day to measure the chemistry of all small infield pools temperature and water conductivity were not analysed for further investigation. All parameters except phosphorus were measured with the multi parameter sensor ISY 6600 by the company eco-Tech (eco-Tech, 2002). To avoid measurable errors, the multi sensor was placed in the middle of a life belt and fixed in that way, that the sensors were placed in 10cm water depth. The life belt was brought near the middle of the pools with help of telescope bars and ropes. The maximum length of 3metres of the connection cable between sensor and laptop allowed a maximum distance between measurement place and shore line. If the pools were not deep enough, a water probe had to been taken and the multi sensor was placed within the probe. The water probes were taken with help of a telescope bar and a plastic tank. The water volume was 1 to 2 litres according to the small depth of the pool and in avoiding disturbances of the sediment into the water column. Measurements were taken within a minute after collecting the water probe. Phosphorus and ammonium were measured 2003 with in situ quick field test developed by Merck AG (http://www.merck.de) (Phosphate quick test kit 114445 by Aquaquant®; Ammonium quick test kit 114423 by Aquaquant®), see figure B06-01. These tests needed a preparation time of 10minutes to 15 minutes. Therefore, 200ml water probes were first collected for several pools and than together investigated. Because, the sensibility of the multi sensor ISY 6600 was not high enough for measured ammonium concentration in the year 2002, ammonium concentrations are only available for the dry year 2003.

Storage effects

In the mid term of 2003 the ISY 6600 multi sensor showed problems in the measuring technique. Parts had to be exchanged and new calibration processes stopped the availability of the multi sensor in the field.

Figure B06-1: water chemistry measurements, phosphorus and ammonium concentrations were measured with in situ investigations kits developed by Merck AG. Water probes were collected over half day time and analysed over mid day or in the evening.

Nitrate analyses

Nitrate concentrations were very variable between small pools as well as among the years. The concentrations vary between 0.31mg/l and 74mg/l. In the middle the concentrations are 7.8mg/l. According to the State Office for water, LAWA (Landesamt für Wasser) quality classes of naturally lakes in Germany, this concentration indicates a water quality of class three, an eutrophic water level one (LAWA, 1999). The nitrate yearly mean concentration of pools differs between 0.67mg/l and 64mg/l within the pools and years. General, the nitrate concentrations were slightly lower in the wet year 2002 with 6.5 mg/l compared to nitrate concentrations of 9.1mg/l in 2003. But highest concentrations were reached in August 2002. Our measurements showed that nitrate concentration varies among pools and years very different. In some pools nitrate concentration did not changed at all. In other pools nitrate concentrations differed among the two years with a factor of up to 45. A trend in nitrate concentration over a year as well as among water levels could not be found. In our study other impacts as water level or water temperature are more important for the water quality. We expect that local intense rain events may have transported nitrate concentrations with soil sediment into the pools leading high concentrations for a short time period.

Five pools had an average nitrate load indicating mesotrophic conditions. Twenty five small infield pools were in meso-eutrophic condition. Eleven pools were in eutrophic condition and only five pools showed very high nitrate concentration over the whole time period and had eutrophic to polytrophic conditions.

Ammonium analyses

The measured ammonium concentrations in the year 2002 were in the range of the error tolerance of the multi sensor YSI 6600 (eco-Tech, 2002). Therefore, these measurements could not be used for interpretations. In 2003 we used a different analysing method, described before.

Ammonium concentrations within the pools occurred between 0mg/l and 3.9mg/l. According to the LAWA standard (LAWA 1999) this are concentrations between oligotrophic and hypertrophic conditions. On average the ammonium concentrations were 0.28mg/l. That indicates mesotrophic conditions for small infield pools. Differences in ammonium concentration within single pools occurred between 0.26mg/l and 3.7mg/l, indicating that small infield pools are temporary very variable in their ammonium concentrations over a single vegetation period. Among the vegetation period a slightly trend of rising ammonium concentration could be visible if the average over the pools will be used for such investigation (see fig B06-2).

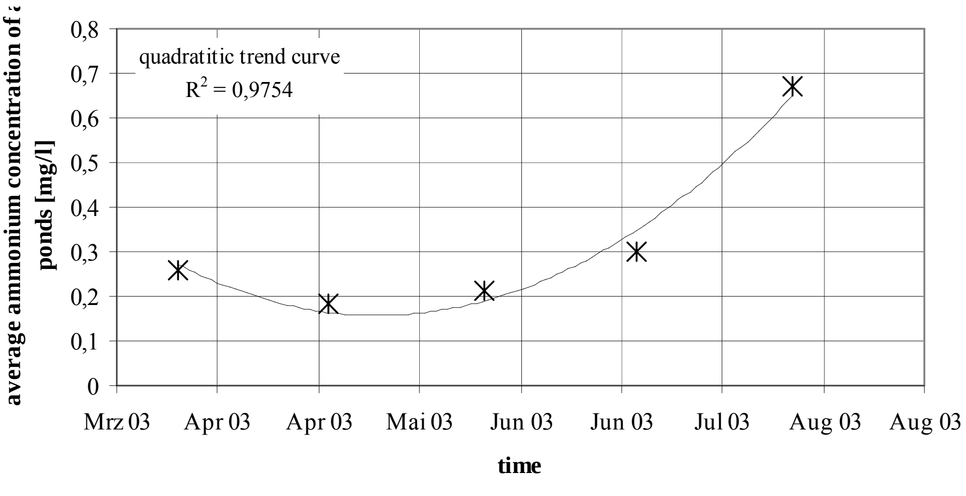


Fig B06-2: Average ammonium concentration over all pools to different times in the year 2003. With lower water level ammonium concentration may rise.

Storage effects

This effect was seen for some of the small infield pools but not for all. Therefore, drying up processes or rising water temperature might raise the ammonium concentration. But in particular, for some pools other effect may have impacts to the pool water ammonium concentration as well. Compared to the nitrate concentrations ammonium concentrations are less in the pool water than nitrate concentration. We had 4 pools with very low ammonium concentrations. Mesotrophic conditions were found in 27 pools. Therefore, more than 70% of the investigated pools had low ammonium contaminations. Nine pools had higher ammonium contaminations and tend to be in a eutrophic nutrition level. Only two pools reached the politrophic water contamination stage. For the other 3 pools the data base was too small for interpretations.

Phosphorus

The phosphorus concentrations were measured only during the vegetation period 2003. We observed values between 0mg/l and 6 mg/l. According to LAWA (1999) the maximum mentioned value for trophic levels is 1.2mg/l. So we measured values up to five times higher than phosphorus concentration occurring in polytrophic water bodies. In average the measurements show phosphorus concentrations of 0.61mg/l. That indicates high phosphorus concentrations and very high eutrophic conditions. For all pools lowest phosphorus values were measured in April with around 0.2mg/l indicating higher contaminations between mesotrophic and eutrophic level (see fig. B06-3). The highest contaminations were observed in July 2003. In average the pools showed polytrophic conditions (see fig. B06-3). Differences in phosphorus concentrations within a pool occurred between almost no variability and very high variability in phosphorus concentration with up to 5.9mg/l differences. The measurements showed, that the phosphorus strain in small infield pools vary spatial as well as temporary in a very strong way. Pool water quality can change from mesotrophic level to polytrophic conditions within a vegetation period. We examined two oligotrophic and two polytrophic pools in the study area. Six small infield pools had nearly polytrophic conditions in average. Eight pools had nearly mesotrophic conditions. Therefore, 40% of the pools had extreme water quality levels either extreme high contaminations or extreme low phosphorus concentrations. We investigated 8 pools with mesotrophic phosphorus water quality and 16 pools with eutrophic water quality level. For the remaining pools the data base for too small for interpretations.

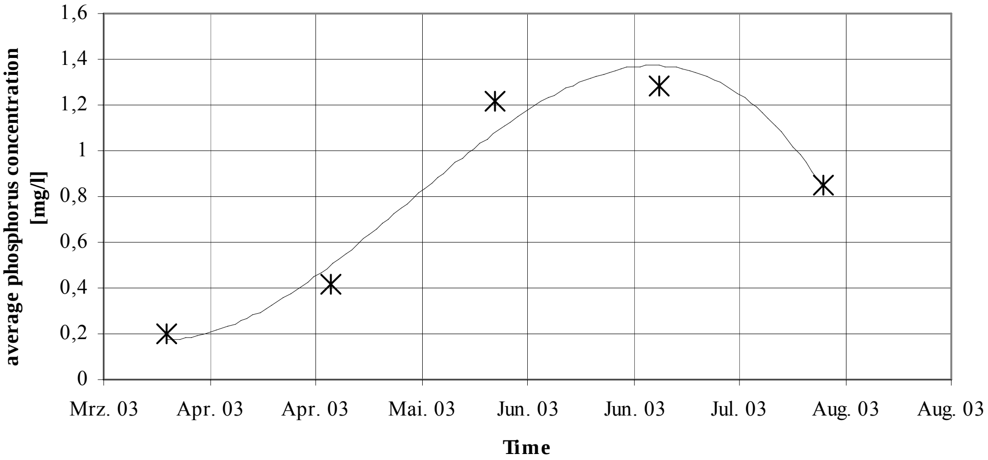


Figure B06-3: Average phosphorus concentration of pools water between April 2003 and August 2003

Storage effects

pH-value

PH-values were measured in a range between 5.2 and 9.1. Differences within pools occurred between 0.2 and 3.2 over the years 2002 and 2003. In 2003 pH-values were higher than in 2002 but no trend could be found (see fig. B06-4).

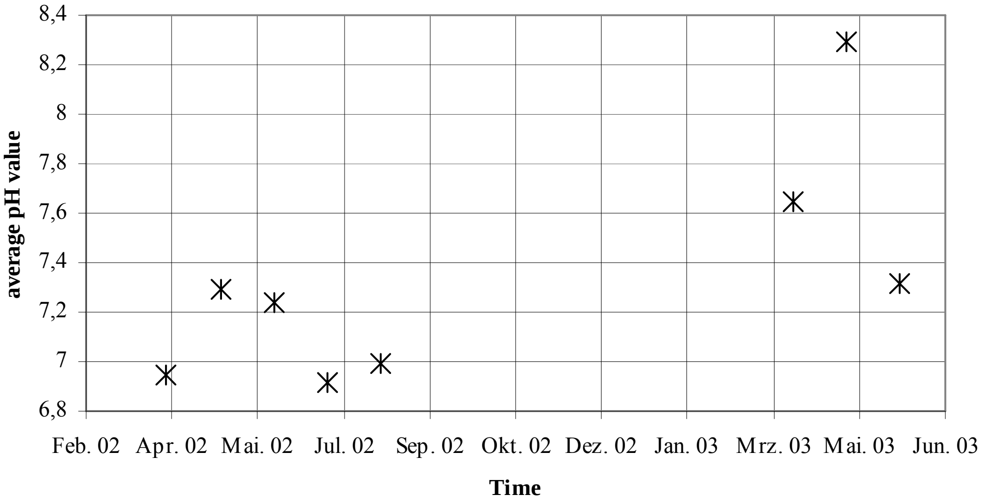


Figure B06-4: Mean pH-values of pool water in the study area. In the drier year 2002 pH values are higher than in 2002.

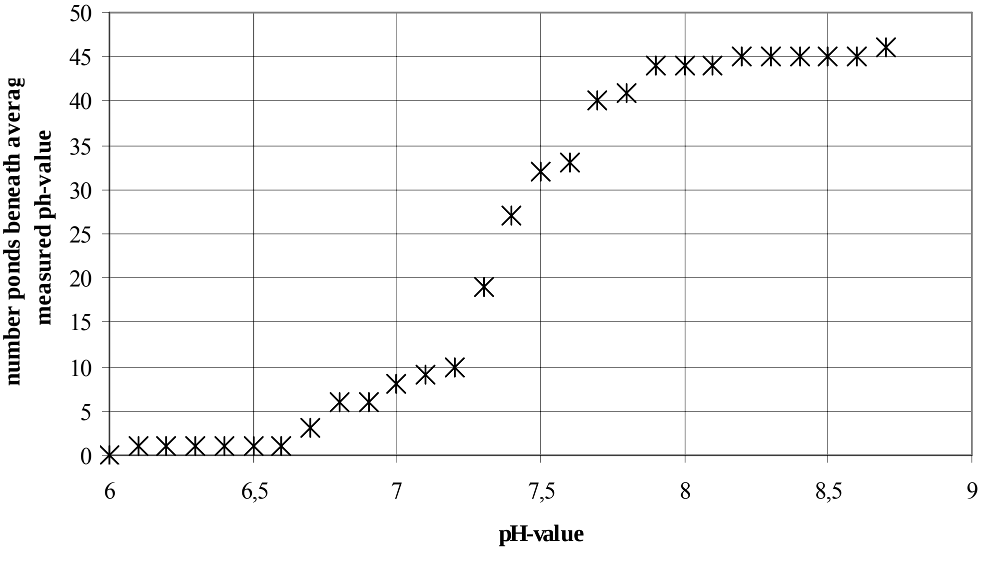


Figure B06-5: Number of pools beneath a certain pH-value. Recognise there is one pool with average pH-value of 6.1 and one with average ph-value of 8.7.

In general, the mean pH-value of the pools is around 7.5. But there are a few pools with lower or higher mean ph-values respectively (see fig.B06-5).

For all measurement, relationships between nutrient concentrations or pH-value to the bed material of the pools could not be found. We expected lowest concentrations of phosphorus and nitrate in the real kettle holes in the southern part of the study area and highest pH-values on the marl hills of the terminal moraine. But always, there are some pools which do not met our expectations. Therefore, we conclude that the impact of agricultural treatment of the catchment area has higher effects on water chemistry conditions than the surrounding bed material and climate.

Box 07: Soil investigation

Intensive soil investigations clarified our expectation of very inhomogeneous soil layers according to the geological map (LUNG 2005). Layers of sandy soils with different grain size and sorting underlie marl layers. The structure of the sandy C-horizons varies between very homogeneous fine sand (grain size 0.06 -0.2 mm) and pepple reach coarse grit (grain size up to 2mm, see fig. B07-1).

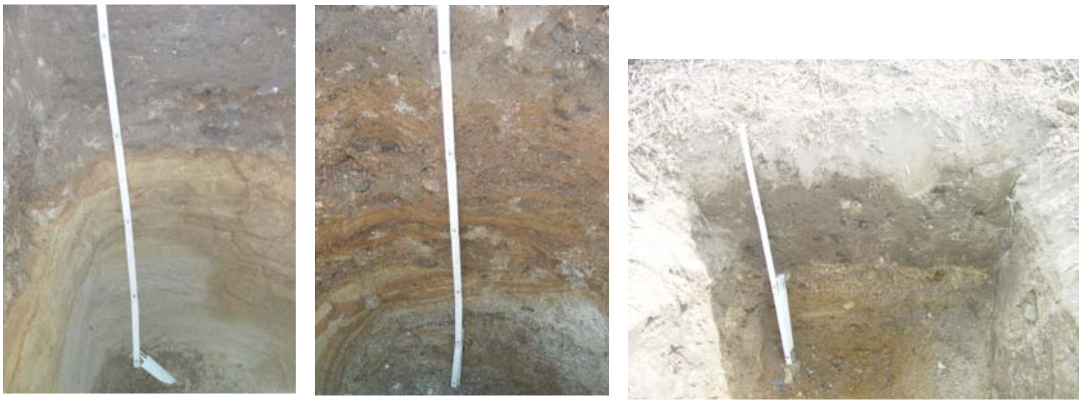


Figure B07-1: Soils with different bed materials. From left to right: very fine grained sandy C- horizon (profile saag2), coarse grit with high amount of pebbles of different sizes and shapes (profiel434421), sandy soil over a dense bedded pebble layer (profile 31322).

Local clay layers with very great values of the soil density and high water impermeability in deeper soil layer are the results of dense soil layers and leaching of the upper soil layers, resulting in a formation of luvisols over planosols (see fig B07-2).

Figure B07-2: Luvisols over planosols from left to right in the sandure region (profile 2221), in the moraine region (38a392), and cambisol over planosol in the sandure region (profile 282).

The soil density varies between 1.41 g per cm^3 and 1.88 g per cm^3. In the moraine area the soil type cambisol (see figure B07-3) has a higher density as the soil type luvisol (see figure B07-4) in the sandure region. This coincides well with the relationship of sediment fraction and soil density. As higher the proportion of coarse sand as lower is the soil density.

Figure B07-3: cambisols in moraine and sandure regions; the profiles are from left to right: profile 31322, 12132, and 2922.

Figure B07-4: luvisols in the sandure region and in moraine areas with low altitude levels. The profiles are from left to right: profile sand3, sand2, and 35361.

The concentration of pebbles in the soil varies between less than 1% to almost more than 80%. Soil layers with high pebbles fraction were found in more than 1m soil depth and very spatial. Due to the great pebble concentrations, the soil density could not be measured.

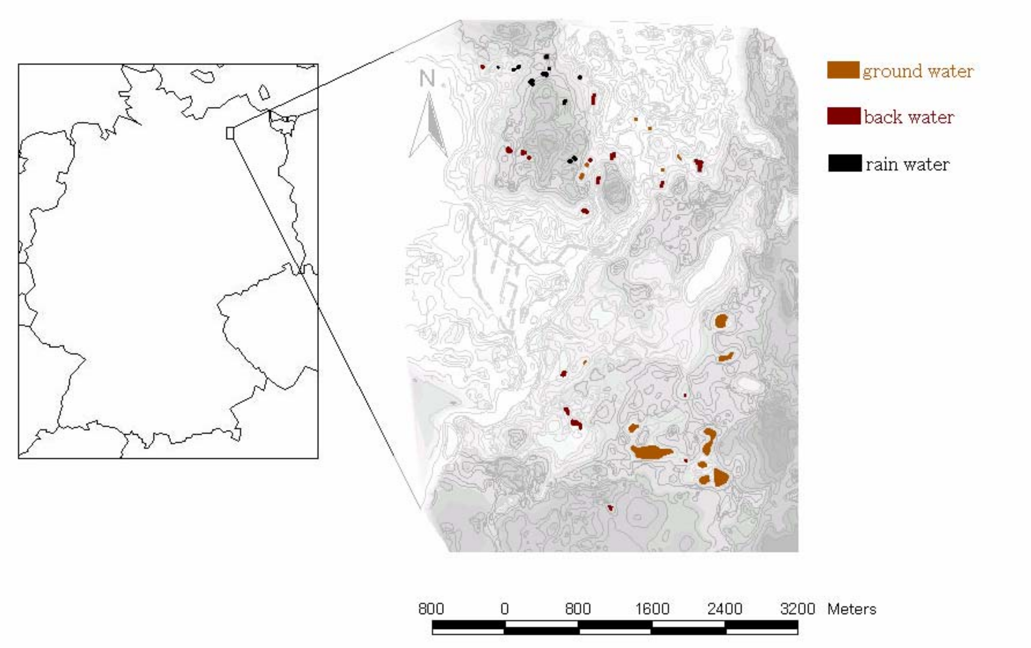
The calcium carbonate concentrations varied between zero and almost 18 volume percent. Highest carbonate concentrations occurred in C horizons, followed B horizons. The Ap-horizons had the lowest carbonate concentrations. This is a typical result of leaching processes. As expected, colluvisols and gleysols (fig. B07-5) next to the small infield pools did not contain any carbonate concentrations. Highest carbonate concentrations were measured mainly in loamy sediments.

Figure B07-5: colluvisols and gleysols next to small infield pools or in the channel; from left to right: profile 321, 181, 171, 04052.

The soil compactness and the soil material are an index for the water permeability which could be estimated according to the KA4 (Boden 1996). The kf-values differ between 7cm per day to more than 650cm per day. As expected, higher values are found in sandy soils. Very low values are found in loamy soil of the terminal moraine. Due to their geographical distribution, and due to the soil investigation, the pools could be related to the morphological bed material. Top soils on higher altitudes in the sandure region are similar to the moraine soil sediments but with less calcium carbonate content. Soils on lower altitude in the sandure and in the channel contain a higher amount of sand fractions. Andy soil layers in the channel region were strongly grain size sorted.

We expected the hydrology of pools in the moraine landscape to be more variable than in the sandure region or channel. There, the pools are mainly feed by ground water. The real catchment area of pools in the moraine landscape can vary among pools and time. Spring tail water and different sediment layers with different water permeability can influence the hydrology of these pools. I grouped the pools according the Hydrogeological map (LUNG 1987) and the soil investigation into groundwater influenced pools in the sandure and channel region, tail water influenced pools in depression zones, and rain water filled pools on hill sides (figure B07-6).

The pools are marked on the map with different colours. The figure B07-7 shows the dependency between spring water level and drying up frequencies of pools. The allocation to certain bed materials, situation in the landscape and distance to the ground water layer allowed to group the pools according to their hydrological connection to the landscape. Table B07-1 shows the main soil profile properties.



FigureB07-6: Pools with associated hydrological impacts. Orange marked pools are ground water influenced, red marked pools are mainly tail water influenced, and black marked pools are mainly rain water filled.

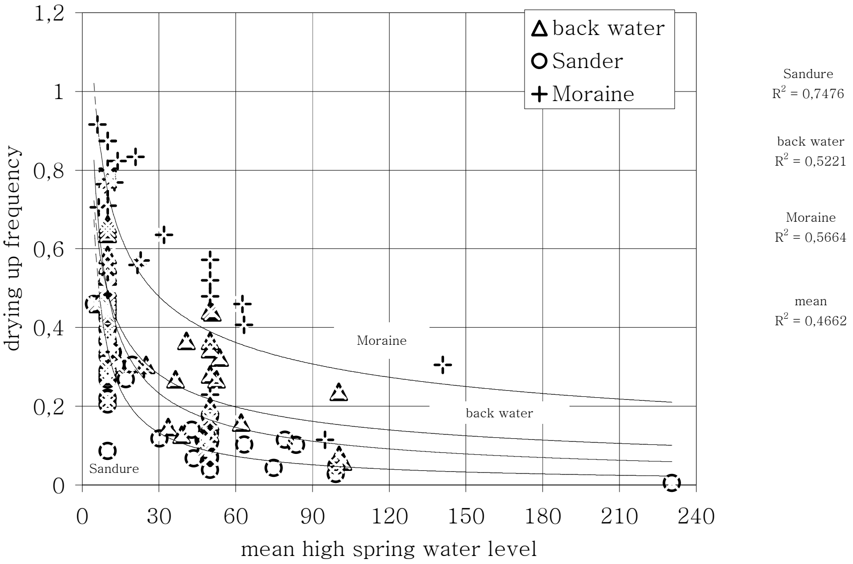


Figure B07-7: Relation between mean spring high water level and drying up frequency according to hydrological impact on the pools.

Table B07-1: Main soil profile properties.

name	soil density [g/m^3]	pH Water	$CaCO_2$ [Vol%]	Stone content %	Layer thick ness	Sedi ments	kF cm/d
04052 Ap	1.71	8.00	10.88	2	36	St3	17.00
04052 B	1.61	8.10	15.24	2	14	St3	17.00
04052 Bs	1.41	7.80	13.74	2	7	St3	>17
04052 C	1.78	8.20	17.37	2	33	Sl2	49.00
041 ApI	1.61	7.80	0.46	2	27	St3	17.00
041 ApII	1.76	7.60	0.31	2	8	St3	17.00
041 ApIII	1.70	7.40	–	2	45	St3	17.00
041 C	flooded			2	40	mS	427.00
051 Ap	1.76	6.90	–	5	37	Ls3	7.00
051 B	1.66	7.50	–	1	33	Lt2	9.00
0608-11 Ap	1.68	8.20	5.06	2	28	Sl2	49.00
0608-11 B	1.58	7.50	7.21	10	12	Sl2	109.00
0608-11 C	1.72	8.00	15.79	2	80	Sl2	49.00
061 Ap	1.70	7.90	1.23	2	45	Sl2	49.00
061 M	1.67	7.70	–	2	35	Ls3	7.00
062 Ap	1.87	8.30	–	5	32	Sl3	15.00
062 B	1.71	7.80	–	5	22	Slu	11.00
062 C	1.69	8.40	11.69	5	29	Sl2	49.00
0811 Ap	1.65	7.30	–	2	37	Sl3	33.00
0811 MI	1.56	7.80	–	2	43	fS	172.00
0811 MII	1.56	7.40	–	2	40	fS	172.00
12132 Ap	1.58	7.80	0.27	2	46	Sl2	109.00
12132 BI	1.60	8.50	11.19	2	34	Sl3	33.00
12132 BII	1.66	8.40	12.57	2	40	Sl3	33.00
12133 Ap	1.72	6.90	–	2	30	Sl3	33.00
12133 B	1.72	7.30	–	2	30	Sl3	33.00
1213F Ap	1.78	6.70	–	2	30	Ls4	14.00
1213F BI	1.77	7.80	–	10	25	Ls3	7.00
1213F BII	1.65	7.30	–	10	65	Ls3	7.00
141 ApI	1.56	6.20	–	2	18	Ls2	20.00
141 ApII	1.65	6.40	–	2	10	Sl2	49.00
141 MI	1.65	6.40	–	2	72	Ls2	20.00
14162 Ap	1.55	7.50	–	2	33	Ls3	13.00
14162 BI	1.61			5	13	Ls2	20.00
14162 BII	1.67	6.50		10	34	Sl2	49.00
14162 C	gravel			90	40	gSms	281.00
151 ApI	1.62	6.00	–	2	36	Sl3	33.00
151 MI	1.63	6.20	–	5	48	Sl3	33.00
151 MII	1.52	6.00	–	5	36	St3	>17
15162 ApI	1.54	6.10	–	2	24	Sl3	47.00
15162 ApII	1.62	6.10	–	2	10	Ls2	20.00
15162 MI	1.66	6.20	–	5	32	Ls2	20.00
15162 MII	1.74	6.80	–	5	54	Ls2	20.00
161 ApI	1.51	5.70	–	5	29	Su2	157.00
161 ApII	1.60	5.20	–	5	15	Su2	88.00
161 MI	1.60	6.60	–	10	16	Su2	88.00
161 MII	Cstones	6.70	–	90	20	gSms	281.00
171 Ap	1.56	7.60	–	5	34	Sl3	47.00
171 B	1.73	8.00	–	5	36	Sl2	49.00
171 M	1.60	7.20	–	5	30	Sl3	33.00
172 Ap	1.58	7.40	0.37	2	38	Sl3	47.00
172 B	1.57	8.10	0.63	2	22	Slu	41.00
172 C	1.67	8.00	11.03	2	30	Sl2	49.00
181 Ap	1.58	6.90	–	5	36	mS	653.00
181 B	1.72	7.40	–	5	22	mS	427.00
181 C	1.74	8.30	–	2	27	Lt2	9.00
191 Ap	1.64	6.80	–	5	39	mS	427.00
191 B	1.71	7.20	–	5	25	Sl2	49.00
191 M	1.54	6.50	–	5	26	mS	653.00

name	soil density [g/m^3]	pH Water	CaCO$_2$ [Vol%]	Stone content %	Layer thick ness	Sedi ments	kF cm/d
2221 Ap	1.51	6.20	–	5	26	fS	172.00
2221 B	1.64	6.50	–	5	10	ffS	106.00
2221 Bh	1.67	6.30	–	5	14	ffS	106.00
2221 Sles	1.52	6.60	–	0	30	gSfs	369.00
2221 Sw	1.64	7.00	–	5	40	Ut4	9.00
2222 Ap	1.65	6.30	–	8	30	mS	427.00
2222 B	1.71	7.20	–	0	30	gsfs	130.00
2222 Sw	1.72	6.60	–	5	60	Su3	32.00
281 ApI	1.67	6.10	–	2	32	Sl3	33.00
281 ApII	plowsole	6.10		0	2	Sl3	15.00
281 BI	1.78	7.20	–	5	66	Sl2	49.00
282 ApI	1.53	7.10	–	10	21	Sl2	109.00
282 BI1	1.70	8.00	–	5	39	Sl2	49.00
282 BI2	1.60	6.40	–	5	20	Su3	32.00
282 BII	1.67	7.60	–	5	40	Su3	32.00
2911 Ap	1.67	6.10	–	20	39	Su3	32.00
2911 Sd1	1.66	6.40	–	5	36	Ut3	8.00
2911 Sd2	1.61	6.50	–	5	20	Slu	11.00
2911 Sw	1.65	8.00	–	10	25	Su3	32.00
2921 Ap	1.77	7.50	–	5	30	Su2	88.00
2921 Sd	1.80	7.70	11.22	5	50	Su2	36.00
2921 Sw	1.65	6.70	0.19	0	40	Su2	88.00
2922 Ap	1.76	6.20	–	30	39	Su2	88.00
2922 SwI	1.69	7.70	–	30	31	Us	10.00
2922 SwII	1.68	7.70	–	20	50	Ls3	7.00
2923 Ap	1.81	7.40	4.99	10	20	Su2	36.00
2923 Sw1	1.69	7.40	0.31	5	55	Us	10.00
2923 Sw2	1.88	7.70	10.77	2	35	Su3	17.00
301 ApI	1.47	6.30	–	5	13	mS	653.00
301 ApII	1.51	6.50	–	10	17	Sl2	109.00
301 ApIII	plowsole	6.30	–	0	4	Sl2	36.00
301 BI	1.55	6.50	–	5	10	mSgs	581.00
301 BII	1.68	6.10	–	5	16	Sl3	33.00
301 BIII	1.65	7.70	–	5	60	Ls3	7.00
302 ApI	1.66	6.10	–	5	9	Sl2	49.00
302 ApII	1.60	6.40	–	2	21	Sl2	49.00
302 ApIII	plowsole	7.20	–	0	7	Sl2	36.00
302 BI	Cstones	7.00	–	10	43	Sl3	15.00
302 BII	1.73	8.30	12.09	10	40	mS	427.00
311 Ap	1.66	7.30	–	2	42	mS	427.00
311 BI	1.74	7.80	–	2	24	fS	106.00
311 B_o	1.72	8.20	0.14	2	54	Ls3	7.00
31322 Ap	1.46	7.10	0.99	10	37	mS	653.00
31322C	Cstones	7.70	11.05	80	23	gS	130.00
321 Ap	1.52	7.20	–	2	40	fS	172.00
321 BI	1.70	7.40	–	2	21	Sl2	49.00
321 M	1.62	7.50	–	2	29	Sl2	49.00
321B_o	1.58	8.30	–	2	30	Sl2	109.00
322 Ap	1.80	7.20	–	2	30	mS	400.00
322 BI	1.76	7.30	–	2	25	Ls4	14.00
322 BII	1.52	8.10	–	2	42	fS	172.00
322 C	1.64	8.20	17.10	2	20	Lt3	10.00
322 M	1.71	7.90	–	2	23	Ls3	7.00
32F Ap	1.73	7.40	–	2	32	mS	427.00
32F BI	1.69	7.90	–	2	22	mS	427.00
32F BII	1.63	8.20	13.82	2	46	Sl2	49.00
32F M	1.68	7.40	–	2	20	Ls4	14.00
331 ApI	1.50	6.70	–	5	30	Sl3	47.00
331 ApII	1.58	6.20	–	0	9	Sl3	47.00
331 MI	1.54	6.30	–	2	11	Sl3	47.00

name	soil density [g/m^3]	pH Water	CaCO$_2$ [Vol%]	Stone content %	Layer thickness	Sediments	kF cm/d
331 MII	1.61	6.50	-	5	20	mS	427.00
331 MIII	1.66	6.50	-	5	50	mS	427.00
34352 Ap	1.63	7.60	3.03	5	27	mS	427.00
34352B	1.67	8.30	16.77	5	61	Ls3	7.00
34352Bg	Cstones	8.20	12.29	60	12	gS	130.00
35361 Ap	1.68	7.40	1.52	1	27	mS	427.00
35361 CI	1.56	8.10	4.79	1	28	fS	172.00
35361 CII	1.80	8.20	9.00	1	55	Su4	20.00
35-372 Ap	1.63	6.80	-	2	30	fS	106.00
35-372 B	1.75	7.10	-	2	70	St3	17.00
371 ApI	1.59	6.50	-	2	30	fS	172.00
371 ApII	1.63	7.30	-	2	14	fS	106.00
371 MI	1.65		-	2	26	fS	106.00
371 MII	1.65	6.70	-	2	30	fS	106.00
372 ApI	1.72			5	26	Sl2	49.00
372 BI	1.64	6.10	-	5	29	fS	106.00
372 CI	1.62	6.60	-	2	45	St3	17.00
372 CII	1.64	6.10	-	1	40	Lt3	10.00
37382 ApI	1.49	5.80	-	2	34	mS	653.00
37382 BI	1.68	6.50	-	5	22	Sl3	33.00
37382 CI	1.71	7.20	-	2	34	Sl3	33.00
381 Ap	1.58	6.30	-	2	37	mS	653.00
381 MI	1.67	6.30	-	2	43	mS	427.00
381 MII	1.51	6.50	-	2	50	Sl2	109.00
38a392 Ap	1.45	6.70	-	2	34	mS	653.00
38a392 B	1.54	7.00	-	2	19	Sl2	109.00
38a392 CI	1.66	7.10	-	2	27	Sl3	33.00
38a392 CII	1.70	7.30	-	2	50	Ls3	7.00
38a392 CIII		too deep		2	70	fS	106.00
391 Ap	1.54	7.10	-	10	34	fS	172.00
391 M	1.66	7.20	-	5	86	fS	106.00
4321 Ap	1.58	7.30	-	30	35	Su2	157.00
4321 B	1.76	7.50	-	50	25	Su3	32.00
4321 C	1.41	7.20	10.24	30	100	gS	369.00
4321 Sw	1.64	6.20	-	10	40	Su3	32.00
4322 Ap	Cstones	7.40	-	30	30	Su2	88.00
4322 B	Cstones	7.70	-	50	30	Su3	32.00
4322 C	Cstones	7.40	9.56	50	60	Ss	126.00
434421 Ap	Cstones	7.00	0.18	30	26	Su3	32.00
434421 B	Cstones	6.10	-	50	24	Su2	88.00
434421 C	1.62	7.30	8.30	30	30	gS	130.00
434421 Sd1	1.61	6.60	-	5	5	mS	427.00
434421 Sd2	Cstones	6.50	-	30	19	Su2	88.00
434421 Sd3a	1.58	6.10	-	5	16	fS	172.00
434421 Sd3b	1.58	6.70	-	5	16	fS	172.00
4422 Ap	Cstones	7.10	1.63	20	27	Su3	32.00
4422 B	Cstones	7.00	-	40	23	gS	130.00
4422 C	1.79	7.30	12.12	2	30	Su2	88.00
4422 Sd	Cstones	7.60	0.24	20	40	Sl3	15.00
Saag1 Ap	1.53	7.10	0.16	10	29	Su3	75.00
Saag1 B	1.73	7.30	-	5	16	mS	427.00
Saag1 C	1.61	7.20	6.32	5	10	gS	130.00
Saag1 Sd	1.78	7.60	17.78	20	47	Sl3	33.00
Saag1 Sw	1.67	7.30	-	15	28	Sl3	33.00
Saag2 ApI	Cstones	6.20	-	20	30	Su3	32.00
Saag2 ApII	Cstones	6.20	-	80	15	Su3	17.00
Saag2 Sd	1.47	7.20	6.56	0	40	Ss	349.00
Saag2 Sw	1.58	8.00	-	0	35	Ss	349.00
Sand1 Ap	1.67	7.40	-	10	27	mSgs	281.00

name	soil density [g/m^3]	pH Water	$CaCO_2$ [Vol%]	Stone content %	Layer thick ness	Sedi ments	kF cm/d
Sand1 C	1.66	7.80	–	30	28	mS	427.00
Sand1 Sw	1.73	7.30	6.95	5	45	mSgs	281.00
Sand2 Ap	1.60	6.50	–	15	30	Su3	32.00
Sand2 B	1.71	7.10	–	15	9	Su4	24.00
Sand2 Sles	1.67	7.10	–	10	26	Su2	88.00
Sand2 Sw	Cstones	8.00	10.00	10	35	Su3	32.00
Sand3 Ap	1.52	7.80	–	8	34	Su3	75.00
Sand3 B	1.56	6.50	–	8	30	mS	653.00
Sand3 C	sampling not possible			0	20	s	Su4
Sand3 Sd	Cstones	7.30	9.66	0	23	Su3	32.00
Sand3 Sw	1.53	6.70	–	0	23	Su3	75.00

Chapter 6:

Plant functional responses to hydrological characteristics of small infield pools

Running title: 'PFG response to hydrological parameters'

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Abstract

Small infield pools are hot spots for species diversity in farmed pleistocene landscapes. Previous studies relating vegetation to environmental conditions of pools have largely ignored the inherent hydrological dynamics of these systems.

To understand the functional response of plants to the dynamic water regime of pools, we divided wetland species into plant functional groups (PFG) and calculated the response of each group to spring water depth and the drying up frequency of the pools. These two hydrological parameters describe both water depth and water dynamics. A novel non-subjective method is presented for grouping wetland plants according to functional trait attributes in such an environment. We use a null model approach based on the fourth-corner-method to calculate the response of plant groups to the hydrological conditions, as well as the preferred site conditions for each PFG. Twenty-four traits were analysed, of which the traits of life cycle, aerenchym, canopy height, turions, floating mats and floating leafs, tussock growth, biomass and height mass ratio were used to identify 10 plant functional groups. These plant functional groups contain all 80 species that were recorded in the 46 pools of an intensely-used agricultural landscape in North-East-Germany.

The resulting PFGs are characterised by different environmental adaptive and competitive strategies to survive in small infield pools. PFGs with surviving strategies were mainly found in sites that had strong shifts between aquatic and terrestrial conditions, whereas PFGs with strong competitive strategies occurred in the more stable environments. Competition is mainly seen in pools on light and well-oxygenated soils. In sites of high aquatic stress species survive by evolving aquatic adapted traits. PFGs with storage traits, like high root investments or high seed production rates, occurred more frequently on sites with high disturbance rates due to large changes in water level.

Keywords: plant, functional groups, fourth-corner method, kettle hole, vernal pool, small infield pools, ponds, trait hierarchy

Introduction

Small infield pools or vernal pools (Burne and Griffin, 2005) are widely distributed and numerous in pleistocene moraine landscapes (Klafs and Lippert 2000), influencing both species diversity (Williams et al. 2004) and the local hydrology (Kalettka 1996). In intensively farmed landscapes they often represent the only hospitable habitat for a wide range of wetland species (Opdam et al. 1990). As hydroperiods of pools are very variable in time and space (Lehsten et al. 2008), these habitats form a dynamic and naturally fragmented landscape for wetland species. In many parts of the world, the number of small infield pools has significantly declined in the last century (Moller and Rordam 1985, Johnston 1994, Shimoda 1997a, Klafs and Lippert 2000, Beja and Alcazar 2003, Wood et al. 2003) and is still declining worldwide (Mouser et al 2005). A decrease in pool density (i.e. number of pools per area) decreases the total habitat size and connectivity between them, thus imposing a higher extinction risk on local populations (Moller and Rordam 1985, Dodd 1990, Sjogren 1991).

Although the general relationships between vegetation and water level or nutrient status of pools have been frequently studied (see Wheeler and Proctor 2000), little can be found concerning the response of species and their traits to the dynamics of water table change or drying-up events (see Pyke 2004). Life cycle, reproductive success, degree of morphological plasticity and germination (timing and success), were found to be altered by flooding events or water level variations (Keddy and Reznicek 1986, Brock et al. 1987, Kellogg et al. 2003, Blom and Voeseneck 1996, Keddy and Constabel 1986, Bliss and Zedler 1998). These morphological traits have been shown to define established-phase plant strategies for a range of species (Grime 1974).

Although traits such as specific leaf area (SLA), canopy height, biomass, or root mass ratio might be expected to contribute to competitive survival (Hodgson et al. 1999), they have rarely been used in studies of PFGs in wetland habitats.

Here, we assume that the pool habitat quality, including its dynamics, causes an adaptive selection of both plant life history strategies and measurable traits, which contribute to increased competitive advantage and result in specific combinations of trait expressions in pool plant communities. Combinations of trait expressions can be classified into functional groups, i.e. non-phylogenetic classifications based on traits leading to a grouping of organisms that respond in similar ways to multiple environmental factors (Gitay & Noble 1997).

Classification approaches for plant species range from deductive to inductive. The latter may be divided into unsupervised (by clustering of species-trait matrixes) and supervised classification, with a pre-selection of traits which are believed to be responsible for a pattern of species occurring on an environmental gradient. Unsupervised classification is highly dependent on input data and ignores the response of species to environmental gradients (Nygaard and Ejrnaes 2004). Supervised classification is manifested in the fourth-corner-problem (Legendre et al. 1997a). It considers the species response to environmental gradients (Nygaard and Ejrnaes 2004). The response can be tested with null models. Two of the published models are the lottery model (Sale 1982) and the environmental control model by Whittaker (1956). The lottery model (Sale 1982) can be used to test whether the occurrences of species or species groups within a certain site are randomly. It assumes a competition-free community assembly. If it can be rejected, this is evidence of competition. The environmental control model (Whittaker 1956) tests whether certain species or species groups occur preferably at certain habitat conditions.

To date, data-defined objective approaches that classify aquatic macrophytes in plant functional groups, have been poorly applied (Willby et al. 2000). The species are mostly grouped a priori according to morphological traits like growth form (Du Rietz 1931) and life form (Raunkiaer et al. 1934) similar to terrestrial plant species grouping (see Kautsky 1988, Rorslett 1989, Murphy et al. 1990, Boutin and Keddy 1993, Ellison and Bedford 1995, McJannet et al. 1995, Weiher et al. 1998, Garcia-Mora et al. 1999, Tabacchi and Tabacchi 2001, Nygaard and Ejrnaes 2004, Houlahan et al. 2006, Bouchard et al. 2007).

For example, Nygaard and Ejrnaes (2004) clustered 530 wetland species according to their environmental response with the same approach as Lavorel et al. (1997). They defined four plant functional groups out of them. These types were used to predict responses to greenhouse environments. Their results show, that predefined PFGs are inappropriate to predict responses of species frequencies to environmental conditions. PFGs are useful only within the environmental properties in which they are determined. Changes in the environment can lead to different traits being functional.

Data-driven approaches to classify wetland plants according to trait similarity were used by Willby et al. (2000) and Xiong et al. (2001). While the first study clustered 120 aquatic macrophytes in 20 plant functional groups, the second study groups the response of single traits over the gradient of litter and silt accumulation. Willby et al. (2000) showed the distribution of the 20 PFGs in relation to environmental conditions, but they did not give the characteristics of each group.

In this study we use the extended fourth-corner-method (Lehsten et al. in press) with a further extension to involve as many traits as are measurable. It is a data based approach which allows us to form plant functional groups of wetland species based on their response to habitat dynamics within small infield pools and their trait similarities. We treated morphological and measurable traits in the same way. Our novel method allows us to group a large number of species non-subjectively. The occurrence distribution of the generated PFGs over the site condition and habitat dynamic can be related to trait attribute ranges belonging to the PFGs.

These generated PFGs will display different plant storage, adaptative and competitive strategies. Storage strategies show how species survive unsuitable environmental periods. Adaptative strategies are morphological characteristic specialised for the given environment, whereas competitive strategies are characterised by traits or trait-syndromes that give the species advantages in competition for resources.

In the context of warmer, longer and drier summer already present in the recorded climatic data and expected to continue for the research area (Christensen et al. 2007) the conditions of small infield pools are predicted to change. Our results can be used to predict the resulting changes of plant functional group distribution among the pools. With changes in the PFG distribution strategy distribution for competition, storage and adaptation will change as well. This allows us to examine potentially disappearing and potentially winning PFGs, using their characteristic competition, survival and storage strategies.

Methods

Study area

The study area is located in central Mecklenburg in the North-East of Germany on a glacial formed landscape (53°40'N and 12°10'E, Fig. A3-1). A total of 46 small infield pools were investigated in an area of 12 km². The study area comprises parts of a terminal moraine of the Pomeranian glacial phase in the north, which passes into the sandure region, followed by heath land in the south. A glacial outburst crosses part of the study area, from northeast to southwest.

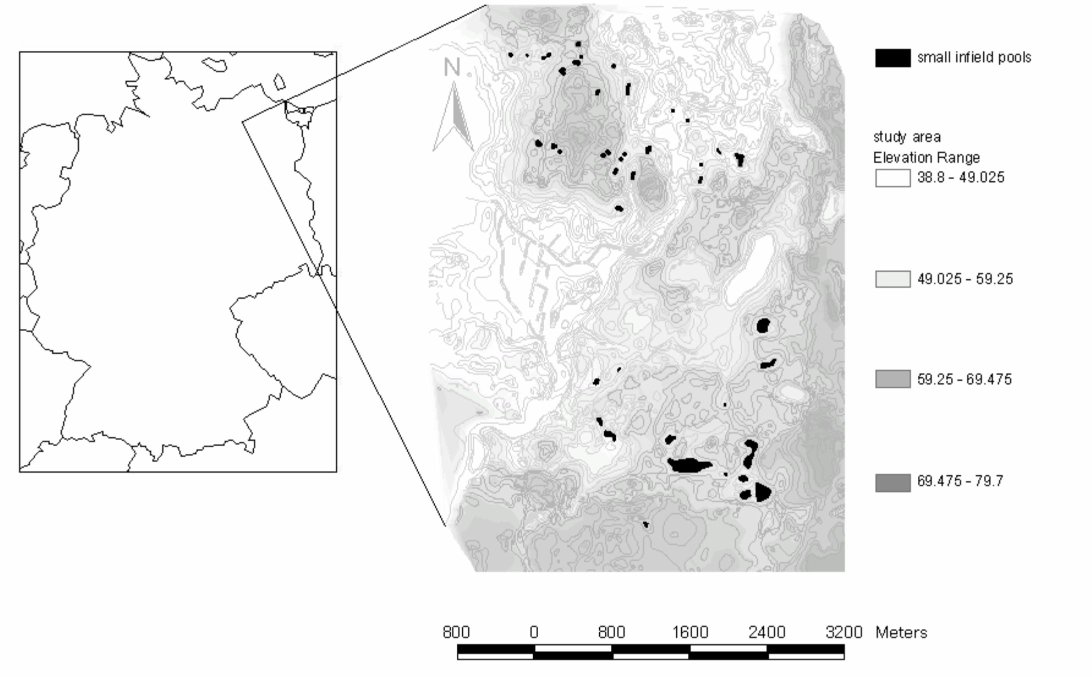


Figure A3-1: Map of the study area (53°40'N and 12°10'E) with the small infield pools investigated in this study. The small infield pools are marked in black.

Abiotic conditions

We used two hydrological parameters to quantify the dynamics of the pool water regime: the spring water table, which describes the water depth at the start of the season, and the drying-up frequency, which describes the frequency of change from aquatic to terrestrial conditions. The data were taken from Lehsten and Kleyer (in prep.). Each of the 46 small infield pools was subdivided into meso-sites according to spring water level and drying up frequencies. For instance, meso-sites close to the bank had a higher drying up frequency than sites near to the centre of the pool. Meso-sites are defined by mean spring water levels of less than 10cm, between 10cm and 50cm, and more than 50cm. Hence, each pool comprised up to three different sites. This results in a total of 101 meso-sites within all pools.

We measured the water chemistry (pH, O_2, Nitrate, Phosphate) in forehand. Their concentration distribution differed strongly over the measuring time period as well as among pools. Hence, significant differences among the pools could not be verified. For detailed information see Box 06.

Biotic measurements

Species inventory

Species composition was recorded every 4 weeks (presence / absence) during the vegetation periods of the years 2002 and 2003. For each species, we also recorded the water depth range of its occurrence in each pool. Since differences between total pool depth and species water depth are equal to differences between pool mean spring water level and the mean spring water level at which the species grows, the species-specific mean spring water level can be estimated for each species as follow:

$$SHW_{sp} = H_{xi} + H_{spxi} - SHW \qquad \text{(A3-1)}$$

SHW_{sp} is the mean spring water level of the place inhabited by species sp, H_{xi} is the total pool water depth in the year x at time i. H_{spxi} is the species-specific water depth in year x at time i. SHW is the pool mean spring water level. Negative values for SHW_{sp} indicate mean spring water below surface i.e. places that are on average not flooded in spring. Species within that zone were assigned to the low spring water level zone (section of the pool with mean spring water level less than 10cm). With this method the plant species observation per pool could be extended to plant species observation per meso-site.

The years 2002 and 2003 were unusually wet and dry respectively (see Lehsten in prep.). Therefore, plant distribution could be examined for both very high water spring water level, with long flooding season, and very low spring water level, representing mostly non-flooded conditions. This is important for annual plant species which may have persistent seed banks and are able to grow during short periods of suitable environmental conditions.

Trait measurements

Species traits were measured for all recorded non-woody species. If applicable, the traits were measured according to the LEDA standard (www.leda-traitbase.org, Kleyer et al. 2008). If possible, we choose 10 well-developed individuals of each species to measure the traits. The following traits were measured non-destructively in the field (see also table A3-1): canopy height (CH), releasing height (RH), start of flowering (SF) and end of flowering (EF), tussock growth form (TG), floating mats of species (FLmat), and the leaf morphological traits like floating / submerged leafs (LF), or leafs above water surface (LAWS). The following traits were retrieved from the literature: life cycle (LSC), presence of aerenchyms (AER) (Anonymous 2000) and turions (T) (Willby at el., 2000). Destructive measurements were taken to determine stem length beneath water surface (WSL), stem diameter at the stem ground (SD), spacer length (SPL), seed number, seed mass, rooting depth (RD), root dry mass, dry and fresh weight of leaves, dry mass and surface area of leaves, and dry mass of roots and the whole individual (BIO).

Table A3-1: names, descriptions, units, and acronyms of all investigated traits

Traits	Description	Unit	Acronym
aerenchyms	ability to evolve aerenchyms	categorical	AER
biomass	dry mass of whole plant	[g]	BIO
canopy height	maximum height of the highest leaf [cm]	[cm]	CH
tussock growth	Growing in tussocks	categorical	TG
start flowering	month of first appearing flower	categorical	SF
floating leafs	ability of leafs to float	categorical	LF
floating mat species	Ability of parts of the plants to float as mats on the water surface	categorical	FLmat
height mass ratio	canopy height divided by biomass	[cm/g]	HMR
end flowering	month of last appearing flower	categorical	EF
leaf dry matter content	dry leaf mass divided by fresh leaf mass	Ln[g/g]	LDMC
leafs above water surface	Ability of leafs to form tissue structure	categorical	LAWS

Traits	Description	Unit	Acronym
life span	annual (1), biannual (2) perenn (3)	categorical	LSC
releasing height	maximum height of seeds	[cm]	RH
reproductive effort	seed mass divided by whole plant dry mass	[g/g]	RE
root depth	depth of main root	[cm]	RD
root mass ratio	dry root mass divided by biomass	[g/g]	RMR
spacer length	spacer length	[cm]	SpL
specific leaf area	area leaf per mass dry leaf	[mm^2/mg]	SLA
specific root mass	root weight divided by root depth	[g/cm]	SRM
specific shoot mass	shoot mass divided canopy height	[g/cm]	SSM
stem diameter	stem diameter 2 cm above ground	[cm]	SD
submerged leafs	Ability for plant to evolve leafs beneath the water surface	categorical	LS
turions	ability to develop turions	categorical	T
water stem length	maximum stem length covered by water	[cm]	WSL

The stem length beneath the water surface was recorded at the first observation in the year, assuming this to be the deepest water level that the species could persist for. The individuals of the submerged plants were collected in June and July and the stem length beneath the water surface was measured as the total length of the individual water plant.

To measure the root traits, ten individuals were dug out and washed in the pool to remove most of the soil. The plant roots were washed carefully to remove soil particles and to separate the roots of the individuals. The washing process was repeated at least five times to ensure clean roots. Since the digging and the washing procedure may have caused some loss of fine roots, only the main roots were measured to determine root traits. Root depth is recorded as the total length of the roots after washing, when holding the plant upright. The shoots of the individuals were collected and cleaned as well. The dry weight was measured in the laboratory after drying at 60°C for 24 hours.

SLA values were calculated, by scanning the watered leaves and estimating the surface area with LAFOREM (Lehsten 2003). The leaves were also dried at 60°C for 24 hours before measuring the leaf dry weight. To measure the leaf dry matter content (LDMC), leafs were collected in the field, shrink-wrapped in plastic bags and deep frozen until further measurement in the laboratory.

Storage effects

The analysis also included the following ratios: reproductive effort (RE, ratio between the seed mass and total biomass), root mass ratio (RMR, root mass divided by total biomass), height mass ratio, (HMR, ratio between canopy height and biomass), specific root mass (SRM root mass divided by rooting depth) and the specific shoot mass (shoot mass divided by canopy height).

Statistics

Traits were discarded from further analysis when their correlation with another trait exceeded 0.5 (r-values; see Tab. 2). Traits with the highest number of correlated relationships to other traits (i.e. exceeding 0.5) were the first to be discarded from the list of traits. This process was iterated until there were no correlated pairs of traits left.

The remaining traits underwent a classification procedure which aimed to group species according to their traits in such a way that the resulting groups showed a significant response to the hydrological regime. Ideally the analysis would take into account all combinations of the remaining plant traits and search for the optimal response groups (see Lehsten et al. in press). However, given the large number of species (80) and uncorrelated traits (17) this method would require an unreasonable computational effort (testing all plant combinations would result in ca. $6*10^{23}$ tests). Therefore, we decided to perform a four step analysis to generate suitable plant functional types instead of searching for the optimal ones. The first step consisted of a single trait – environment relationship analysis. With the results of this single trait analysis we constructed a trait attribute range hierarchy, which is afterwards used to classify the species into PGs. The third step included the testing of the PG with the fourth corner method to proof their functionality and, if possible, to reduce the number of PGs. Finally, we calculated the PFG responses to the hydrological regime from the final set of PFGs. An explicit justification for our approach is given in Box 08. An overview of the method is given in figure A3-2.

Single trait analysis

In the single trait analysis PFGs were generated based on one trait only. This analysis is performed for each trait separately. In general, optimising PFGs involves three parts. First, for each trait a large number of classifications of plant groups were generated. Second, the response of each plant classification to the hydrological regime was tested using a null model. In a third step, an optimisation criterion was applied to choose the best classification.

Generating all possible plant group classifications in the first step was not feasible. Therefore, to generate a sufficient set of plant classifications it is necessary to limit the maximum number of plant groups per classification. We classified each continuous trait into three classes at most (this does not apply for categorical traits for which the full set of possible classifications was used). There are 3160 possibilities to group 80 species in up to three classes if only one trait is involved and each species has a different trait attribute. In the second step, the test of response was performed with an extension of the 'fourth-corner-method' using the 'lottery model' (Legendre et al. 1997b, Lehsten et al. in press) for each classification.

Finally, in the third step, the optimisation criterion selected that plant classification which had the highest average number of significant responses per PFG. A detailed description of testing the responsiveness of the classification and choosing the optimal classification as well as an evaluation of the statistical merits of the method is given in Lehsten et al. (in press). A program performing all three steps including several null models for different kinds of data and ecological questions can be obtained from the second author.

Trait attribute range hierarchy

The single trait analysis resulted in a functional classification for each trait with up to 3 attribute ranges (trait classes). We counted the number of species in each class. Over all traits and classes, the class which contains the highest number of species is regarded as the most important trait class in determining the occurrence of species. We constructed a trait class hierarchy by ordering all traits classes according to their contained species number.

Generating Plant types

As most plant species carry the trait attribute of the highest rank (by definition), this attribute is expected to have the highest functionality for species survival. Species which do not carry this trait evolved towards a different strategy. Hence, these species formed the first plant type which potentially differs in their survival strategy from all other species.

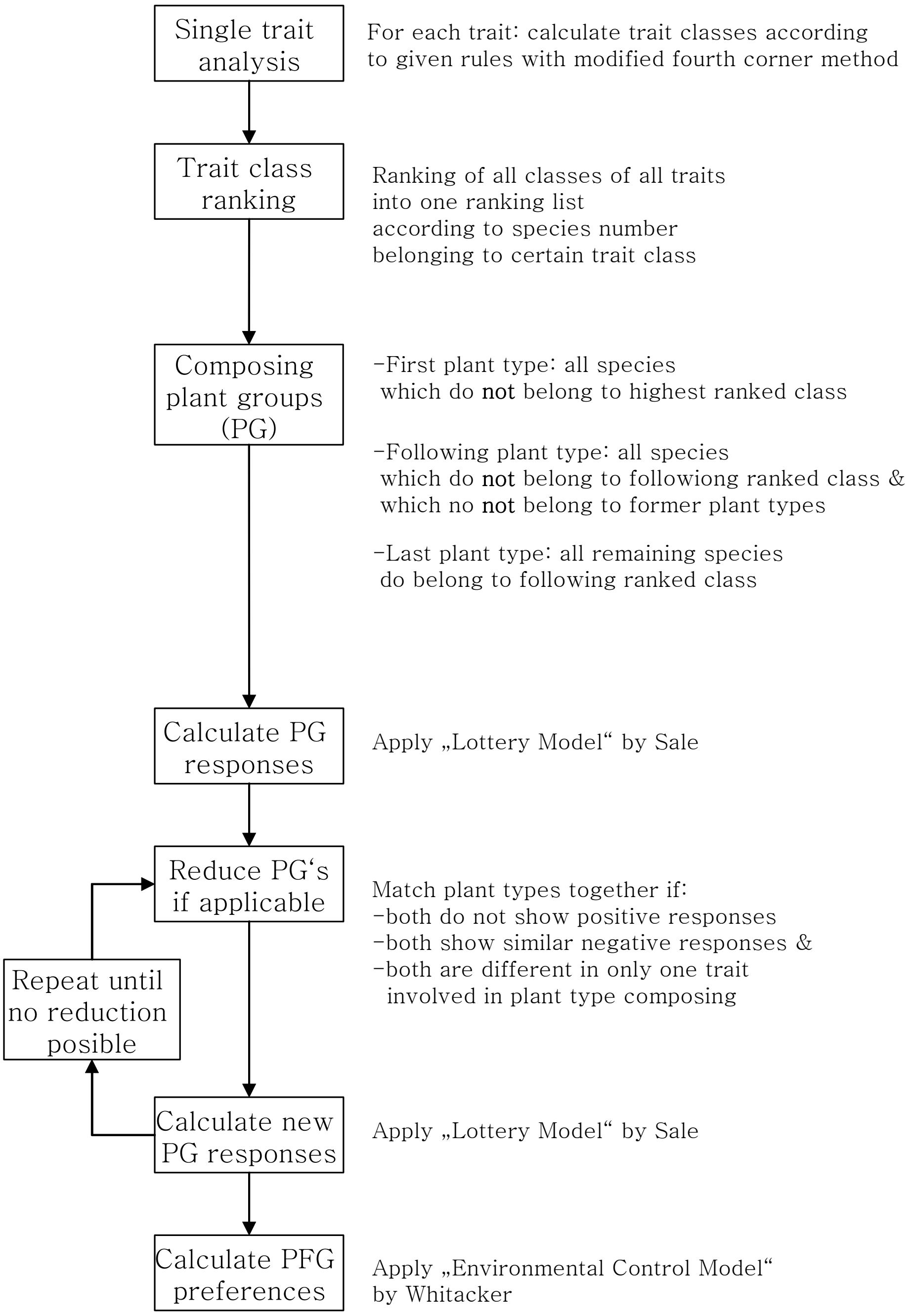
The second (next) plant group contained all species which are not already assigned to the first plant group (former plant groups) and which do not carry the second (next) trait attribute in the trait hierarchy. In general, the plant group x contained all species which were not already assigned to the forgoing generated plant groups (one to x-1) and which do not carry the attribute number x in the trait hierarchy. The procedure stops when the remaining species can not be grouped according to the trait belonging to the following trait class in the hierarchy. This is they case when they all belong in the same class of the trait which is next in the trait attribute hierarchy. It is not important whether the species belong to the trait class responding in the trait hierarchy or to another trait class of this trait.

Testing the generated plant types

The responses of species of a single trait grouping can not be expected to be directly transferable to responses of trait combinations. Therefore, we tested the final grouping for responsiveness. We collated PFGs which differ only in one trait and show a similar response to the hydrological regime. After plant type collation we tested the responsiveness again to derive the final plant functional groups.

The test was performed with the 'lottery model' which can be used to test plant group responsiveness, hence reflecting the reaction of PFG occurrence to changes in the hydrological regime.

Additionally, the 'environmental control model' was used to test the PFG site conditions preferences of the final PFGs (for further details see Lehsten et al. in press).



For each trait: calculate trait classes according
to given rules with modified fourth corner method

Ranking of all classes of all traits
into one ranking list
according to species number
belonging to certain trait class

-First plant type: all species
which do **not** belong to highest ranked class

-Following plant type: all species
which do **not** belong to followiong ranked class &
which no **not** belong to former plant types

-Last plant type: all remaining species
do belong to following ranked class

Apply „Lottery Model“ by Sale

Match plant types together if:
-both do not show positive responses
-both show similar negative responses &
-both are different in only one trait
involved in plant type composing

Apply „Lottery Model“ by Sale

Apply „Environmental Control Model“
by Whitacker

Figure A3-2: Overview of the method. After analysing each trait separately, all classes of all traits were sorted according to the number of species falling into the particular trait classes. All species which do not belong to the highest ranked trait class form the first plant type. Species not belonging to the following trait class and which are not members of a former defined plant types form the next plant type. This step is repeated until all remaining species do belong to one class of the next trait which will be the last plant type. The composed plant types were tested with a fourth-corner-method and their responses to environmental conditions were calculated. The number of plant types can be reduced according to the given rules and the new set of PFGs had to be tested until the final set of PFGs is found.

Results

The site classification according to the hydrological regime of the pools derived in (Lehsten and Kleyer 2008) is displayed in figure A3-3. Each site type, defined by mean spring high water level and drying up frequency is labelled with a number between one and twelve. The site types nine and twelve did not exist in the investigated area. The mean spring high water level (SHW) varies between 5cm and 3m. The average mean spring high water level over all small infield pools is 50cm. The drying up frequencies varies between 0.005 and 0.9. The mean drying up frequency over all pools is 0.3. This leads to high temporal and spatial dynamics.

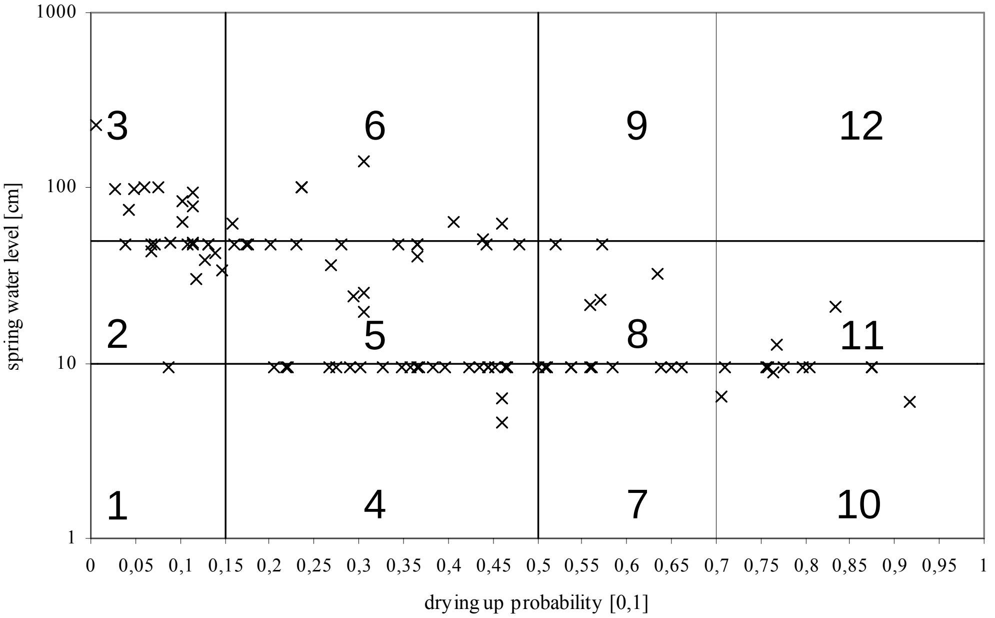


Figure 3: Average spring water levels and drying up frequencies of 101 sites in the investigated 46 small infield pools classified into 12 site condition types.

One species (*Eriophorum angustifolium*) was excluded from the analysis, because of it's rarity in the investigated area and the lack of trait data in the literature.

The correlation factors of the pair-wise trait correlations are listed in table 3. From the 24 traits, 17 could be seen as uncorrelated with a threshold below 0.5.

For each of the 17 traits a single trait analysis was performed to find the trait ranges most strongly responding to the hydrological regimes. A list of the trait classes and the number of species belonging to each class is given in table A3-2.

Table A3-2: Functional hierarchy of plant traits.

Trait	Acronym	Trait limits	Species number	Rank
Aerenchyms	AER	yes	77	1
life span cycle	LSC	not annual	74	2
Canopy height	CH	<108cm	72	2
Turions	T	no	70	4
submerged leafs	LS	no	65	5
spacer length	SpL	<18cm	62	6
root mass ratio	RMR	<0.46g/g	62	6
Biomass	BIO	<12g	62	6
height mass ratio	HMR	<4.3m/g	59	9
Specific shoot mass	SSM	0.008 - 0.14g/cm	56	10
Specific leaf area	SLA	16 - 53mm²/mg	55	11
leaf dry matter content	LDMC	4.6-5.9ln(g/g)	54	12
water stem length	WSL	<5.5cm	53	13
root depth	RD	>5.5cm	42	14
reproductive effort	RE	>0.08 g/g	37	15
reproductive effort	RE	<0.06g/g	36	16
root depth	RD	<4.5cm	23	17
water stem length	WSL	>17cm	19	18
Specific leaf area	SLA	<16mm²/mg	19	18
root depth	RD	4.5-5.5cm	15	20
leaf dry matter content	LDMC	>5.9ln(g/g)	15	20
Specific shoot mass	SSM	<0.008 g/cm	13	22
height mass ratio	HMR	4.3-5.2cm/g	13	22
Tussock growth	TG	yes	12	24
submerged leafs	LS	yes	12	24
Specific shoot mass	SSM	>0.14g/cm	11	26
leaf dry matter content	LDMC	<4.6ln(g/g)	11	26
Turions	T	yes	10	28
root mass ratio	RMR	0.46-0.62g/g	10	28
Biomass	BIO	12g-25g	10	28
water stem length	WSL	5.5-17cm	8	31
root mass ratio	RMR	>0.62g/g	8	31
height mass ratio	HMR	>5.2cm/g	8	31
Biomass	BIO	>25g	8	31
reproductive effort	RE	0.06-0.08g/g	7	36
spacer length	SpL	>18cm	6	37
Specific leaf area	SLA	>53mm²/mg	6	37
life span cycle	LSC	annual	6	37
Canopy height	CH	108cm-172cm	5	39
Aerenchyms	AER	no	3	40
Canopy height	CH	>172cm	3	41

We ranked the traits according to the species number within each trait class (table A3-2) and generated the plant groups (table A3-3, table A3-4) according to the procedure described in the methods section. Either we named each PG according its trait class responsible to distinguish it from the following generated PG or by its vegetation type defined by Wheeler and Proctor (2000). This happened if all species of this PG belonged to the same vegetation type. The first plant type consisted of the three species without aerenchyms (PT 1: No aerenchyms).

Out of the remaining 77 species the second plant type is formed by the 8 species which are not perennial or biannual (PT 2: Annuals). Out of the remaining 69 species the next group was formed by the six species which are taller than 108cm in average (PT 3: Reed fen). The fourth group consisted of all eight species with turions (PT 4: Turions). The fifth and sixth group are separated by leaf morphology either forming floating mats or floating leafs (PT 5: Quaking mats and PT 6: Floating leafs). The next group consisted of the 12 species which have the tussock growth form (PT 7: Tussock). The following group contained 10 species which have a high root mass ratio, (PT 8: Sedge fen). The ninth group is formed by all remaining species which have a biomass of more than 12g dry mass in total. These 12 species also have a biomass of less than 20g (therefore, PT 9: medium biomass). The 10 remaining species had a biomass of less than 3 g. They were grouped according to the preceding trait in the ranking list, height mass ratio (PT 10: High HMR, 5 species). The last five species had a medium specific shoot mass ratio, the next one in the ranking list (PT 11: Medium SSM).

Table A3-3: Generated plant groups with trait attributes and species number. Note that empty cells indicate non-defined trait attributes, e.g. the first plant type with no aerenchyms can be either annual or perennial. See text and table 1for acronyms.

Traits	PT 01	PT 02	PT 03	PT 04	PT 05	PT 06	PT 07	PT 08	PT 09	PT 10	PT 11
AER	no	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
LSC		annual	not	not	not	not	not	not	not	not	not
CH			tall	small	small	small	small	small	small	small	small
T				yes	no	no	no	no	no	no	no
FL mat					yes	no	no	no	no	no	no
FL						yes	no	no	no	no	no
TG							yes	no	no	no	no
RMR								high	low	low	low
BIO									midd	low	low
HMR										high	low
SSM											midd
Number sp./PFG	3	6	6	8	11	6	12	9	8	5	6

The responses of the generated plant groups were tested with the fourth-corner statistic. The last two groups showed similar responses to the environmental conditions. As they differ only by one trait, we combined them to the plant group “Low biomass”. Subsequently, we calculated the fourth corner statistic for the new groups. The results of the fourth corner analysis are displayed in figure A3-4 and A3-5 for the “Lottery-Model” and the “Environmental Control model” respectively. The plant species for each PFG are given in table A3-4.

Table A3-4 Species composition of the plant functional groups

PFG number	PFG	Species number	Species
1	No AER	3	*Alopecurus pratensis; Holcus lanatus; Rumex optusifolius*
2	Annual	6	*Bidens cernua; Bidens tripartita; Gnaphalium uligunosum; Oenanthe aquatica; Polygonum minus/Persicaria minor; Ranunculus sceleratus*
3	Reed Fen	6	*Phalaris arundinacea; Phragmitis australis; Schoenoplectus lacustris; Scirpus sylvaticus; Typha angustifolia; Typha latifolia*
4	Turions	8	*Ceratophyllum demersum; Ceratophyllum submersum; Elodea canadensis; Lemna minor; Lemna trisulca; Potamogeton acutiformis;Spirodela ployrhiza; Utricularia vulgaris*
5	Quaking Mat of Species	11	*Callitriche stagnalis; Hottonia palustre;Hydrocolyle vulgaris; Myosotis palustris; Nuphar lutea; Polygonum amphibia; Potamogeton natans; Potentilla palustre; Ranunculus aquatilis; Ranunculus circinatus; Viola palustris*
6	Floating Leafs	6	*Alopecurus aequalis; Alopecurus geniculatus; Berula erecta;Glyceria fluitans; Glyceria notata; Sium latifolia*
7	Tussock Growth Form	12	*Calamagrostis canescens; Carex canescens; Carex elata; Carex paniculata; Carex pseudocyperus; Carex rostrata; Carex vesicaria; Carex vulpina; Deschampsia caespitosa; Juncus effusus; Juncus inflexus; Molinia caerulea*
8	Sedge Fen	9	*Acorus calamus; Carex acuta; Carex acutiformis; Carex flacca; Carex hirta; Carex nigra; Carex riparia; Iris pseudacorus; Lythrum salicaria;*
9	Medium BIO	8	*Alisma plantago-aquatica; Cirsium oleraceum; Lycopus europaeus; Lysimachia vulgaris; Peucedanum palustre; Rorippa palustris; Rumex maritimus; Sparganium erectum*
10	Low BIO	11	*Agrostis canina; Alisma lanceolatum; Carex lasiocarpa; Eleocharis palustris; Epilobium palustre; Galium palustre; Juncus articulatus; Lysimachia thyrsiflora; Mentha aquatica; Ranunculus flammula; Scutellaria galericulata*

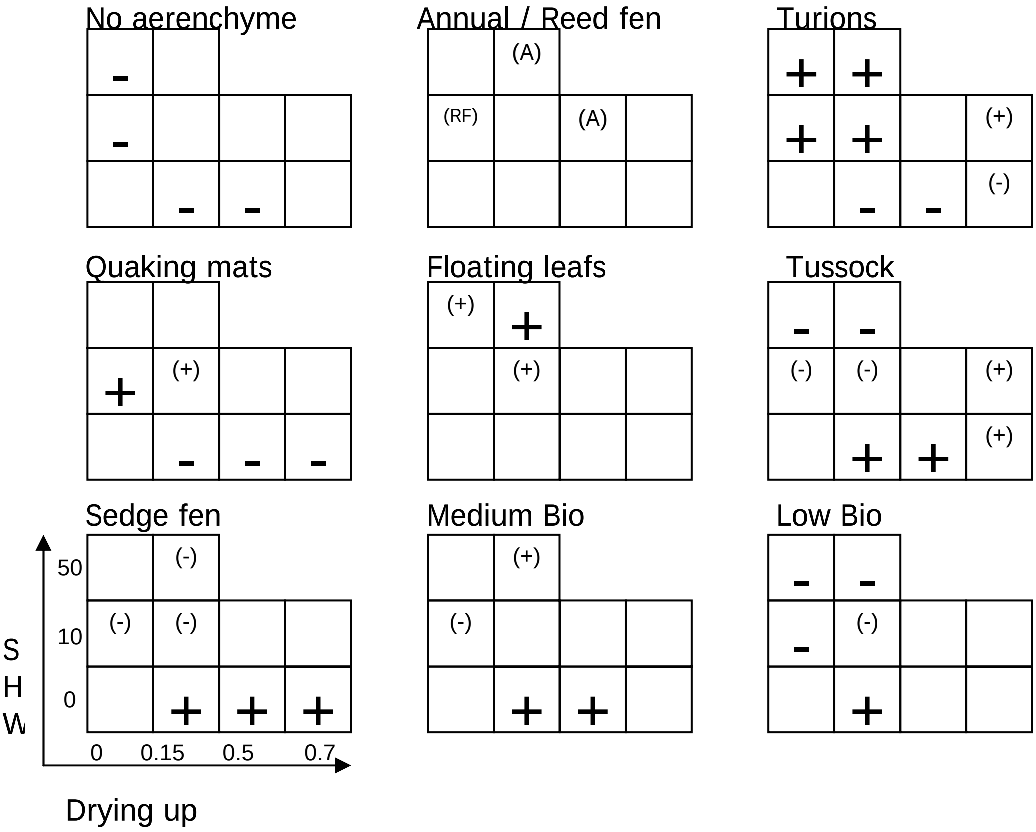
The “Lottery-Model” by Sale (1982) analysed the occurrences of PFGs at certain site conditions. Whether the PFG prefers or avoids the site conditions shows which PFG is most likely to occur, i.e. be most competitive on these conditions.

The plant group “no aerenchyms” showed only negative responses or non-significant responses to all site conditions. These species are typical for the surrounding agricultural landscape and occurred only occasionally within the pools. Therefore, they could not be seen as wetland species. The plant types “Annuals” and “Reed fen” did not show any positive significant responses within the small infield pools. “Annuals” occurred on the site types 6 and 8. They indicate sites with high and random hydrological dynamics. The PFG “Reed fen” occurred on site type 2. This site type has medium water level and low water level fluctuations. But, these 3 occurrences were not significant after a Bonferoni-Holm correction.

The remaining plant functional groups could be classified into PFGs typical for low spring water level (further called wetland PFGs) and PFGs typical for aquatic situations with low drying up frequencies and mean spring high water level more than 10cm (further called aquatic PFGs).

The PFGs “Turions”, “Quaking mats of species”, and “Floating leafs” occurred significantly more than expected on sites with an aquatic environment (spring water level higher than 10cm and drying up frequency less than 0.5), The aquatic PFGs occurred significantly less than expected on sites with low spring water level, except for the PFG “Floating leafs” which had a non-significant occurrence probability.

Unlike the previous PFGs, the wetland PFGs occurred more often than expected by the null model in low spring water environments and occurred less than expected in aquatic environments (PFGs “Tussock” and “Low biomass”). Before a Bonferoni-Holm correction, the PFG “Medium Biomass” occurred more often than expected than by the null model on aquatic sites with high water level fluctuation (high spring water level more than 50cm and drying up frequency between 0.15 and 0.5). An overview of the PFGs and their occurrence probabilities is given in figure A3-4.



No aerenchyme

	0	0.15	0.5	0.7
50	-			
10	-			
0		-	-	

Annual / Reed fen

	0	0.15	0.5	0.7
50		(A)		
10	(RF)		(A)	
0				

Turions

	0	0.15	0.5	0.7
50	+	+		
10	+	+		(+)
0		-	-	(-)

Quaking mats

	0	0.15	0.5	0.7
50				
10	+	(+)		
0		-	-	-

Floating leafs

	0	0.15	0.5	0.7
50	(+)	+		
10		(+)		
0				

Tussock

	0	0.15	0.5	0.7
50	-	-		
10	(-)	(-)		(+)
0		+	+	(+)

Sedge fen

	0	0.15	0.5	0.7
50		(-)		
10	(-)	(-)		
0		+	+	+

Medium Bio

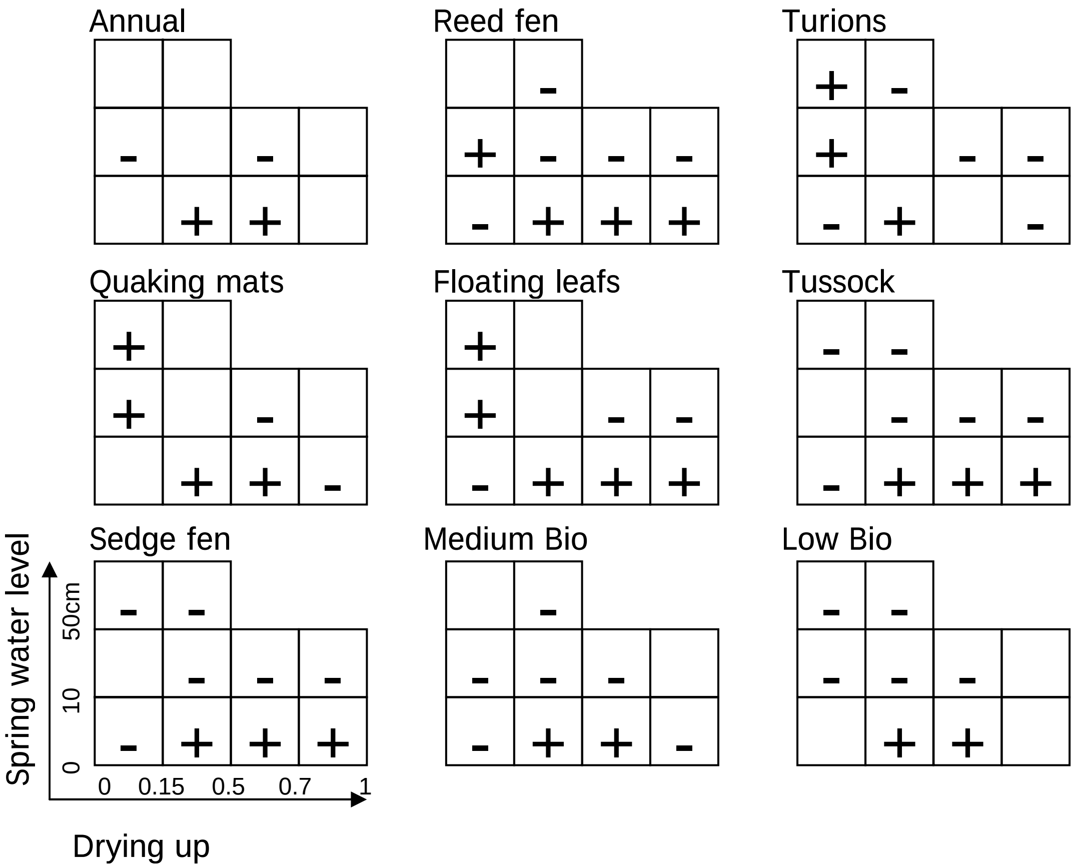
	0	0.15	0.5	0.7
50		(+)		
10	(-)			
0		+	+	

Low Bio

	0	0.15	0.5	0.7
50	-	-		
10	-	(-)		
0		+		

Figure A3-4: Occurrences of the optimised plant functional groups calculated with the “Lottery Model” by Sales (1982). Plus and minus signs on the different site conditions indicate negative and positive responses ($p<0.05$) respectively. Values in brackets are p-values which became non-significant after the Bonferoni-Holm correction.

The “Environmental Control Model” by Whittaker (1956) shows the preferences/ avoidance of a site by a PFG. Our results showed that all plant functional groups preferred sites with low spring water level. Only aquatic-adapted plant functional groups like the PFGs: “Turions”, “Reed fen”, “Quaking mats of species”, and “Floating leafs” preferred additional aquatic sites with spring water level higher than 10cm and drying up frequencies lower than 0.5. Therefore, similar to the results of the “Lottery” model, the plant types could be classified into aquatic PFGs and wetland PFGs. The two plant types “Annuals” and “Reed fen”, which where not competitively advantageous at any sites could now be allocated to the wetland PFGs and aquatic PFGs, respectively. The preferences of the PFGs to the different site types are displayed in figure A3-5.



Annual

-		-	
	+	+	

Reed fen

	-		
+	-	-	-
-	+	+	+

Turions

+	-		
+		-	-
-	+		-

Quaking mats

+			
+		-	
	+	+	-

Floating leafs

+			
+		-	-
-	+	+	+

Tussock

-	-		
	-	-	-
-	+	+	+

Sedge fen

-	-		
	-	-	-
-	+	+	+

Medium Bio

	-		
-	-	-	
-	+	+	-

Low Bio

-	-		
-	-	-	
	+	+	

Figure A3-5: Site preferences of the optimised plant functional groups, calculated with the “Environmental Control Model” by Whittaker (1956). Plus and minus signs indicate positive and negative preferences, respectively.

Discussion

No direct relationships between nutrient level and vegetation were found. This may be due to the high spatial and temporal dynamics of the trophic status of the small infield pools, where agricultural treatments within the catchment area are expected to have the strongest impact on pool water chemistry (see Box 06). In general, the measured nutrient concentrations in the fens are slightly but not significant lower than in the other pools. All pools had moderate to high nitrification levels, which may have lead to no detectable significant differences in nutrient levels. Therefore, we decided to use the hydrological regime as the only environmental condition in the analysis.

Our results indicate that the species in small infield pools have different storage, adaptative, and competitive strategies. Most of them have characteristics of competitive ability and storage/ environmental adaptative based strategies. But some concentrate on storage effect and environmental adaptative strategies like “Annuals”, “Turions”, and “Floating leafs” and not to invest in being competitive on resources.

Furthermore, our results indicate that plants responded to increasing drying-up frequencies at low water level by increasing root biomass at the expense of shoot biomass, as well as by decreasing root biomass with rising high spring water level. Sites with high spring water levels are occupied by PFGs that are especially adapted to water stress.

The storage strategies employed by the PFGs are distributed differently over the sites. PFGs with high reproductive effort (“Annuals”, “Medium biomass”) occurred significant only on sites with unpredictable and highly dynamic environmental conditions (drying up frequencies of around 0.5). PFGs with high root mass ratio occurred significantly more often than expected by the null model on sites with low spring water level or with very low water level changes. And, the PFG with turions occurred significantly only on aquatic sites.

Competition in the small infield pools is mainly for two resources, light and soil oxygen. All PFGs prefer sites with low spring water level, since there the soil oxygen and nutrient levels are highest. But, only PFGs with high investment in root biomass seem to be advantageous competitors on these sites. The other PFGs are therefore forced into deeper spring water zones. Competition for light involves several strategies. The PFGs adapted to aquatic sites either cover the water surface to keep the place occupied (PFGs “Turions” and “Quaking mats of species”) or grow tall like the PFGs “Reed fen” and “Floating leafs”. Both strategies require special environmental conditions for the PFGs, which limits the occurrence of these PFGs, for instance to stable water bodies for the PFG “Reed fen”.

All wetland PFGs had the strategy to invest in growth to gain light. PFGs with higher root mass ratio do not grow as tall as PFGs with lower root mass ratio. Therefore, it could be assumed that there is a trade-off between the competition on light, and storage in roots, on low spring water levels. This was also seen on the distribution of these PFGs. Higher root mass ratio occurred more at drier sites (higher drying up frequencies) where as taller species are more frequent at sites with lower drying up frequencies. The PFG “Annuals” avoided stress due to oxygen deficit and space competition via seed dormancy. Here, the trade-off between root mass ratio and canopy height is not evident.

Our analysis included morphological as well as measured traits. Neither the traits forming the final PFGs, the attribute ranges, the number of species per PFG, nor the number of resulting functional groups were predefined. Therefore, we can consider our novel method to derive plant functional groups to be non-subjective. To our knowledge, this was the first time a non-subjective approach was applied to form plant functional groups in temporary wetlands.

Some of our generated PFGs are comparable to predefined PFGs by morphological characteristics or to vegetative forms. These are the PFGs “Annuals”, “Reed fen”, “Turions”, “Quaking mats of species”, “Floating leafs”, “Tussock growth form”, and “Sedge fen”.

Ellison and Bedford (1995) found a similar relationship between water depth and annual species. With rising water depth the occurrence of this plant type declines. But they did not find the relationship between annual species occurrence and early drying up incidence. Also, tussock species grow with rising, but still low water level.

The wetland species *Typha latifolia* and *Phalaris arundinacea* responded to flooding treatments in the same way (Kercher and Zedler 2004) and were in the same plant functional group according to our method. This PFG „Reed fens“

comprised only of plant species belonging to the main vegetation type "Reed fens" or "swamp", as per Wheeler and Proctor (2000). These vegetation types are typically found on eutrophic sites with low to medium water level.

We defined two wetland PFGs which are not comparable to former predefined PFGs. These are "Medium biomass" and "Low biomass". Both occurred more often than expected by the null model on sites with low spring water level and medium drying up frequencies (around 0.5), indicating random changes between aquatic and terrestrial situations. Both PFGs evolved their own surviving, storage, and competition strategies, which are not comparable to other PFGs.

Some species of the PFG "low biomass" used the supporting tissue of other species to gain height to compete for light. Hence, nutrient and space availability was limited due to the species employed. The supporting individuals (mainly tussocks) provide stable environments for these species. Therefore adaptation or storage strategies to dynamical environments are not necessary. This resulted in low biomass, low reproductive effort, and lower root mass ratio. Other species of this PFG are typical species for nutrient poor wetlands and bogs. Their biomass is reduced owing to the environmental conditions with low nutrient supply. Therefore, its distribution is limited to sites with stable and low water level conditions, regardless their nutrient resources. The PFG "Medium biomass" also occurred more frequent (but not significant after the Bonferoni-Holm correction) on aquatic sites with high spring water level (more than 50cm) and medium drying up frequencies (between 0.15 and 0.5). These site characteristics represent a high dynamic in hydrological conditions. The PFG survives long periods of unsuitable situations via seed dormancy (seed mass is 21% of the total biomass) and shorter periods of unsuitable situation via storage in roots (also 21% of the total biomass is invested in roots). Furthermore, this PFG invests in stem mass and canopy height but less in stable leafs (lowest height mass ratio, second highest canopy height, high SLA values). This indicates a fast leaf growing aiming for light resources to build up a tall and stable stem under suitable environmental conditions. The PFG "Medium biomass" is less adapted to aquatic environments than aquatic PFGs, but, it can survive unsuitable situations via storage effects (both in roots and seeds). Once growing, it is a successful competitor for light and space. Therefore, species of this PFG are especially qualified to persist on sites with very high dynamic in environmental conditions.

Expected trends in PFG occurrences in small infield pools

When the hydrological regime changes in small infield pools, the species composition can change as well. As Lehsten et al (2008) showed a hydrological trend of higher annual water level fluctuation with similar mean high spring water level is already detectable in the simulated data. With the given expected increase in mean temperature of 3.2 degree over the next 100 years for the study area (Christensen, 2007) we expect sites with low disturbance impact by water level changes to become rare. This can cause a high extinction risk for the PFGs “Reed fen” and “Floating mats of species”, which are adapted to such environments.

The PFG “Sedge fen” could be subdivided by the trait biomass which the next trait in the hierarchy. Species with a biomass less than 3g could have been associated to the plant type “Small sedge fen”, whereas species with a biomass higher than 9g could have been associated to the plant type “Tall sedge fen”. The last group had the same occurrence probability as the PFG “Sedge fen”. However, the plant type “Small sedge fen” occurred significantly less than expected by the null model on most of the site types. For a few site types its occurrence probability was not significantly different to that expected by the null model. According to Wheeler and Proctor (2000) the vegetation type small sedge fen is related to sites with oligotrophic to mesotrophic eutrophication levels, whereas the vegetation type tall sedge fen occurs on sites with higher eutrophication level. Therefore, the low occurrence of this plant type small sedge fen could be explained by the higher eutrophication level of most of the sites. Therefore, this plant type could be seen as a relict of former lower eutrophicated situations, due to the lower farming impact on the surrounding fields.

Constrain of the adaptability of the generated PFGs

According to Du Rietz (1931) the number of species increases with increasing variability of habitats. Species adapt to the environment with morphological traits. We used traits to group wetland and aquatic macrophytes in PFGs. Trait combination essential to survive in other environmental conditions or higher the competitive factor to other species / PFGs growing there are not necessary for PFGs in small infield pools. Therefore, extending as well as reducing the habitat types will result in different PFGs. B. Nygaard and R. Ejnaes (2004) had to deal with changing PFGs due to different sets of environmental conditions. They determined 4 PFGs out of 250 species and their occurrences in Danish wetlands. The application of these PFGs in an experiment with a very low subset of species and site conditions failed. That means the derived groups and their responses to the environment are only valid for the investigated area. Changes in environmental conditions e.g. due to agricultural practices or climate change may result in different PFGs or changes in their response, as was also found by Diaz and Cabido (1997). Therefore, our PFGs are unique for small infield pools in agricultural treated landscapes. They explain the occurrence of species, their strategies to persist in such environment, and their threats to environmental changes. Their application to other site conditions would fail as they show only a snapshot of species and hence of PFGs that occur worldwide.

Conclusion

Our novel approach to generate Plant Functional Groups in aquatic or temporal aquatic habitats is, to our knowledge, the first successful application of non-subjective PFG determination in European and North American wetlands. We showed, that some of the plant functional groups we created can be related to wetland vegetation types classified by earlier work. Furthermore, we could show which PFGs occurred randomly in the sites. These are PFGs which underlie either extinction or establishing processes, and PFGs with consistent seed input from the surrounding environment. And third, we could determine PFG typical strategies in environmental adaptation, storage effect and competition. These different strategies are responsible for the different occurrence probabilities of the PFGs. Our results suggested that small infield pool conservation should be kept as an active habitat management regime by keeping/creating the hydrology dynamic for the plant types which need to be protected. Our methods here can be applied to estimate the required conditions for focal species. Even with the actual situation of wetlands in general and of small infield pools in particular, a correct management of these features can protect and even recreate the habitat quality, and therefore enhance the species inventory of focus. As already pointed out by Darwin (1859), most species are able to (re-)colonise restored pools since active vectors like water birds can disperse their seeds, or even small plant parts, very effectively. This high chance of re-colonization makes them a promising field of work in nature conservation.

BOX 08: Numbers of possible groupings depending from species number and limited attribute number

The number of possible grouping of species rises with the number of species, number of involved traits, and number of allowed groups per traits. For 80 species and 24 with up to three groups per trait there are ca.10^{80} different permutations possible. To group 80 plant species in any possible way results in $6*10^{23}$ permutations. This value is much smaller. Hence it would be appropriate to group all species into all possible combinations and test each combination against the environmental conditions. After this procedure, the groups might be found according to the used rules. But the trait attributes (and therefore the traits) responsible for describing the groups are still missing. Actually, the effort seems to be equal. For each species combinations all traits had to be classified, whereas the class borders are unknown as well as the importance of the trait attributes for the special environment. For instance, in a group A there are species with releasing heights between 10cm and 90cm. In another group B in that combination there are plants with releasing heights between 50cm and 60cm. And a third group C inhibits plant species between 70cm and 90cm. Which are the releasing height class borders? Is there only one releasing height attribute between 10cm and 90 cm? Or inhibit group A a low and a high range of releasing height, whereas group B is defined by species with medium releasing height and group C by species with tall releasing heights? Does group A has no description in releasing height at all? But for the other groups releasing height is an important trait for building plant functional groups? Is the trait releasing height important for describing plant functional groups in the investigated habitats? Such a classification analysis has to be done for each trait and has to be tested.

Therefore, both methods are infeasible for finding plant functional groups out of a greater number of species and traits.

If a single trait analysis will be applied beforehand, the 80 species will be grouped in maximal 3 groups for each trait. These are up to 3111 different runs per trait. Hence for 24 involved traits these are less than 80000 different runs. For each trait that classification with the highest number of significant occurrences per attribute and in total will be choose as the best classification. Classes will be matched together if their occurrences on all site types are equal and the resulting class has the same occurrence probabilities. (Example: Canopy height is classified in 3 groups: small, medium, and tall. On all site types group ‘one’ and group ‘two’ are negative significant. Matching these two groups into one will result in a new group ‘one-two’. This new group is also significant negative on all sites types. Hence, group one and two belongs into the same class ‘one-two’.)

Box 09: PFG characterisations

In general the generated PFGs could be subdivided into aquatic PFGs which evolve different morphological features to survive in flooded habitats and into wetland PFGs. But, the characteristics specialising the aquatic PFGs lower their competition level on riparian sites. Further, surviving or storage strategies differ strongly among aquatic PFGs in small infield pools.

The PFG “Turions” uses an aquatic morphological trait strategy in establishing turions to survive winter and dry period in these buds. This PFG does not invest in other storage effects traits like seeds or roots. The spacer length is short compared to other aquatic PFGs, indicating that species with turions defend the occupied space rather to reach new areas. Therefore, on the one hand, this PFG may a better competitor on sites with higher spring water level since it defence the space. But also, it survives shorter periods of unsuitable conditions due to the ability to evolve turions as storage effect. Its occurrence on 4 different aquatic site conditions can be explained by this two mentioned factors defending the place and re-establish after dry periods.

The aquatic PFG “Quaking mats of species” follows a competition strategy in light resources and invest in root storage. Hence, the investment in stem and seeds is limited. Therefore, its occurrence regulation to spring water depth between10cm and 50cm can be explained in the limited stem length. It avoids environments with higher drying up frequencies as it is adapted to aquatic situations in leaf and stem morphology. This PFG has a higher spacer length, indicating a faster occupying of new sites if the hydrological habitat qualities change.

The PFG “Floating leafs” invests in changing leaf morphology as survival strategy. Storage in roots or seeds is low. If the environment conditions reach the PFG requirements with low competition pressure (when other species have to avoid the changed situation) species of this PFG can use the resources and grow to a canopy height of 50cm. These species use the possibility of changing environments within a vegetation period. The spacer length is low, indicating only a slow spread into neighbouring sites. Therefore, their strategies can explain their positive response on sites with higher drying up frequencies but still aquatic situation. Their higher SLA values (resulting in lower tissue investment in leafs) can also be explained by the same strategy. They grow fast to use the changing situation. Leafs will be carried by the water column during flooding events.

In contrast to the PFG "Sedge fen" we could group the PFG "Reed fen" to the aquatic PFGs. Both PFGs prefer sites with low stress situation indicated by low spring high water. But, the taller PFG "Reed fen" also prefers sites with intermediate stress and low disturbance as it is adapted to permanent flooding (aerenchyms and tall canopy height). The PFG "Sedge fen" invest in high root mass ratio, whereas the PFG "Reed fen" invest nearly the same amount of the biomass in standing crop, which allows it growing taller. But the water depth of its occurrence is limited. This results in a higher occurrence probability for "Reed fen" on undisturbed flooded sites with a competition effect on light resources and a surviving strategy during flooding events due to the long water stem. After a Bonferoni-Holm correction this response effect was not significant anymore. It is unpropitious on sites with higher disturbance since its investment in canopy height can be lost by mechanical disturbances.

The PFG "sedge fen" does not occur on deeper flooded sites because of the shorter water stem length. It invests in roots to survive inappropriate situation via storage effect, resulting in lower standing crop bio mass with lower canopy height compared to the PFG "Reed fen". Therefore, the PFG "Sedge fen" has its distribution only on sites with low spring high water. Compared to the PFG "Reed fen", the PFG "Sedge fen" has shorter spacer. That could results in a lower vegetative spreading velocity which indicates the tendency of these species to occupy the area rather than moving to other sites with changing conditions.

The PFG "Tussock" follows a competition and surviving strategy. In creating its own environment in growing in a tussock of different height levels it survive smaller water level changes. Also, on the same time this strategy defends the occupied space against other species. Tussock species invest in leafs to keep them alive over the vegetation period, resulting in lower SLA values. It invests in root mass to keep the space occupied. But the root mass ratio is smaller than that of "Sedge fen" or "Reed fen" probably also due to investment in standing crop by strong leafs. Because of its competition strategy the investment in storage via seeds is not essential. The biomass is low due to intra-specific competition resulting in lower canopy height. Therefore, this PFG has a positive response only on sites with low spring high water level and intermediate drying up frequencies. Sites with stable conditions (either mainly flooded or mainly dry) will be occupied most likely by aquatic or terrestrial plant species respectively than by tussock species.

The PFG “Annual” follows the same strategy as the PFG “Floating leafs”. Species out of this group emerge in periods or seasons of suitable environmental conditions. During unsuitable situations, they outwear in seed dormancy. Therefore, it occurs most likely on sites with higher disturbances (frequently changes between aquatic and terrestrial situation). Because it avoids aquatic situation, its distribution is slightly switched to drier environments than the PFG “Floating leafs”. But, its occurrence is not significant anymore after a Bonferoni-Holm correction.

The PFG „Medium biomass“ invests in reproductive effort second most strait after the PFG „Annuals“. It can be assumed that the strategy of this PFG is seen in surviving unsuitable periods in seed dormancy. Its average SLA values of 37cm²/g indicates fast growing species. Also, this PFG invests most in supportive tissue compared to all PFGs in small infield pools. Both factors indicate a competition strategy of light resources, seen in the second highest PFG after the PFG “Reed fen”.

A completely different strategy operates the PFG „Low biomass“ compared to the other PFGs of small infield pools. Some of these species are growing in the direction of the light with help of other species. The results are thin and week stems and low ratio of supportive tissue. The height mass ratio of this PFG is very high compared to the other PFGs. Only the aquatic PFGs “Turions” and “Quaking mats of species” have comparable or higher height mass ratios. They do not need supportive tissue as they are carried by the water. The PFG “Small biomass” invests neither in reproductive effort nor in roots. Therefore, it needs stable environmental conditions to survive with its strategy. These conditions are found on tussocks species. Because of the high competition on nutrient resources, these species can not effort higher investments in any storage or competition effects.

Box 10: Traits and their ranges among the generated PFGs

Traits which are not involved in creating plant functional groups can show a significant distribution over the resulting PFGs. We give a short overview of “dry matter content”, “height mass ratio”, “water stem length”, “root depth”, “specific leaf area”, “reproductive effort”, and “specific shoot mass”. Table B10-1 gives an overview of the trait ranges among the PFGs.

Leaf dry matter content values range between 4% and 82% of dry matter content. Ranges within a single plant functional group vary between twice of the lowest value up to the ninth of the lowest value. In general, low values are in the plant functional group “Annual”, “Turionen” and “High biomass” with up to 14% of dry matter content. Medium values are found in “Quaking mats”, “Sedge fen”, and “Small biomass”. High values are in PFGs “No aerenchym”, “Reed fen”, “Floating leafs”, and “Tussock growth form”.

The height mass ratios in ln(cm/mg) vary between 0.6 and 10. Except for the PFGs “Turions” and “Quaking mats” the values of height mass ratio within a single PFG do not differ so much. Small mean values are found in the PFGs “Reed fen”, “Sedge fen”, and “High biomass” with less than 2.1. Medium values occur in the PFGs “No aerenchym” and “Tussock growth form”. High mean values of more than 3.6 are representative in the PFGs “Floating leafs”, “Small biomass”, Quaking mats of species”, and “Turions”.

In each PFG occur at least one specie with no or very small water stem length. PFGs which do have species with long water stem are “Reed fen”, “Turions”, and “Quaking mats of species”. There, the maximum water stem length is more than 100cm. PFGs with a maximum water stem length of less than 30cm are “Annuals”, “Floating leafs”, “Tussock growth form”, “Tall sedge fen”, “Medium biomass”, and “Low biomass”. Only the PFG “No aerenchym” does not have water stems.

Root depth varies between 1 and 60cm. PFGs with high root depth more than 24cm are “Reed fen” and “Sedge fen”. Medium root depth between 6cm and 16cm is found in the PFGs “No aerenchym”, “Quaking mats of species”, “Tussock growth form”, and “Medium biomass”. PFGs with low root depth less than 5cm in mean value are “Annuals”, “Turions”, “Floating leafs”, and “Low biomass”.

Mean SLA values vary among the PFGs. Low values are found in the PFGs “Reed fen”, “Sedge fen”, and “Tussock growth form”. High values are found in the PFGs “Annuals”, “Turions”, “Quaking mats of leafs”, and “Medium biomass”. Medium values between 24 and 33mm²/mg are representative in the PFGs “No aerenchym”, “Floating leafs”, and “low biomass”.

The reproductive effort is in general low between 4% of the dry biomass and 12% of dry biomass. Only in two PFGs the reproductive effort is significant higher with 24% of dry biomass in the PFG “Medium biomass” and nearly 50% in “Annuals”. Very low reproductive effort with less than10% is found in the PFGs “Tussock growth form”, “Floating leafs”, and “Small biomass”.

The specific shoot mass varies between 0.01g/cm and 0.86g/cm. Among the PFGs mean values are between 0.02g/cm and 0.15g/cm. Highest values are found in the PFGs “Annuals”, “Reed fen”, “Tussock growth form”, and “Medium biomass” with more than 0.09g/cm. All other PFGs have mean values of less than 0.05g/cm.

Table 01: Plant functional groups and their minimum, maximum, and average trait attributes.

	Terres. Species	Annuals	Reed fen	Turi ons	Quaking mats of species	Floating leafs	Tussock growth form	Sedge fen	High bio mass	Low bio mass
AER	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	0,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0
max	0,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0
mean	**0,0**	**1,0**	**1,0**	**1,0**	**1,0**	**1,0**	**1,0**	**1,0**	**1,0**	**1,0**
LSC	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	3	1	3	3	3	2	3	3	2	3
max	3	1	3	3	3	3	3	3	3	3
mean	**3**	**1**	**3**	**3**	**3**	**2,8**	**3**	**3**	**2,7**	**3**
CH	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	36,0	2,0	111,0	0,0	0,0	26,5	27,4	18,0	51,8	8,6
max	53,2	118,0	220,0	18,3	30,0	92,0	103,0	105,0	105,0	79,7
mean	**36,8**	**50,5**	**171,3**	**2,3**	**10,7**	**48,5**	**68,7**	**57,2**	**73,4**	**42,1**
T	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	0,0	0,0	0,0	1,0	0,0	0,0	0,0	0,0	0,0	0,0
max	0,0	0,0	0,0	1,0	0,0	0,0	0,0	0,0	0,0	0,0
mean	**0,0**	**0,0**	**0,0**	**1,0**	**0,0**	**0,0**	**0,0**	**0,0**	**0,0**	**0,0**

	Terres. Species	Annuals	Reed fen	Turi ons	Quaking mats of species	Floating leafs	Tussock growth form	Sedge fen	High bio mass	Low bio mass
Flmat										
min	0,0	0	0,0	0	1,0	0,0	0,0	0,0	0,0	0,0
max	0,0	1	0,0	1	1,0	0,0	0,0	0,0	0,0	0,0
mean	0,0	0,4	0,0	0,3	1,0	0,0	0,0	0,0	0,0	0,0
LF										
min	0,0	0	0,0	0	0	1,0	0,0	0,0	0,0	0,0
max	0,0	1	0,0	1	1	1,0	0,0	0,0	0,0	0,0
mean	0,0	0,4	0,0	0,8	0,9	1,0	0,0	0,0	0,0	0,0
SpL	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	0	0	14	0	0	0	0	0	0	0
max	5	8	51,3	10	50	10	0	20,9	31,7	5,4
mean	**4**	**1,6**	**21,9**	**1,5**	**15,0**	**4,2**	**0**	**8,9**	**6,3**	**2,3**
TG	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	0	0	0	0	0	0	1	0	0	0
max	0	0	0	0	0	0	1	0	0	0
mean	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**0**	**0**
RMR	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	0,1	0,04	0,12	0,001	0,08	0,10	0,05	0,60	0,09	0,04
max	0,22	0,29	0,62	0,31	0,67	0,21	0,67	0,70	0,32	0,31
mean	**0,16**	**0,13**	**0,40**	**0,04**	**0,36**	**0,17**	**0,27**	**0,64**	**0,21**	**0,18**
Bio	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	0,5	0,06	5,39	0,001	0,011	0,34	0,36	0,68	12,08	0,09
max	24,86	20,58	96,3	0,5	68,6	17,48	9,8	47,3	16,96	2,94
mean	**1,2**	**5,8**	**42,1**	**0,15**	**9,0**	**4,3**	**4,0**	**13,7**	**14,4**	**0,99**
WL	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	0,0	0,0	0,0	0	0,5	0	0,0	0	0,0	0,0
max	0,0	19,0	100,0	150	130	11	10,0	30	30,0	10,0
mean	**0,0**	**3,9**	**54,2**	**58,9**	**49**	**4,2**	**2,8**	**5,9**	**7,7**	**2,6**
RD	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	5,0	1,0	10,0	0	2	3	5,0	5	5,0	2,0
max	10,0	10,0	58,0	5	50	12	15,0	30	50,0	6,0
mean	**6,5**	**4,0**	**31,0**	**2,1**	**13,9**	**5,8**	**8,9**	**17,5**	**16,0**	**4,1**
SLA	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	21,90	18,20	7,63	14,3	13,7	24,8	4,30	10	15,70	7,60
max	45,20	49,70	20,65	58,6	89,7	55,21	28,20	45,2	65,10	44,60
mean	**32,9**	**34,7**	**15,3**	**33,6**	**39,7**	**36,8**	**15,9**	**18,8**	**36,9**	**27,8**

	Terres. Species	Annuals	Reed fen	Turi ons	Quaking mats of species	Floating leafs	Tussock growth form	Sedge fen	High bio mass	Low bio mass
RE	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	0,08	0,32	0,00	0	0,001	0,0204	0,00	0,0012	0,00	0,01
max	0,37	0,66	0,41	0,1868	0,1438	0,3372	0,21	0,3805	0,57	0,32
mean	**0,12**	**0,47**	**0,10**	**0,05**	**0,06**	**0,15**	**0,05**	**0,07**	**0,25**	**0,09**
SSM	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
min	0,01	0,01	0,02	0	0,0008	0,0109	0,00	0,0109	0,07	0,01
max	0,36	0,86	0,35	0,1	0,1808	0,1433	0,09	0,1612	0,20	0,06
mean	**0,03**	**0,15**	**0,11**	**0,03**	**0,04**	**0,05**	**0,04**	**0,06**	**0,15**	**0,02**
LN(HMR)										
min	0,76	1,16	0,91	2,30	0,60	2,95	1,98	0,85	2,26	1,23
max	4,32	4,77	3,45	10,13	7,17	4,39	4,33	2,49	3,43	2,41
mean	3,64	3,12	2,10	5,95	3,63	3,66	3,19	1,58	2,75	1,70
LN(LDMC)										
min	4,63	4,11	5,41	3,80	4,23	5,15	5,54	5,09	4,36	4,10
max	6,11	5,44	6,10	5,74	6,25	6,39	6,71	5,80	6,28	5,81
mean	**5,72**	**4,73**	**5,76**	**4,65**	**5,17**	**5,73**	**5,88**	**5,56**	**5,64**	**4,97**

Box 11: Plant species and PFG diversity

Plant species diversity versus PFG diversity

We calculated the PFG diversity for each site and related it to the species diversity (fig. B11-1). An exponential trend curve over the mean values has a correlation factor of r^2=0.97 (a linear correlation using all data points instead of means results in an $r^2$of 0.92). That gives a strong indication that despite strong differences in species numbers per PFG, PFG diversity is positively related to species diversity.

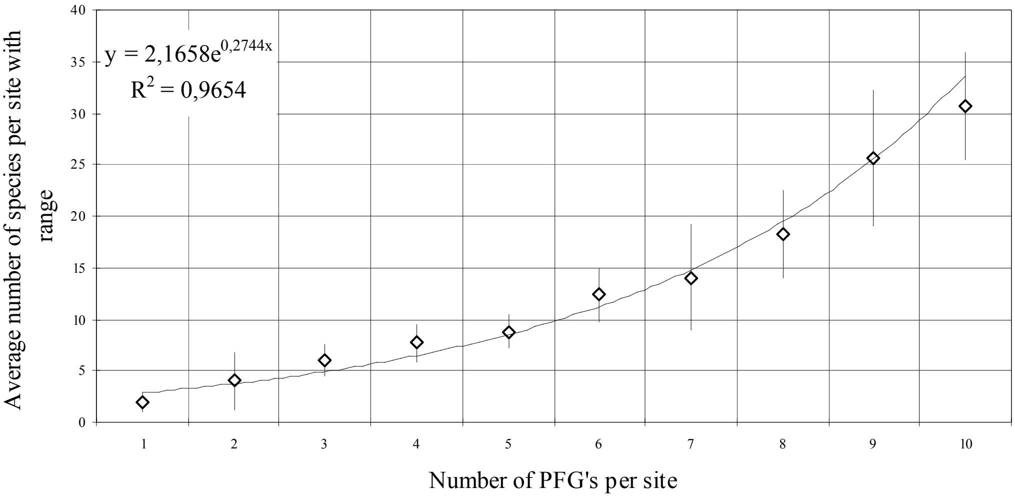


Figure B11-1: PFG number per site versus species diversity of the sites. An exponential trend curve has an r^2=0.97.

According to the species area model (see Keddy 2005) the number of species increased with increasing area. Because, the number of PFGs is fixed by the investigation, sites with greater areas will inhibit a higher number of species but a limited number of PFGs. Therefore, the PFG species number correlation can not be linear but rather modelled by an exponential function for which we found the best correlation.

Storage effects

PFG diversity versus disturbance and stress intensity

The number of PFGs responding positively to each site type is shown in figure B11-2. It varies along the gradient of high spring water level and along the gradient of drying up frequencies. Highest number of positive responses is found in sites with low spring water level and intermediate drying up frequencies between 0.15 and 0.7. The lowest number of positive PFG responses is found in sites forming the corners of the investigated site condition matrix (extreme values of high spring water level and drying up frequencies).

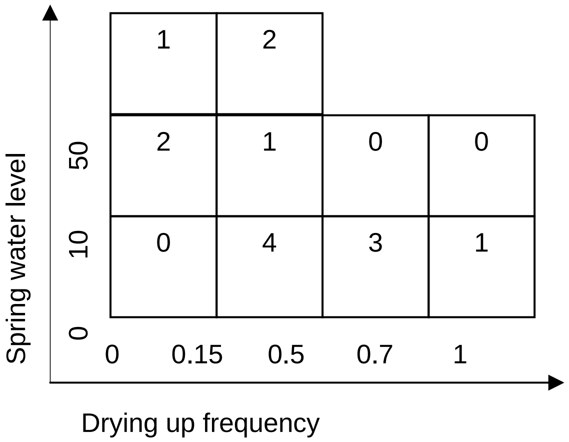


Figure B11-2: Number of positive response PFGs per site type

Species richness and biomass distribution in small infield pools

The basic unimodal relationship between standing crop biomass as indicator for disturbance and productivity intensity and biodiversity is also found in hydrophyte communities with highest biodiversity at 150-200g dry weight of standing crop in artificial waterways (Dodson et al. 2000, Willby et al. 2001, Desilets and Houle 2005).

The result that species richness is low at high and at low levels of stress (Grime 1973, Keddy 2005) was also found in our study (see fig. B11-2). High stress induced by low resource availability in environments with high water level and low drying up frequencies reduced species diversity. We found out that not only decreasing stress intensity lowers species richness lowers only with. Also, the disturbance intensity had to be recognised in such investigation.

With higher resource availabilities resulting from longer drier periods, species diversity increases until a certain level. Than the species diversity will decrease with rising resources (Desilets and Houle 2005). In our study the resource gradient ranges from high spring water level (high stress) and low drying up probability (low disturbance) to low spring water level (low stress) and high drying up frequencies (high disturbance). Species richness and PFG diversity is highest on a gradient of stress and disturbance. Rising stress causes lowering species diversity whereas rising drying up frequencies show a peak in species diversity on intermediate drying up frequencies. A finer differentiation of high spring water level and drying up frequencies would be appropriate to identify the relationship of stress and disturbance intensity to species richness. But, this entails to involve a larger set of pool investigations.

We have not tested the relationship between species richness and total above biomass.

But, high biomass accumulating PFGs occur in sites with low stress (low spring water level) on a gradient of disturbing rate by drying up frequencies. These PFGs are “Tussock growth form”, “Sedge fen” and “Medium biomass”. Therefore, in our case highest biomass can be expected at lowest stress level (Willby et al. 2001, Desilets and Houle 2005) or in not poor nutrient environments with low fluctuating levels (Bakker et al. 2007). The high biomass production at high drying up frequencies can be explained in the context of low disturbances on these sites. Spring water levels will drop down fast to lead the side dry up for most of the years. Hence, species need to adapt to emerge later in the year or to survive short periods of flooding. In the context of terrestrial plant species these sites would have the lowest disturbance level.

Box 12: PFG extinction risk – An example on the group “Small Sedge Fen”

According to the carousel model by Maarel and Sykes (1993) and Sykes et al. (1994) species within a small infield pool can reach new free niches due to periodical changes in environmental conditions. Successions are changes in vegetation composition. Hence, due to long term changes in the environmental conditions of small infield pools species composition will change (Diaz and Cabido 1997) rather in a succession way than at random as predicted by the carousel model. If species went extinct randomly the linear correlation of species and PFG diversity would become invalid as Fonseca and Ganade (2001) showed. Therefore, species within the small infield pools are expected to disappear due to environmental changes. Here, the carousel model works only for plant species and PFGs which have the opportunity to reach potential free niches in the water pools. Species, which can not survive in the changed environment and which do not find potential new niches will become extinct. An example in our case could be the PFG “Small sedge fen”, which can be subdivided from the PFG “Sedge fen”. All species within the PFG “Sedge fen” are similar except for the trait “biomass”. The group can be divided into a group of species with a total biomass of less than 3g and into a group of species with a total biomass of more than 9g. The species of the group with less biomass can be related to the vegetation form “Small sedge fen”, whereas the other species can be related to the vegetation form “tall sedge fen” according to Wheeler and Proctor (2000). The plant type “Small sedge fen” exists in the study area with 4 species, mainly found in the less eutrophicated glacially formed kettle holes with high turf accumulations. McNamara et al. (1992) showed that such vegetation appears only in ombotrophic water. With connection to the groundwater, water movements should at least periodically appear downwards. The edges of such kettle holes are covered by fen vegetation which filters the incoming lateral flow waters. Hence, species related to nutrient poor water like small sedges and sphagnum species can exist only in small infield pools big enough to filter the nutrient rich lateral water flow from the surrounding agricultural treated environment (Ripl et al. 1996) by their edge vegetation (Merbach et al. 1996) and precipitation evaporation rates which allow a ground water downwards flow periodically. Higher nutrient supply due to agricultural treatment or by mineralization processes of organic substrate in drier periods result in an increase in emergent plant biomass (Willis and Mitsch 1995) and shifts to aggressive growing plant species (Craft et al. 2007). That could explain the poor occurrence of the PFG "small sedges". Hence, there is a high risk of disappearing of small sedge fens in small infield pools in the background of higher evaporation rate with time (Lehsten and Kleyer 2008) and very high nutrient supply into the water bodies of small infield pools (Ripl et al. 1996). Though our study could not relate nutrient level to the vegetation it is expected that changes in the chemical composition of the pool water have changed the vegetation profound in the last century (Carpenter et al. 1998). Therefore, we assume that the plant group "small sedge fen" could be a relict of former site conditions and could be extinct soon.

Synthesis

In the DFG funded thesis „Speichereffekte reproduktiver Kapazität bei Pflanzen von Kleingewässern in Beziehung zur zeitlichen Variabilität der Habitatqualität“ (Storage effects of reproductive capacity of plants in small infield pools in relation to the temporary variability of habitat quality) I examined the impact of the dynamic of environmental conditions on the vegetation characteristics of small infield pools. These features are important island habitats and provide some of the few remaining semi-natural landscape elements for amphibian and wetland species within intensively managed, homogeneous agriculturally-dominated pleistocene landscapes. The importance of pools in general and temporary in particular in conservation management as well as in the scientific frame works changed from negligible water bodies (Ratcliffe 1977) to one of the most threatened habitats on the world (Oertli et al. 2005, Cereghino et al. 2008). This is also seen in the fact that nowadays pools are recognised as wetland types of international importance in the Ramsar Convention (Ramsar Resolution VIII.33) (Oertli et al. 2005). Furthermore, during the first European Pond Workshop held in Geneva, Switzerland, in October 2004 (Oertli et al. 2005), the European Pond Conservation Network was founded (EPCN, http://campus.hesge.ch/epcn/). This implies the strong need of international cooperation of scientific research in pool ecology and management.

Wetland communities in general are seen by some authors as the most threatened vegetation types throughout the world (Gopal and Junk 2000). However, till now, the relationship between survival of wetland species and the underlying hydrological conditions of wetland habitats are far from fully known (Kennedy et al. 2003).

Till now, pool research covers mainly pool ecology by observations (Cereghino et al. 2008). Study times differ between a few months (Della Bella et al. 2008) to several decades of observations (Winter and Rosenberry 1998, Biggs et al. 2005). In general, the pool environment conditions depends strongly on climate, agricultural treatment of the rain run off catchment area, and on changes in the hydrological system (e.g. melioration impact) (Davies et al. 2008a). All three threats are already mentioned as strong impacts to pool conditions (Oertli et al.

2005). Also, pools and the species composition they host react highly sensitive to changes in these threats (Carchini et al. 2005, Menetrey et al. 2005, Ruggiero et al. 2005). But potential resulting changes in species compositions are rarely modelled (Pyke 2005).

It is known that periodical water level cycles in prairie potholes are found to alter wetland vegetation either by vegetation fluctuation or by vegetation succession (van der Valk 2005). Such vegetation fluctuations occur with small water level cycles of less than 50cm, i.e. seasonal wetlands. Successions are changes in vegetation composition and occur with changes in the hydrological regime (Tulbure et al. 2007).

Such prolonged periods of low water levels can be caused by melioration impact as it happened in North East Germany in the last century (Kalettka 1996) as well as by climatic changes influencing the hydrological regime of small infield pools in a drastic way and the growing season.

Both impacts in turn can change long term vegetation structure (Pedersen and Sandjensen 1993, Dahl and Birks 1998). Therefore, small infield pool vegetation structure underlies a high risk to alter in a succession way rather than in a fluctuation way. But, this could higher the extinction risk of some species in the future.

But, practical pool conservation and management is rarely based on scientific research (see Cereghino et al. 2008). This often results in wrong management decisions with negative consequences for the nature.

Pools differ functional to other aquatic systems (see Cereghino et al. 2008). The often in nature conservation applied species-area models ('big is best') will be challenged by pool functions (Scheffer et al. 2006). On regional landscape level the pools show collectively a much higher biodiversity than rivers or lakes in the same landscape (Williams et al. 2004, Biggs et al. 2005). Also, even if single temporary pools have a lower biodiversity level and comprise a lower amount of aquatic species than permanent pools they provide often the only habitat condition for endangered species (Collinson et al. 1995, Pyke 2005). Their rarity index is comparable to permanent pools (Collinson et al. 1995). They constitute biodiversity hot spots in their landscapes (Cereghino et al. 2008). Among pools as well as among years the biotic and environmental amplitudes are greater than thus of rivers and lakes (Davies et al. 2008a). Also they occur with a factor of 100 more often than bigger lakes in the landscape (Oertli et al. 2005). Due to their number and variability they are important for studying relationships between environmental conditions, connectivity and the species they harbour. Therefore, pools provide good model systems for understanding and testing theoretical and fundamental ecological targets (De Meester et al. 2005). It is clear that the conservation of such environmental gradients at the landscape scale is essential for the conservation of among-pool variability (also called beta diversity) and total landscape biodiversity (also called gamma diversity) (Cereghino et al. 2008).

Therefore, the protection of the pool network should be rather a pool conservation issue than the focus on protecting a few pools (Biggs et al. 2005).

In that background the aim of my study was to examine, describe and predict the variety of hydrological characteristics of small infield pools, to find relationships between plant species occurrence and environment according to their trait syndromes, and to predict finally the potential plant type composition in small infield pools.

As all pools are situated within intensively agricultural managed fields, they all underlie similar agricultural impacts of nutrient contamination. Due to agricultural intensification and urban expansion many habitats of small infield pools changed within the last century with higher nutrient supply (Carpenter et al. 1998). Higher nutrient level cause higher eutrophication levels (Wheeler and Proctor 2000) with phosphorus being the major reason for high eutrophication (Schindler 1974). Both eutrophication and hydrology regimes influence strongly the species compositions of small infield pools (Van der Valk 1981, Arts and Denhartog 1990, Arts et al. 1990, Jeffries 1998, Willby et al. 2001, Brönmark and Hansson 2005, Deil 2005a, b). Also, high water level fluctuation causes high nutrient dynamic in the water bodies. My results in the nutrient measurements show very high dynamics in nutrient concentration within a single vegetation period as well as among years. The nutrient levels within a pool alter in higher amplitudes than the mean eutrophication levels of all investigated pools. But, I could not model this dynamics with climatic and water level data. Though, the buffer effects of pools morphology and pool sediment could have resulted in different mean eutrophication levels, no significant differences were detected. It could be only shown that all investigated sites have meso-trophic to eutrophic nutrient levels. Therefore, the impact of local and temporal nutrient inputs by farming activities seems to be the strongest source for current water eutrophication. Therefore, I did not expect differences in plant responses to nutrient supply among pools.

Hence, the habitat quality with respect to plants of small infield pools differs mainly in hydrological characteristics. Fine-scale hydrologic conditions are among the key factors structuring wetland communities (Weiher and Keddy 1995a, Weiher et al. 1996). Hydrological conditions expressed in mean water and mean annual water level fluctuation as for example used by Magee and Kentula (2005) miss the high variability of small infield pool environment. Changes in the environment due to dry periods can not be predicted, accordingly. Therefore, very weak relation of plant species distribution and environmental conditions may result from ignoring the strong habitat quality dynamic of changes between aquatic and terrestrial systems within as well as among years as Kazmierczak et al. (1995) found out.

In the same meso scalic climate region, small infield pools react to weather dynamics similar but with different extent. This results in different hydrological dynamics among pools as well as among hydrological years.

The strongest change in habitat quality is the change between aquatic and terrestrial environment for plant species. Hence, the drying up frequencies of the habitats have a higher ecological relevance than the water level fluctuations. Also, the germination time of most plant species is in spring season. This leads the mean high spring water level being more important for plant species than the yearly mean water level.

Hence, the hydrological parameters mean high spring water level and drying up frequency are key elements determining the dynamic and the suitability of pools for plant species. Therefore, these parameters are required to understand and predict the species composition in small infield pools.

To gain knowledge on how small infield pools function and the way that they are affected by climatic change requires a model applicable to large numbers of small infield pools regardless of their origin, morphology and interaction with the surrounding ground water system. I applied a time series model developed for ground water modelling and showed that the requirements for modelling the hydrology of small infield pools can be met by using climatic time series data, such as evapotranspiration and precipitation (recorded from the German weather administration) and daily water level observations of two year duration. Infiltration through the pool sediment layer into the next groundwater layer, water gain by lateral or artesian ground water transports into the pools were captured by an evaporation factor and a noise model respectively. I simulated 50 years long time series of water level fluctuation in 16 pools and could predict a decrease in the minimum water level and an increase in the yearly fluctuation over time in the pools. These trends are caused by rising mean annual temperatures in the study area and may be a result of changing climate.

The relationships between trends in climate and trends in hydrological characteristics can be used to calculate further hydrological trends by applying simulated climate change scenarios. Hence, future changes in the habitat quality of small infield pools can be predicted and nature conversation efforts can be adapted to the changes in environmental conditions of small infield pools.

However, two years daily time series measurements are very expensive to perform and can normally only be done on a limited number of pools. But, as the response functions in the hydrological models for precipitation and evaporation are predefined in form of a Poisson III distribution and meso-scalic meteorological data are equal for all pools within the same meso scalic climate, calculated mean high spring water levels and drying up frequencies can be related to measured hydrological characteristic data of a single hydrological year. Hence, to infer the spring water level and drying up frequency for a large number of pools I derived such transfer functions.

This allowed me to characterise a higher number of small infield pools within the same meso-scalic climate without available water level measurements at high temporal resolution. The resulting pool hydrological dynamics corresponded to their origin (kettle holes, pools in agriculturally-treated depressions due to anthropogenic soil compression, and marl or constructed holes).

To implement conservation plans for small infield pools, it is necessary to identify the species response to the dynamic of the environment. I developed a method to generate functional groups (PFGs) of plant species with respect to their response to the environment and their trait syndromes. The generated PFGs should be specific in their competition as well as surviving strategies. In natural environments both competition (biotic internal forces) and plant strategies (persist at the occurring environmental conditions, hence seen as abiotic external forces) structure a species community by rules (Weiher and Keddy 1995a, b).

This tends to limit the co-occurrence of some species (Weiher et al. 1998).

Species of a plant functional group have similar responses to environmental factors and similar competition strategies, but may differ strongly from each other in other traits. Hence, both types of traits (morphological and measurable) are required to explain the plant group distribution in small infield pools. But, this entail that the creation of plant functional groups is manifested neither on the involved traits nor in the number of traits responsible for a defined plant functional group. Furthermore, the number of species from different guilds (Weiher et al. 1998) or PFGs does not have to be similar (Weiher et al. 1998)

I applied a null model approach based on the fourth-corner-method and derived plant functional groups (PFGs) in a non-subjective approach. I calculated the response of the PFGs to the combined environmental factors spring water level and drying up frequency. I also identified the preferred site conditions for each plant functional group.

I observed eighty non-woody wetland and aquatic plant species in the 46 studied small infield pools in North-East-Germany. However, detection probabilities may vary among species and between years in an unpredictable way (Schmidt 2005) resulting by different responses to different environmental condition. Therefore, with a diaspore bank analysis I verified the observation of the total set of plant species in the sites. I analysed twenty-four traits. The resulting PFGs are defined by the traits: aerenchyms, life cycle, canopy height, turions, floating mats of species, floating leafs, tussock growth form, and biomass. The PFG-responses are comparable to relationships of plant syndromes to spring water depth retrieved from the literature. I could divide the PFGs belonging to the environment of small infield pools into aquatic macrophytes PFGs e.g. “Turions”, “Quaking mat of species”, “Floating leafs”, and “Reed fen” and wetland PFGs e.g. “Tussock”, “Sedge fen”, “Medium biomass”, and “Low biomass” by its respond to different site conditions.

With spring water level as stress gradient due to anaerobic conditions in root systems and drying up frequency as disturbance indicator, all generated PFGs prefer mainly habitats with low stress and medium drying up frequencies ($0.15<P<0.7$). Only the aquatic PFGs also prefer sites with low disturbance and higher stress as they are adapted to this kind of stress due to their morphology.

The derived PFGs have unique strategies to survive unsuitable environmental conditions and to compete against other PFGs. Strategies in storage effects are strongly coupled to competition strategies for light, soil oxygen, and nutrients. Because of their unique strategies different PFGs have different occurrence probabilities within the sites conditions of small infield pools. Highest PFG diversity is found on sites with intermediate disturbance level and low stress impact. PFG diversity declines with rising stress intensity resulting by extreme values for drying up frequencies (either low or high drying up frequencies).

I could prove the linear relationship between species diversity and PFG diversity. The applied method of grouping species into PFGs maintained the diversity among different environmental conditions. This relationship also shows if plant species went extinct, they do not disappear randomly (Fonseca and Ganade, 2001). Therefore, species and resulting PFG losses are caused by changes of the environmental conditions and underline the former statement that the small infield pools plant species composition will alter rather in a succession than in a periodic way.

One of the first applications of the plant functional groups was the simulation of vegetation responses to climate change (Woodward and Cramer 1996).

The estimation of the extinction risk of plant functional groups requires simulating the water level of the small infield pool using climate change scenarios. However, even with the presented data it is possible to predict some changes in the functional vegetation community of the small infield pools if the climate changes as expected by the IPCC (Christensen et al. 2007).

I showed that the yearly fluctuation level increased over the last 50 years, caused by warmer, dryer vegetation periods but the spring water level remains. These rising habitat dynamic will increase disturbances for plant species within the pools (Mitsch and Gosselink 1993, Kennedy et al. 2003). I expect this trend to continue in the near future according to the regional climate projections of the IPCC which expects an increase of the annual mean temperature of 3.2 degree for the study area within the next 100 years (Christensen et al. 2007). This causes changes in the physical habitat properties seen in more frequent and longer periods of terrestrial conditions. Sites with low or medium spring water level and low drying up frequency will change into sites with similar spring water level but higher drying up frequencies. This is expected to alter the species and PFG composition of small infield pools.

Species belonging to the functional groups “Tall sedge fen”, “Tussock growth form” and “Medium biomass” will then dominate most of the sites. “Annual” species and “Reed fen” species will become very rare. The only group of aquatic plant species that is expected to persist in the small infield pools are species with turions. For all other aquatic plant species there is a very high risk of extinction in most of the small infield pools.

The species compositions that I observed in the small infield pools are the result of climate conditions of the last decade. The results of my study show that small infield pools are already becoming unsuitable for several wetland species. Hence, conservation strategies for small infield pools should include the effects of climatic changes.

Pools provide ideal model systems for studying meta-populations and meta-communities and their processes (Jeffries 2005, Cereghino et al. 2008). They fit nicely in the island ecology theory as they are suitable patches within an unsuitable environment (Cereghino et al. 2008). Compared to real islands, they react much faster, are easier to manipulate, occur more frequent, and they are much easier accessible. Hence, pools play a significant role in understanding re-colonisation and persistence processes of population during and after strong disturbance events. Searching for traits or trait syndromes of such species population may play the key factor for further ecological studies. Therefore, future research can be seen in identifying meta-communities and their reaction to environmental dynamics in the landscape.

Further, Davies et al. (2008b) showed that conservation effort in reducing nutrient/pesticide/sediment input or manipulating the hydrology on the pool scale can easier implemented than on river or lake catchment area sizes. This and the knowledge of the species response to different dynamics in the environmental conditions allow defining management strategies for certain species of interest as well as for pools in the landscape.

Construction of new pools according to nature conservation needs can easily be conducted (Williams et al. 2008). They will be rapidly colonised with several wetland species and macrophytes (Santamaria 2002).

Finally, even with the actual situation of high risks of wetland and pool losses due to human impacts, changes in climate and the resulting high risk for species extinction there is a chance to reverse the nowadays pool situation. But, it also implies a fast reaction in research as well as in applying research result by practitioners before endemic pool species become extinct (Collinson et al. 1995, Pyke 2005).

Summary

Small infield pools in the Pleistocene landscape are widespread and important habitats. They are characterised by their high hydrological dynamic among years and pools. They act as island habitats for amphibian and wetland species within an intensively treated, homogeneous agricultural landscape. And sometimes they provide the only suitable habitat for endangered and endemic species. However, the properties that make them attractive for several wetland species as well as the traits or trait syndromes which allow species to survive in such high dynamical systems are largely unknown. The dynamic in the habitat conditions is mainly driven by the hydrological regime. But, even though they are protected by law in some countries, changes in the environment affecting the hydrological regime and hence the species compositions are often ignored.

Therefore, with this study I did not try to correlate species occurrence to short time habitat qualities. I described the long time habitat quality of small infield pools before I investigated plant species responses.

To gain knowledge of how small infield pools function requires a model that can be applied to many small infield pools regardless of their origin, morphology and interaction with the surrounding groundwater system. I used a time series model developed for groundwater modelling. This model requires only two climatic time series (evapotranspiration and precipitation) and an observed daily water level time series. My results show that it is possible to simulate the water level dynamics for a large number of small infield pools with a minimum input time series of 2 years time span. Furthermore, it was obviously, that a decrease in the minimum water levels and an increase in the yearly water level fluctuations over time occurred in most of the pools. These trends are caused by rising temperatures in the study area. Therefore, there is a high risk of changing habitat quality within small infield pools if the climate alters in the study area as it is expected already. But also, this will effect the species composition of small infield pools. To define the habitat quality of small infield pools I choose the parameter mean spring water level and drying up frequency. Both parameters together explain best the habitat quality for plant species. Mean spring water level is an expression of the (oxygen) stress during germination time by the water column

above the surface. The drying up frequency is an expression for the disturbance intensity seen in the frequency of drastic changes between aquatic and terrestrial conditions. For the modelled pools these parameters could be calculated for different meso sites (defined by mean spring high water) within the pools. But for pools without a modelled water level time series I had to find transfer functions.

Zusammenfassung

Ackerhohlformen sind weit verbreitete Elemente in pleistozänen Landschaften. Sie zeichnen sich durch ihre hohe räumliche und zeitliche hydrologische Dynamik aus. Sie sind wichtige Habitate in homogenen landwirtschaftlich intensiv genutzten Umgebungen. Sie agieren als Inselhabitate für Amphibien, Sumpf- und Wasserpflanzen, für die sie teilweise die einzigen verbliebenen Lebensräume darstellen. Trotz intensiver wissenschaftlicher Bearbeitung sind sowohl die Eigenschaften, der Ackerhohlformen die das Vorkommen der Arten ermöglichen als auch die Eigenschaften, die es den Arten ermöglichen in solch dynamischen Systemen zu überleben, weitestgehend unbekannt. Die Dynamik der Habitatqualität der Ackerholformen ist weitestgehend durch deren Hydrologie charakterisiert. Auch wenn diese Landschaftselemente in einigen Ländern Europas unter Schutz stehen, wird bei Bestandsaufnahmen die hydrologische Dynamik, welche die Artenzusammensetzung bestimmt, häufig ignoriert. Aus diesem Grund habe ich in meiner Arbeit in einem ersten Schritt die hydrologischen Verhältnisse und deren Reaktion auf ändernde Umwelteinflüsse der Ackerhohlformen ermittelt, welche dann in einem zweiten Schritt mit ihrer Artenzusammensetzung in Beziehung gesetzt wurde.

Zur Ermittlung der Wasserstandsdynamik der Ackerhohlformen verwendete ich Menyanthes, ein Zeitreihenmodell, welches für Grundwassermodellierungen entwickelt wurde. Dieses Model benötigt als Eingangsdaten lediglich die zwei klimatischen Zeitreihen Niederschlag und potentielle Transpiration sowie eine Pegelstandszeitreihe für jede zu modellierende Hohlform. Dementsprechend ist mein Modellierungsansatz auf eine Vielzahl von Hohlformen unabhängig ihrer Entstehung, Morphologie, und Interaktionen zum Grundwasserleiter anwendbar. Meine Resultate zeigen, dass tägliche Wasserstandsdaten über einen Zeitraum von zwei Jahren ausreichen, um die Wasserstände mit Hilfe von meteorologischen Daten für beliebig lange Zeiträume zu simulieren. Weiterhin konnte ich zeigen, dass die jährlichen Pegelminima einen Abwärtstrend und die jährlichen Pegelschwankungen einen Aufwärtstrend während der zweiten Hälfte des 20. Jahrhunderts in fast allen Ackerhohlformen des Untersuchungsgebietes haben. Diese Trends werden durch steigende Jahresmitteltemperaturen verursacht.

Deshalb besteht aufgrund der erwarteten Klimaänderung die Gefahr der Änderung der hydrologischen Verhältnisse und damit auch der Habitatqualität. Für die ökologische Charakterisierung der hydrologischen Habitatqualität verwendete ich die beiden Parameter langjähriges Frühlingshochwasser und Austrocknungshäufigkeit. Das Frühlingshochwasser ist ein Maß für den Sauerstoffstress, dem die Arten während der Keimungsphase unterliegen. Die Austrocknungshäufigkeit ist ein Ausdruck für die Störung des Systems durch den Übergang von aquatischen zu terrestrischen Bedingungen. Für die modellierten Ackerhohlformen konnten diese Parameter für verschiedene Standorte innerhalb jeder Hohlform (definiert durch die Wassertiefe des Standorts) ermittelt werden. Da aus logistische Gründen nur für einen Teil der im Untersuchungsgebiet liegenden Hohlformen tägliche Wasserstände gemessen werden konnten, entwickelte ich Transferfunktionen die eine Charakterisierung von im Gebiet liegenden Hohlformen mit monatlich gemessenen Wasserständen ermöglichte. Für die hydrologisch modellierten Ackerhohlformen konnte ich das langjährige Frühlingshochwasser und die Austrocknungshäufigkeit aus Beziehungen zwischen hydrologischen Langzeitparametern aus den Simulationen und Kurzzeitaufnahmen der aufgenommenen Datenreihen ableiten. Die Transferfunktion der langjährigen Frühlingshochwasser ist eine lineare Funktion aus den gemessenen Frühlingshochwasser und Pegelfluktuationen eines hydrologischen Jahres. Die Austrocknungshäufigkeit ist beschrieben durch eine Funktion des Quotienten aus dem Maximumwasserstand und der Pegelfluktuation eines hydrologischen Jahres.

Die Beziehung der Austrocknungshäufigkeiten zum mittleren Frühlingshochwasser konnte der Genese der Ackerhohlformen zugeordnet werden (echte Sölle und Pseudosölle, Mergel- und andere Gruben, feuchte Senken).

Zur Bestimmung der Reaktion der Pflanzenarten auf die Habitatqualität gruppierte ich diese anhand von Ähnlichkeiten in relevanten Eigenschaften und Reaktionen dieser Eigenschaften auf die Habitatqualitäten. Für den Funktionalitätstest dieser Pflanzengruppen verwendete ich ein Nullmodell, basierend auf der 'fourth-corner' Methode.

Zur Auswertung einer großen Anzahl von Arten und Eigenschaften entwickelte ich eine vier Schritte umfassende Methode. Mit dieser Methode konnten alle 80 kartierten Sumpf- und Wasserpflanzen anhand der 24 aufgenommenen Arteigenschaften in 10 funktionale Pflanzengruppen eingeteilt werden. Dabei erwiesen sich nur die Eigenschaften: „Aerenchyme“, „Lebenszyklus“, Pflanzenhöhe“, „Turionen“, „Schwimmenden Pflanzenmatten“, „Unterwasserblattformen“, „Horstwuchsform“, „Wurzel- zu gesamter Biomasse“ und „Biomasse“ als funktional.

Die funktionellen Pflanzengruppen sind über die untersuchten Habitattypen unterschiedlich verteilt. Sie sind charakterisiert durch verschiedene Anpassungs-/Überdauerungs- und Konkurrenzstrategien. An aquatischen Standorten mit einer hohen hydrologischen Dynamik unterscheiden sich die funktionellen Gruppen hauptsächlich anhand ihrer Überdauerungsstrategien. Diese Strategien sind durch morphologische Ausprägungen gekennzeichnet, welche eine Anpassung an aquatische Lebensräume mit variablen Wassertiefen ermöglichen. An eher flachen Uferstandorten unterscheiden sich die funktionalen Pflanzentypen hauptsächlich durch ihre Konkurrenzstrategien. Konkurrenz tritt auf um Licht und Bodensauerstoff.

Mit steigenden Austrocknungshäufigkeiten auf Uferstandorten sinkt die Anzahl der vorkommenden Arten und Pflanzengruppen und der funktionale Pflanzentyp „Seggenried“ setzt sich durch. Die Ergebnisse zeigen, dass morphologische Eigenschaften nicht ausreichen, um die Auftretenswahrscheinlichkeit von Sumpf- und Wasserpflanzen zu erklären. Es sind zusätzliche Eigenschaften notwendig, welche die Konkurrenzstrategie charakterisieren.

Es ist gelungen die Hydrologie der Ackerhohlformen mit rezentem Klima in Beziehung zu setzen. Diese Beziehungen können benutzt werden, um Veränderungen im Wasserhaushalt aufgrund von Veränderungen des Mesoklimas abzuschätzen. Die entwickelten Transferfunktionen sind ein vielseitiges Hilfsmittel, um hydrologische Langzeitparameter für eine Vielzahl von Ackerhohlformen im gleichen mesoskaligen Klimabereich abzuleiten ohne tägliche Wasserstandsaufnahmen über einen längeren Zeitraum durchführen zu müssen. Dies kann die Bestandaufnahme und Kartierung der in Deutschland unter Schutz stehenden Biotope „Ackerhohlform“ erweitern um nicht nur die rezenten Arten sondern auch das naturschutzfachliche Potential zu ermitteln. Weiterhin kann das Wissen über die Strategien der funktionellen Pflanzengruppen genutzt werden, um die aktuelle Gefährdung als auch den potentiellen Gefährdungsgrad durch Klimaveränderungen von Arten und Artengruppen zu ermitteln. Meine Ergebnisse können auch verwendet werden um die Konstruktion neu zu erstellender Ackerhohlformen an die Ansprüche der zu schützenden Arten anzupassen.

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Curriculum vitae

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Educational history

1981- 1988	Public school “Ehm-Welk-Oberschule” Ueckermünde
1988 -1993	Special school for mathematics, techniques and science, ‘Albert Einstein Gymnasium Rostock’
1993 -1994	Architectural internship
1994 -1997	Student of Landscape management and environmental protection at the University of Rostock
1997 -1998	Visiting student at the University of East Anglia Norwich, GB; at the School of Environmental Sciences Main subjects: Applied geophysics, Ocean physics, Conservation Biology,
1998 - 2000	Degree 'Diplomingenieur für Landeskultur und Umweltschutz' of the University of Rostock
2000-2002	Maternity leave
2001	Study of Mathematics at the University in Oldenburg
2002-2005	DFG founded Dissertation at the Institute of Biology and Environmental Science at the University of Oldenburg
2005-2007	Maternity leave
2007-2009	Dissertation at the Institute of Biology and Environmental Science at the University of Oldenburg

Accompanying digital data files:

Water log files

- Data log files: for each pool a file of the logged daily water levels
- Model files 2002: model files, model results and simulations in separated files for each pool, graphical model statistic in separated files
- Model files 2003: the same as in 'model files 2002', but for 2003
- Model files 2002-2003: the same files as in 'model files 2002', but for both years modelling

Climate files

- Climate study area – Reimershagen
- Climate Schwerin
- Trends in climate

Water level observation files

- Manually observations
- Drying up frequencies and spring water level correlations
- Drying up frequence calculations
- Small infield pools categories

Chemistry files

- Water chemistry

Soil files

- Soil investigations: Soil drilling
  - Soil analysis
- Soil profile pictures: Soil profiles

Green house files

- Seed experiment

Plant species files

- Data: trait, enviroenmental, and species observation data; data provided for 'SUE'
- Results: Single trait analysis
  - PFG's

Erklärung

gemäß § 10 Abs. 2 der Promotionsordnung der Fakultät für Mathematik und Naturwissenschaften der Carl-von-Ossietzky-Universität Oldenburg.

Hiermit erkläre ich ehrenwörtlich, die vorliegende Arbeit in allen Teilen selbständig und nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben.

Lund, den 25.01.2009

Dörte Lehsten