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Diploma thesis

Effects of nutrients and water level on *Phalaris arundinacea* growth



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Annotation

This thesis is an extension of my Bc. thesis. Based upon previously conducted research in a wet grassland, Mokrý Louky, near Třeboň, Czech Republic, a mesocosm experiment was designed for investigating the effect of two nutrient regimes (non fertilized / fertilized) and three flooding regimes (saturated / spring flood / flooded) on *Carex acuta* and *Phalaris arundinacea* plants to determine the effect of management type for restoring a more diverse wet meadows system.

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I hereby declare that this thesis has been fully completed by myself with use of the cited references.

České Budějovice 28.4.2011

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Miroslava Káplová

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1 Introduction

The spread of invasive plants into natural habitats is a ubiquitous global problem with negative economic and ecological impacts (Kercher *et al.*, 2007). The trend of the past several decades of increased anthropogenic disturbances, abandonment of traditional management, and a dramatic increase in nutrient supply has resulted in rapid invasion of more tolerant, fast-growing, and morphologically plastic plants like *Phalaris arundinacea*, with a subsequent change in plant composition (Kercher *et al.*, 2007). This all has led to a large decrease in biodiversity, together with perturbations in ecological functioning of many wet meadows (Benstead *et al.*, 1999). Wetlands are some of the most important ecosystems on Earth and for the functions they perform they are sometimes called as “the kidneys of the landscape” (Mitsch and Gosselink, 1986). Therefore, due to the excess water, inflow and accumulation of sediments from agricultural and urban lands, and other contaminants, they are considered to be particularly susceptible to invasions. Knowing which factors are most influential in shifting native vegetation towards dominance by invasive species should help determine appropriate management actions (Miller and Zedler, 2003).

This thesis is an extension of a bachelor thesis (Káplová, 2009) that reported previously conducted research in a wet grassland Mokré Louky in the Třeboň Basin Biosphere Reserve, Czech Republic. Historically, the grassland area was dominated by sedges (*Carex acuta*) and grasses (*Alopecurus pratensis*) (Holubičková, 1959; Prach, 1993). Due to intensive management actions and the 2002 floods, the grassland became dominated by *Phalaris arundinacea* (> 80% cover in 2005). Cessation of fertilization and mowing, starting in 2005, has led to the re-establishment of *C. acuta* in parts of the grassland.

The experimental area was divided into two parts with significantly different nutrient levels. A nutrient richer site, with close proximity to a still fertilized field, had been receiving more nutrients through run-off. Differences in nutrient availability between sites resulted in an almost twice as large net aboveground primary production in the richer site in 2007 and 2008. Moreover, the sites differed in species composition between those years. In the nutrient poorer site, *Carex acuta* and *P. arundinacea* were co-dominants, while cover of *P. arundinacea* was about 80% in the richer site.

Therefore, based on these outcomes we designed a mesocosm experiment to investigate the effect of two nutrient regimes (non fertilized / fertilized) and three flooding regimes (saturated

/ spring flood / flooded) on *C. acuta* and *P. arundinacea* plants to determine the effect of management type for restoring a more diverse wet meadows system.

2 Objective and Hypotheses

Objective: Determine effects of hydrologic and nutrient conditions, both separately and interactively, in governing wet meadow structure.

Hypotheses:

- 1) *Phalaris* dominates in nutrient-richer conditions.
- 2) *Phalaris* plants are restricted by constant vs. intermittent flooding regime.
- 3) Which species become the dominant under certain environment conditions depends upon changes in the species biomass allocation pattern as well as the ability to spread vegetatively.

3 Literature review

3.1 Biological invasions

3.1.1 General info

Disturbances in natural habitats caused by shifts in hydrologic regime, traditional management, and amount of nutrient supply, especially in urban and agricultural areas, increase the vulnerability of the landscape to the spread of some species that can take advantage of a partially or completely vacant niche in the new range (Lavergne and Molofsky, 2004). These invasive species pose a serious threat to native plant communities and are an important contributor to loss of biodiversity (Vitousek *et al.*, 1996) with the annual economic

impact estimated to range from millions to billions of US dollars (Lavergne and Molofsky, 2006).

Kercher and Zedler (2004b) describe “invasive plants” as species or strains that rapidly increase their spatial distribution by expanding into existing plant communities. Invasive wetland plants then divide based upon their origin. They are often exotic (e.g., *Lythrum salicaria* L. [purple loosestrife]; Edwards *et al.*, 1998), but not always. Some are native (*Typha domingensis* Pers. [southern cattail] in the Florida Everglades; Davis, 1991), others are hybrids (e.g., *Typha x glauca* Godr., which is a cross between the native *T. latifolia* and the exotic *T. angustifolia* L. [narrowleaf cattail]; Smith, 1967), while some are exotic strains of a species that is native (e.g., *Phragmites australis* [Cav.] Trin. Ex Steud. [common reed] in the U.S.; Saltonstall, 2002); (Zedler and Kercher, 2004). Moreover others species can be native strains that display invasiveness in response to environmental change. Lynch and Saltonstall (2002) described one population of *Phragmites australis* that invaded a wetland along Lake Superior and was hypothesized to be exotic, but genetic analysis proved it to belong to the native strain (Zedler and Kercher, 2004).

One example of this last type of expansive species is *Phalaris arundinacea* L. or reed canary grass (*Phalaris* hereafter). This erect, cool season perennial grass is native to Eurasia. For instance, *Phalaris* is grown on several thousand hectares in Sweden and Finland for the production of pulp and paper, and for energetic use (Lewandowski and Schmidt, 2006). However, due to the existence of many genotypes, their hybridization and cultivation for many purposes, it can become very aggressive under certain conditions. It has recently spread across North America and nowadays occurs in 43 of the United States plus Canada (Kercher and Zedler, 2004b). Unfortunately, most of the studies and experiments conducted on *Phalaris arundinacea* are from North America, where this grass poses a serious problem to their wetlands and natural habitats as it can suppress native vegetation and spread over large areas (Kercher *et al.*, 2007; Lavergne and Molofsky, 2004; Zedler and Kercher, 2004; etc.). Not many papers have been published yet about *Phalaris* and its spread in the Czech Republic or Europe. Therefore, most sources for this literature review are American with European comparison, where possible. *Phalaris* is capable of spreading large distances via seed and rhizome fragments and, once established in a wetland, can undergo rapid clonal spread and form dense monotypic stands with few coexisting species (Kercher *et al.*, 2004; 2007; Kercher and Zedler, 2004b). More information about this species is presented in chapter 3.2.

Invasive introduced plants can have deleterious impacts on the structure of native communities, including both plant and animal species, and can alter various ecosystem

processes, such as fire regimes, nutrient cycling, and hydrology (Lavergne and Molofsky, 2006). Spyreas *et al.* (2009) found that vegetation density, height, biomass, and total cover increased with increasing *Phalaris* dominance. On the contrary, diversity and floristic quality, and therefore, biological integrity of native plant communities, declined with increasing *Phalaris* cover in the experimental study and across the larger region. Therefore, plant species richness and floristic conservation values generally showed a negative relationship with *Phalaris* cover (Spyreas *et al.*, 2009; Káplová *et al.*, 2011).

3.1.2 Factors responsible for increased invasions

Although it is estimated that only 1% of introduced species actually become invasive, the damage that an invasive species can cause on native communities makes it one of the most pressing ecological problems (Lavergne and Molofsky, 2004). There are several factors that are responsible for the increase in invasive plant species. In general, when anthropogenic disturbances coincide with increased site fertility, more tolerant, fast growing, and morphologically plastic plants like *Phalaris* can invade very rapidly (Green and Galatowitsch, 2002; Kercher *et al.*, 2007). Kercher and Zedler (2004b) hypothesized that *Phalaris* and *Typha latifolia* should be competitive dominants under a variety of hydrologic conditions, at least where nutrients are abundant, as in urban and agricultural landscapes. Gaudet and Keddy (1995) found that the relationship between competitive performance of plant species grown with *Lythrum salicaria* and pattern in the field are correlated with distribution along natural gradients of fertility and standing crop.

There are several possible means by which invasive plants can disperse and establish in new areas. These include deliberate introduction for forage, erosion control, and ornamental use, increase in accidental introductions due to increased global travel and trade, and increase in habitat disturbance that can provide new opportunities for invasive plant species (Lavergne and Molofsky, 2004). The introduced species must either contain sufficient genetic diversity that will allow it to adapt or alternatively possess sufficient phenotypic plasticity (Baker, 1974). By altering morphological, reproductive, and physiological responses, invasive species can expand across altitudinal and latitudinal ranges consisting of variable vegetation, soils, temperature, and rainfall regimes (Herr-Turoff and Zedler, 2007). Invaders that reproduce vegetatively (clonal species) generally have a greater ecological impact on native communities than non-clonal species (Maurer and Zedler, 2002). Morphological plasticity is a

species' ability that contributes to survive sudden environmental changes and enable the species to spread into favorable microhabitats (Herr-Turoff and Zedler, 2007).

3.1.3 Wetlands & invasion threats

Wetlands are increasingly valued for ecosystem services, such as improving water quality through nutrient removal and filtration of sediments and chemicals, controlling and storing surface water, recharging groundwater, and providing wildlife habitat (Green and Galatowitsch, 2002). More general information, characteristics, and evaluation of wetlands and wet grasslands are presented in Káplová (2009). Estimates of global wetland area range from 5.3 to 12.8 million km². About half of the global wetland area has been lost, but still they contribute more to annually renewable ecosystem services than their small area implies (Zedler and Kercher, 2005).

Wetlands seem to be especially vulnerable to invasions. Even though ≤ 6 % of the earth's land mass is wetland, 24% (8 of 33) of the world's most invasive plants are wetland species (Zedler and Kercher, 2004). The great sensitivity of wetlands and riparian habitats to plant invasions is due to their function as landscape sinks. Therefore they receive debris, sediments, water, nutrients, salts, heavy metals, other contaminants, and species propagules from adjacent areas. Moreover, water circulation encourages plant dispersal. The disturbance caused by the accumulation of material can create canopy gaps where aggressive species can invade and capitalize on newly available resources (Zedler and Kercher, 2004). Hence, wetlands are highly dependent on the landscape context and particularly human activities and utilization. Establishment of buffer zones around sensitive wetlands may help to control water quality and release from urban and agricultural areas as well as the ban of agronomic or domestic use of deleterious species or strains (Lavergne and Molofsky, 2006).

Zedler and Kercher (2004) estimated the potential invasion threat for wetlands depending on the water source. Therefore, wetlands fed by surface water from agricultural and urbanized watersheds tend to have many invasive species (Galatowitsch *et al.*, 1999). Species richness is low and plants are of low "quality" (Kercher and Zedler, 2004a). On the other hand, wetlands that are not fed primarily by surface water (e.g., slope wetlands, vernal pools, and high-altitude fens, bogs, and pools) have small watersheds, depend more on rainfall or groundwater than on surface-water runoff tend to be species rich and relatively free of invasive plants.

Their high species richness is generally attributed to low nutrient concentrations in groundwater (Zedler and Kercher, 2004).

Eutrophication, a disturbance caused by excess of nutrients particularly in wetlands surrounded by agriculture or urban development, lead to shifts in plant community composition, decreases in plant species diversity and losses of rare or uncommon species in wetlands of western Europe and North America (Herr-Turoff and Zedler, 2005). It has been shown that wetlands are very sensitive to plant invaders, especially grass species (Galatowitsch *et al.*, 1999; Zedler and Kercher, 2004). Kercher *et al.* (2004) present that once invaded by *Phalaris*, wet meadows retain few species. In their experiment, native sedge meadows supported 60 or more species but 15 or fewer when invaded by *Phalaris* (Kercher *et al.*, 2004). Furthermore, many wetland invaders, like the clonal grass *Phalaris*, form monotypes, which alter habitat structure, lower biodiversity, change nutrient cycling and productivity (often increasing it), and modify food webs (Zedler and Kercher, 2004).

3.2 *Phalaris arundinacea* L. (reed canary grass)

3.2.1 Species description

Phalaris arundinacea L. (Poaceae) is a 1 to 2 m tall, long-lived perennial grass with a C3 photosynthetic pathway. This a cool season grass that begins growth early in the season, well in advance of warmseason (C4) grasses and other wet prairie vegetation (Maurer and Zedler, 2002). Spring emergence of new shoots occurs at the expense of reserve carbohydrate stored in the rhizomes (Čížková- Končalová *et al.*, 1992). The native range of *Phalaris* is circumboreal, including Eurasia and a small part of North America. Non-native strains had been repeatedly introduced to the United States shortly after 1850 for forage, soil stabilization, and wastewater treatment. Following repeated introductions, *Phalaris* became an aggressive invader that has spread throughout North America, taking over natural wet prairies, stream-banks, and wetlands. It now constitutes a major threat to native wetland vegetation and is classified as a pest in nine states of the U.S. (Lavergne and Molofsky, 2004).

Phalaris is capable of reproducing vegetatively or sexually by seeds (Kercher *et al.*, 2007). It produces dense crowns and prominent networks of vigorous underground rhizomes, allowing for aggressive vegetative spread. By tillering young clones, *Phalaris* can cover an area of one square meter and will consist of 100 tillers by the end of the first growing season

(Klimešová and Čížková, 1996). Moreover, it has a very high annual seed yield. Seeds exhibit dormancy (Vose, 1962), some seeds remain dormant and can germinate after storage for three years and thus can constitute an important component of seed banks. Germination requires light, seeds germinate within six days of wet (Zedler and Kercher, 2004), and is best in moist soils with highest germination rates in water-saturated soils (Lavergne and Molofsky, 2004).

Phalaris typically grows best under cool and moist conditions. It is found in a large array of wet habitats, such as wet meadows, wetlands, and lake shores and floodplains. *Phalaris* grows along extensive altitudinal and latitudinal gradients (Lavergne and Molofsky, 2004; Prach, 1992). Due to its early season growth, rapid vegetative spread, rapid stem elongation, wide physiological tolerance, and morphological plasticity, *Phalaris* possess ability to be highly competitive under a wide range of ecological conditions (Lavergne and Molofsky, 2004). Many factors, such as physical disturbance, intermittent water runoff, flooding, and nutrient enrichment can enhance *Phalaris* invasion in natural wet habitats (Green and Galatowitsch, 2002; Maurer and Zedler, 2002; Kercher and Zedler, 2004a). Miller and Zedler (2003) found that a transition from native vegetation to invasive taxa might occur in response to changes in water depths or hydroperiod (frequency and duration of high water levels) due to runoff from urban and agricultural lands. Comparisons of water levels in native wet prairie adjacent to monotypic stands of *Phalaris* in Wisconsin showed that *Phalaris* occurred where water was deeper, inundation was prolonged, and/or high water levels occurred more frequently (Miller and Zedler, 2003).

Phalaris has been observed to colonize preferentially post-disturbance moist devegetated sites and achieve rapid and near- total dominance over native wetland plant communities (Green and Galatowitsch, 2002). It can outcompete native plant species and form monospecific stands due to several traits it benefits from. Its plants can grow into tussocks as well as swards, it grows over a longer season than most native plants, it can make use of nutrient pulses, it has a broad ecological niche, it displays morphological plasticity, and its hollow stems allow great height growth per biomass investment (Zedler and Kercher, 2004). Empirical evidence clearly shows that *Phalaris* has deleterious effects on the integrity and function of ecosystems it is currently invading (Lavergne and Molofsky, 2006) together with concomitant loss of plant and insect diversity.

3.2.2 Spread of *Phalaris arundinacea*

Much more work has been conducted on studying the spread of *Phalaris* in North America than in the Czech Republic. Galatowitsch *et al.* (1999) report that *Phalaris* was originally introduced to the United States from Europe shortly after 1850 and it is believed to have become more aggressive following repeated introductions of agronomically-important cultivars from northern Europe for forage and stream bank erosion control since the 1930's (Kercher *et al.*, 2004). Other uses of the species include wastewater treatment (Vymazal, 2001), use as a bioenergy crop, ornamental plants, and for pulp, paper, and fiber production. Low alkaloids cultivars are used as a pure or mixture forage crop, or as persistent perennial cover for permanent pastures (Lavergne and Molofsky, 2004).

Nowadays, in southern Wisconsin, over 40,000 ha of wetlands are dominated (>80% cover) by this species (Berntal and Willis, 2004 as in Herr-Turoff and Zedler, 2005). It is also found in more than one half of Illinois' wetlands and is the most dominant plant in 74% of them (Spyreas *et al.*, 2009). Moreover, *Phalaris* is classified as a pest species in nine states of North America (Galatowitsch *et al.*, 1999).

Native to the temperate zones of the Northern Hemisphere, *Phalaris* is widely distributed throughout Eurasia where it has different cytotypes (Fig. 1, Lavergne and Molofsky, 2004). Differences between the spread of *Phalaris* in North America and Czech Republic are in the original distribution of the species. While *Phalaris* occurs more around standing water in America, it is found mostly along running water in the Czech Republic. This can probably refer to a lower oxygen deficiency tolerance in Czech genotypes, because this trait can differ among different genotypes. Phytosociological and ecological surveys of *Phalaris* population in alluvia along the Berounka River, Czech Republic, were done by Kopecký (1961). Current research, guided by Neil O. Anderson, is taking place at the Faculty of Science, South Bohemian University, Czech Republic. The purpose is to test whether genetic variation differs along the Czech rivers, but with no published results yet. However, under certain conditions, especially soil eutrophication, or abandonment of regular mowing, *Phalaris* can rapidly spread along the whole wet meadow and change species rich meadows into a monotonous stand (Káplová *et al.*, 2011; Prach and Straškrabová, 1996; etc.)

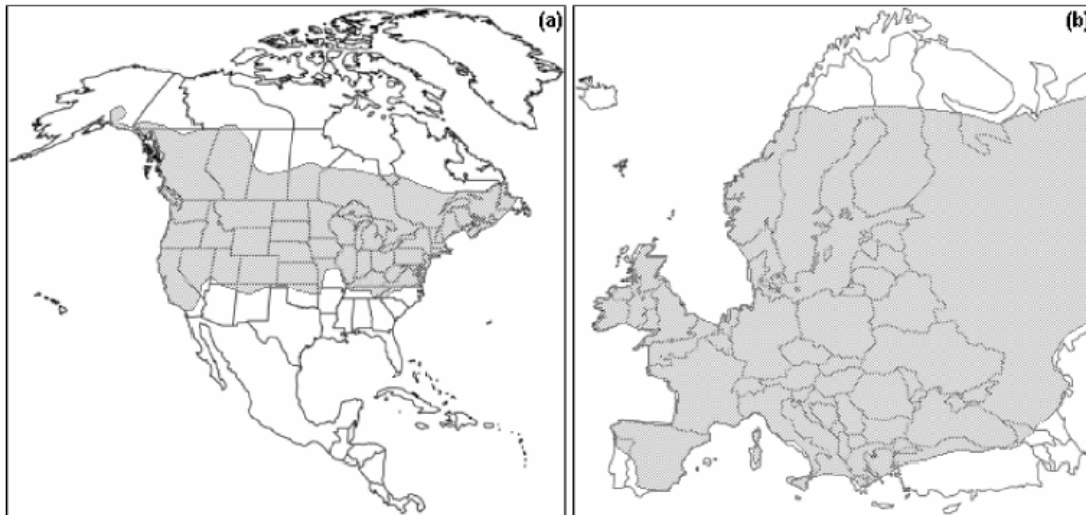


Fig. 1: Current geographical range of *Phalaris arundinacea* in its invasive range in (a) North America and in its native range in (b) Europe (Lavergne and Molofsky, 2004).

3.2.3 Abiotic factors influencing invasiveness

3.2.3.1 Disturbances

Areas subjected to physical disturbance (i.e., biomass destruction) are usually more vulnerable to invasions. The role of disturbance in facilitating plant invasions was recognized by Elton (1958). Disturbances that intensify with agricultural and/or urban development are thought to promote the spread of invasive plants, such as *Phalaris* (Kercher and Zedler, 2004a). Therefore, Larson (2005 in Kercher *et al.*, 2007) indicated *Phalaris* as a symptom of anthropogenic disturbances, perhaps even a “human symbiont”. In wetland or riparian habitats, large biomass destruction can be human induced or result from erosion after massive flooding. In its invasive range, *Phalaris* germinates best under post disturbance conditions such as canopy gaps and in moist to waterlogged soils. In its native range, *Phalaris* can persist after intense flooding that removed other species (Lavergne and Molofsky, 2004). Although physical disturbances may enhance *Phalaris* invasion, there are no data to suggest that *Phalaris* requires a disturbance to become established (Lavergne and Molofsky, 2004).

As articulated by Davis *et al.* (2000), the most invasible condition occurs when increases in the gross supply of resources coincide with decreases in the uptake of resources by the resident plant community. Kercher *et al.* (2004) found lower species richness and diversity on sites with visible indicators of hydrologic disturbance and negative relationships between the

abundance of invasive *P. arundinacea* and measures of site quality, as expressed in their model (Fig. 1).

Habitats that contain *Phalaris* have generally lower native plant species diversity. While no negative relationship was found between native species diversity and *Phalaris*, it may show that *Phalaris* preferentially establishes in habitats containing lower species diversity (Lavergne and Molofsky, 2004).

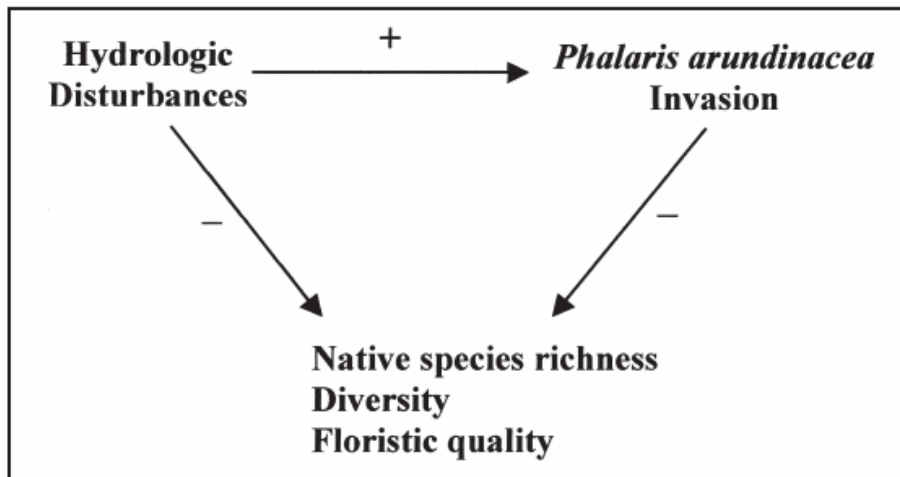


Fig. 2: Conceptual model suggesting the interrelationships of hydrologic disturbances, *Phalaris arundinacea*, and native species. “+” and “-“ signs indicate positive and negative relationships, respectively (Kercher *et al.*, 2004).

3.2.3.2 Hydrologic regime & water level

Human activities can alter water levels and the hydrologic regime in wetlands. As a result of flooding, inhibited oxygen diffusion into soils can subject root cells to anoxia. Many wetland plants tolerate inundation through morphological adaptations, such as aerenchyma, adventitious roots, and elongated shoot internodes, or by relying on energy stored in rhizomes (Miller and Zedler, 2003).

Water regimes can affect vegetative spread and thus influence invasion success of *Phalaris*. For example, initial water conditions can affect its vegetative establishment. In a greenhouse experiment, vegetative tillers survived and grew better in moist and water-saturated soils compared to flooded conditions (Maurer and Zedler, 2002). In outdoor mesocosms, flooding reduced the growth of *Phalaris* in comparison to water-saturated soil (Miller and Zedler, 2003). Hydrologic cycles may also impact the spread of *Phalaris*. Vegetative establishment and spread of *Phalaris* seem to be favored only under short-term flooding or cyclic

inundations occurring two to three days per week (Lavergne and Molofsky, 2004). On the contrary, Kercher *et al.* (2007) found no increase in *Phalaris* biomass with intermittently-flooded mesocosms receiving low levels of nutrient inputs, but *Phalaris* biomass increased by ~35% when low levels of nutrients coincided with prolonged floods. Although high levels of nutrient addition nearly tripled *Phalaris* biomass under intermittent flooding, the absolute increases in *Phalaris* biomass were five and 12 times greater when floods lasted four and 14 weeks, respectively. These authors also mentioned a possibility that, in the absence of prolonged flooding (i.e. under the intermittent flood regime), added nutrients were taken up by resident plants, leading to little increase in nutrient availability for *Phalaris* (and hence comparatively little invasion) in that treatment (Kercher *et al.*, 2007).

A similar effect of prolonged flooding was found by Herr-Turoff and Zedler (2007) in a wet prairie mesocosm study treated with three flooding durations and three levels of nutrient addition. From their results, *Phalaris* invasion was extensive under constant flooding; invasion accelerated with longer durations of flooding and with high nutrient addition. *Phalaris*' aboveground biomass was 200–900% larger under constant flooding than under early-season or intermittent flooding. Similarly, *Phalaris* increased its biomass >100% with high nutrient addition than with low or no nutrient additions (Herr-Turoff and Zedler, 2007). The effect of increased surface water was also demonstrated by Kercher and Zedler (2004a) in an outdoor mesocosm study, in which *Phalaris* grew in competition with 15 herbaceous native North American species. Dominance of *Phalaris* was reduced under intermittent flooding (flooded for two days every two weeks), while floods lasting four weeks or longer caused several sensitive native species to decline and more tolerant *Phalaris* plants to grow and spread rapidly into the large gaps created during the dieoff of the natives (Kercher and Zedler, 2004a).

However, Miller and Zedler (2003) had different results when they compared the growth of two species (*Phalaris arundinacea* and *Spartina pectinata*) alone and together under four hydroperiods (varying inundation frequency and duration) each at two water depths (surface saturation and flooding to 15 cm). Flooding reduced belowground biomass and increased total shoot length and shoot: root biomass of each species. *Phalaris* produced the most biomass, shoots, and total shoot length when wetter and drier conditions alternated weekly, while *Spartina* grew best with prolonged (four weeks) inundation. This suggests that periodically low water levels or times of drawdown are important for *Phalaris* (Miller and Zedler, 2003). Lavergne and Molofsky (2006) demonstrated that high water levels, exceeding 40 cm, and long term flooding such as 10 weeks, significantly reduced *Phalaris* growth but did not kill

individual plants, which can usually resprout and vegetatively reproduce even after a severe flood (Lavergne and Molofsky, 2006).

Results from mesocosm studies also depend on soil composition, nutrient level, and may differ from natural conditions. In Wisconsin wetlands, for example, survival and growth of transplanted rhizomes were higher in wet prairies but limited by prolonged flooding (Maurer and Zedler, 2002). Miller and Zedler (2003) also suggested that changes in water level are not the direct cause of *Phalaris*' dominance of wetlands or the loss of native grasses like *Spartina* in wetlands receiving stormwater runoff. However, stormwater runoff from urban and agricultural land carries nutrients and sediments. Hence, changes in water quality appear to be more influential than altered hydrologic regimes in explaining dominance of *Phalaris* in wetlands receiving stormwater runoff (Miller and Zedler, 2003).

3.2.3.3 Nutrients

Nutrient enrichment may be the human impact with the greatest influence on the success of plant invasions. Wetlands are particularly sensitive because they can be subject to repeated agricultural water runoff from surrounding cultivation areas (Galatowitsch *et al.*, 1999). In response to eutrophication, emergent wetland plants tend to produce more biomass, higher shoot: root ratios, more tillers, and taller shoots (Maurer and Zedler, 2002). Under natural conditions, nutrient runoff to wetlands is likely to increase competitive dominance of *Phalaris*. This may explain the observed correlation between aggressive spread of *Phalaris* in wetlands in close proximity to cultivated areas of Minnesota (Galatowitsch *et al.*, 2000) and also *Phalaris* dominance in a study site closer to a still fertilized field in a wet grassland (Mokré Louky) near Třeboň, Czech Republic (Káplová, 2009).

Elevated nitrogen (N) levels accelerate expansion of *Phalaris*. Kercher and Zedler (2004a) found that nutrient enrichment caused a greater relative increase in *P. arundinacea* than in native wet prairie species. Hence, *Phalaris* is commonly presumed to have high nutrient uptake that contributes to higher N retention in a wetland. *Phalaris* growth responded more to changes in nitrate-N compared to changes in ammonium-N, so fertilizer that increases nitrate-rich runoff and subsurface drainage are major contributors to *Phalaris* invasions (Iannone *et al.*, 2008). The extraordinary capacity of *Phalaris* to use NO₃-N inputs for growth is illustrated in its doubling of shoot biomass in response to a NO₃-N dose level between 12 and 48 g m² (Green and Galatowitsch, 2002). On the other hand, in their study Herr-Turoff and Zedler (2005) did not find support for the presumption of *Phalaris* retaining more N than

native plant assemblages. These authors tested a wet prairie under selected environmental conditions (low hydrologic disturbance, namely, intermittent flooding).

In contrast to the common assumption that *Phalaris* is a superior competitor to sedge meadow species under both N-rich and N-poor conditions (Wetzel & van der Valk, 1998; Green & Galatowitsch, 2002), *Phalaris* may, like other nitrophilic species, lack traits to confer a competitive advantage under N-poor conditions (Perry *et al.*, 2004). Therefore, desired plant species may outcompete *Phalaris* if N is limited. A greenhouse study showed that *Carex hystericina* outcompeted *Phalaris* if soil N was immobilized by incorporating a high carbon C: N amendment (pine sawdust, Perry *et al.*, 2004). According to their results, in soil without carbon added, competition with *Phalaris* reduced *Carex* biomass by 91%, while competition with *Carex* did not influence *Phalaris*, as is commonly observed in sedge meadows. *Phalaris* biomass was five times greater than *Carex* biomass in mixed stands. Conversely, in soil depleted of available N via carbon enrichment, competition with *Carex* reduced *Phalaris* biomass by 82%, while competition with *Phalaris* reduced *Carex* biomass by only 32%, indicating that *Carex* is the superior competitor for N. *Carex* biomass was six times greater than *Phalaris* biomass in mixed stands in the carbon-enriched soil (Perry *et al.*, 2004). Greater N absorption capacity of *Carex* roots probably accounts for the greater *Carex* N uptake efficiency under N-poor conditions. Low-N soils might be achieved via carbon enrichment, vegetation harvests and reduced N inputs (Perry *et al.*, 2004).

Reduction of both N and light is likely the reason why the target community decreased *Phalaris* invasion (Iannone *et al.*, 2008). Results emphasize the importance of fast establishing a perennial community in order to achieve long-term reduction of resources and *Phalaris* invasion. *Phalaris* could outcompete target species in low-light but not low-N environments. Understanding if there is a tradeoff of higher N retention when *Phalaris* displaces native species becomes critical when deciding to control its invasions or justify its use in treatment wetlands (Herr-Turoff and Zedler, 2005).

3.2.4 Biotic factors

3.2.4.1 Competitive ability

Early growth and rapid vegetative spread make *Phalaris* very aggressive in wet prairies and marshes of North America (Lavergne and Molofsky, 2004). *Phalaris* exhibits winter-hardiness due to the storage of nonstructural carbohydrates in its roots (Čížková- Končalová *et al.*, 1992). This feature enables it to overwinter in the rhizome stage and produce tillers

early in the following year. Therefore, *Phalaris* begins to sprout earlier than many sedge meadow plants. Additionally, reserve carbohydrates allow *Phalaris* to be productive into the fall and through the prolonged seasonal growth, thereby suppressing native plant species (Zedler and Kercher, 2004). In natural conditions, the species can exhibit high rates of aboveground biomass production, because of high stem elongation and leaf production (Lavergne and Molofsky, 2004). Production of dry biomass varies between 5 to 11 t . ha⁻¹, and rarely can be 12-13 t . ha⁻¹ (Rychterová, 2007).

Phalaris is also a good competitor for belowground resources because of its prolific root system and its ability to increase allocation to roots when grown in low moisture or dry conditions. In addition, the root system has a high nutrient uptake capacity (Dubois, 1994), relatively high water use efficiency, and elastic cell walls, which help in maintaining turgor despite a loss of water (Lavergne and Molofsky, 2004).

Although North American populations of *Phalaris* seem to be competitively superior to many native plant species, no studies have explicitly compared the competitive ability of European native and American invasive genotypes of *Phalaris* (Lavergne and Molofsky, 2004). However, it has been observed that, due to its different competitive effects on different native species (Green and Galatowitsch, 2002), *Phalaris* alters the dominance relationships within natural communities and reduces species diversity (Lavergne and Molofsky, 2004; Káplová *et al.*, 2011).

3.2.4.2 Morphological plasticity

Morphological plasticity occurs when an organism or genotype produces different phenotypes under varied environmental conditions by altering biomass allocations and morphological traits in shoot and root systems (Herr-Turoff and Zedler, 2007). This trait can facilitate the spread of invasive macrophytes across variable environments (Baker, 1974). By shifting biomass allocations from root to shoot systems and producing a more extensive canopy relative to shoot biomass, plants can increase their ability to capture resources across increasing nutrient and light gradients (Herr-Turoff and Zedler, 2007).

Morphological plasticity could accelerate invasions in disturbed areas with ample light, nutrients, and variable water depths, conditions typically found in wetlands downstream from developed landscapes. There is some evidence that *Phalaris* modifies its biomass allocation patterns, producing higher shoot: root ratios with increasing nutrients (Maurer and Zedler, 2002) and flooding (Miller and Zedler, 2003; Kercher and Zedler, 2004b). On a nutrient

gradient, *Phalaris* could adjust its root: shoot ratio more than co-occurring native species in sedge meadows (Green and Galatowitsch, 2001).

Herr-Turoff and Zedler (2007) explored canopy plasticity of *Phalaris* under three flooding durations and three levels of nutrient addition. *Phalaris* grew as a sward with intermittent and early-season flooding but shifted to tussocks under constant flooding. While forming tussocks, *Phalaris* tolerated longer durations of flooding and more than doubled its aboveground biomass (Herr-Turoff and Zedler, 2007). Similar morphological forms were also observed by Conchou and Pautou (1987) who found *Phalaris* growing as “isolated individuals” in dry areas and as “clumps” in wetter areas. Maurer and Zedler (2002) found that their *Phalaris* clones allocated approximately 30% more resources to root than shoot growth in low nutrient conditions, but nearly 75% more resources to rhizome and tiller growth than roots in high nutrient treatments. They concluded that nutrient addition can cause a three to 15% decrease in the root: shoot ratio and allow a 50% increase in clonal spread (Maurer and Zedler, 2002).

This plastic response gives *Phalaris* a competitive advantage under limiting resources. As summarized in Lavergne and Molofsky (2004), plants tend to increase their biomass allocation to belowground structures when water supply or nutrients is decreased. For lower soil nutrient levels, *Phalaris* had a higher root: shoot ratio than native species (Green and Galatowitsch, 2001). Conversely, when water level or flooding frequency increases, *Phalaris* showed a decrease in root biomass allocation and an increase in shoot biomass (Miller and Zedler, 2003). This shift may help in decreasing biomass and oxygen demand of the root system in conditions of greater availability of water and diffusion of nutrients. *Phalaris* can take advantage of increased nutrient inputs through increased biomass production, (Wetzel and van der Valk, 1998), decreased allocation to roots (Green and Galatowitsch, 2001), and higher rates of clonal spread and tiller production (Maurer and Zedler, 2002).

3.2.5 Implications for Practice

Due to complex interactions among disturbance factors, simple reductions in fertilizer use, flooding, or sedimentation alone will not likely suffice to protect wetlands from this tolerant, fast-growing, and morphologically plastic invader (Kercher *et al.*, 2007). *Phalaris* appears to grow best where water levels are highly variable, and where nutrients and sediments flow into the site. Thus, management actions to decrease the volume of stormwater runoff might

simultaneously reduce nutrient and sediment loading, thereby lessening chances that remnant native wetlands would become dominated by *Phalaris* (Miller and Zedler, 2003).

Current methods of controlling invasive vegetation focus on eradication of existing populations, and are often effective only in the short term. Manipulating resource availability to give native species a competitive advantage over invasive species could reduce ecosystem vulnerability to invasion and might more effectively control invasive vegetation (Perry *et al.*, 2004). Mechanical methods alone are not a sufficient control strategy for *Phalaris* because it can vigorously regrow from rhizome fragments and the seed bank. Hence, *Phalaris* control must be integrated into a whole ecosystem management strategy (Lavergne and Molofsky, 2006). Maurer and Zedler (2002), in agreement with Iannone *et al.* (2008), emphasize the importance of planting or encouraging the growth of native species that emerge early in the growing season and rapidly develop dense canopies. Secondly, the flow of nutrient-rich waters into wetlands must be reduced and/or eliminated to reduce the spread of *Phalaris* monotypes and other clonal invaders. Thirdly, they recommend quick action to eradicate new clones before they spread. Frequent monitoring and immediate removal of new clones is essential to prevent spread.

3.3 *Carex acuta* (syn. *Carex gracilis*)

3.3.1 Species description

Carex acuta is a rhizomatous, perennial plant characterized by a shortened stem with meristems that produce long leaves. It usually attains heights between 1,2 and 1,5 m (Soukupová, 1994) and can be found in almost all of Europe except for the mountainous regions with altitudes higher than 1000 meters above sea level (Soukupová, 1986). The tillers are polycyclic. In the first season they develop as vegetative shoots with a rosette of leaves; in the next season a reproductive culm is formed (Soukupová, 1994). The highest value of *C. acuta* total aboveground biomass estimated by Kuncová (2007) was 352 g . m⁻² in an unmown wet area of Mokré Louky in the Třeboň Basin Biosphere Reserve, Czech Republic.

The correlation between some quantitative aspects of ground water regimes and the occurrence of some plant communities in wet meadows in Netherlands was tested in a study by Grootjans and Ten Klooster (1980). The *Caricetum gracilis* community was characterized by water levels at or above the surface over four to five months. These plant species occurred where ground water levels were high with early spring floods and higher groundwater levels

were more frequent than lower ones. As found in the Lužnice river floodplain, *Carex acuta* tolerates high water levels and associated oxygen deprivation quite effectively (Klimeš, 1996). Also, the *Caricetum gracilis* colonizes predominantly meso- to eutrophic habitats (Hroudová, 1988).

In an outdoor experiment, Soukupová (1994) tested the influence of waterlogging on *Carex acuta*. Three different waterlogging regimes were established in relation to the soil surface: (a) terrestrial, with a water level between 0.20 to 0.12 m below the soil surface, (b) limosal, with a water level between 0.05 m below and above the soil surface, and (c) littoral, with a water level between 0.15 to 0.20 m above the soil surface. Maximum biomass production in terrestrial treatments of *Carex*, reached 1.66 kg . m⁻² after three seasons. The most stressed plants in the littoral/ limosal treatments produced 1.46 kg . m⁻². Thus total biomass of the sedges in the littoral treatment was reduced by about one eighth. The roots showed the greatest reduction of all component parts with decreases in biomass of 27% (Soukupová, 1994).

4 Methods

4.1 Mesocosm experiment

A mesocosm experiment was established in 2009 at the Institute of Botany, Třeboň, Czech Republic, to determine the combined effects of nutrient additions and water level on the growth and spread of *Carex acuta* and *Phalaris arundinacea*. The experiment consisted of 12 basins (187 cm long x 106 cm wide x 15 or 40 cm deep, depending on particular water level) with six pots in each (72 pots altogether) and with two nutrient and three water level treatments (see below). A similar experiment pattern was used in Kercher *et al.* (2007).

4.1.1 Plants setting

During the first year of the mesocosm experiment, *P. arundinacea* and *C. acuta* plants (aboveground with attached belowground structures) were collected at Mokré Louky (Wet Meadows) near Třeboň, Czech Republic in April 2009. 500 plants of each species were planted separately in 0,4 L plastic cups with sand and placed into tubs (Fig. 3), to which were added 12 g NPK fertilizer per tub.

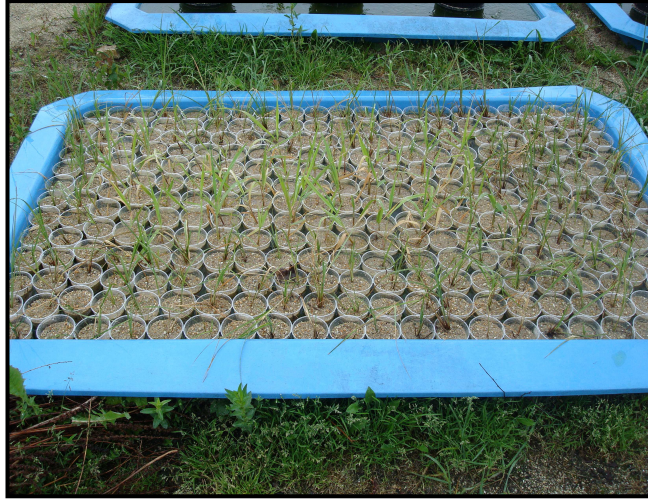


Fig. 3: Separately planted plants in 0,4 l plastic cups.

Unfortunately, many *P. arundinacea* plants died during the acclimation period. Therefore, only 288 plants of each species were planted into 72 pots with sand (15 L) respectively (four plants of *P. arundinacea* and four plants of *C. acuta* per pot) in July 2009. The small number of *P. arundinacea* plants limited us to only having pots containing both species and prevented us to have pots containing only plants of one species. Plants were separated by their height and then planted into the pots using one high, two medium and one small sized plant per each species. Six pots were placed into each tub (Fig. 4). Nutrient and water level treatments were then assigned randomly to each tub (Fig. 5).



Fig. 4: Part of the basins with pots.

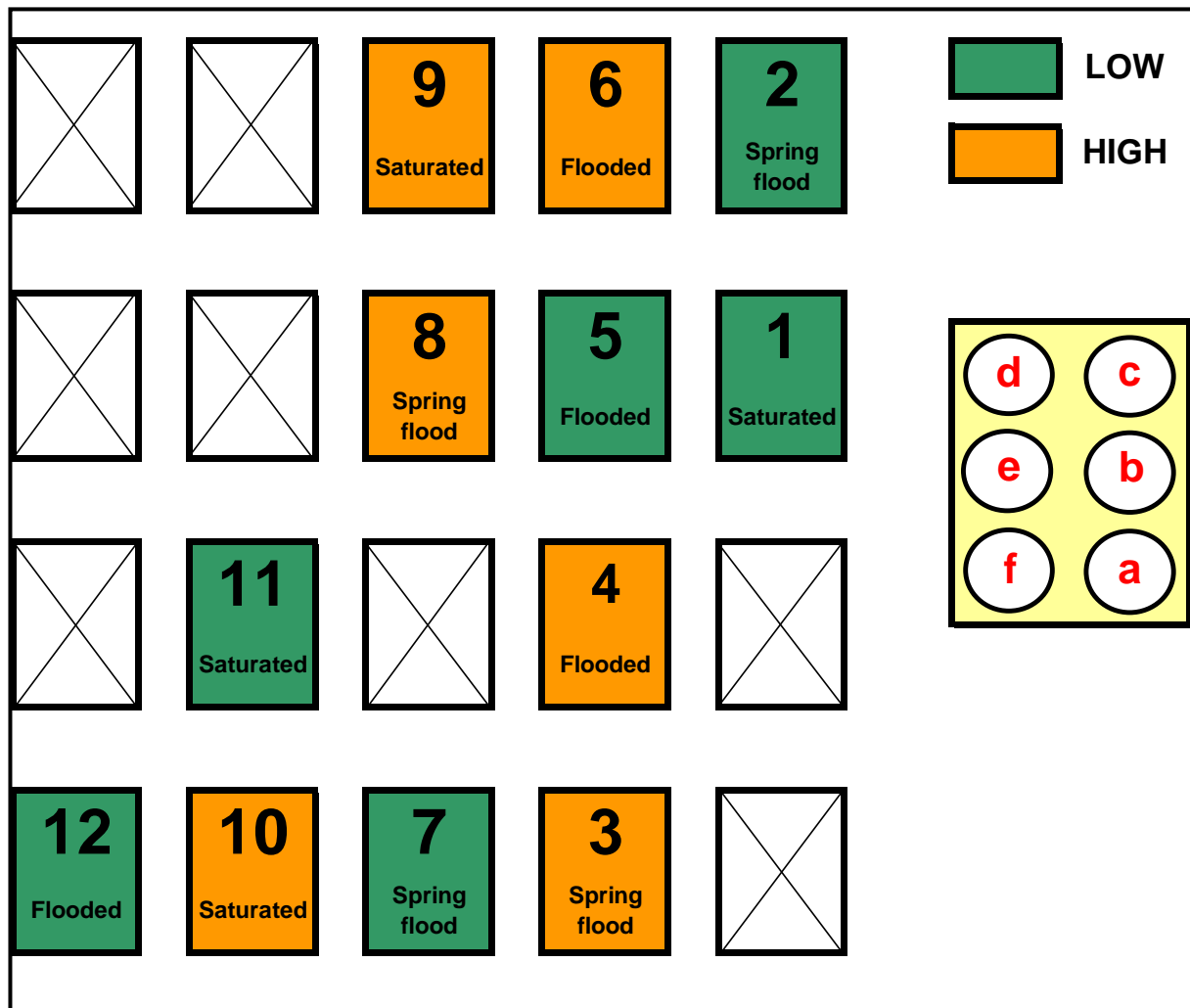


Fig. 5: Distribution and treatment type of particular basins.

4.1.2 Nutrient enrichment

For this experiment, we used two levels of nutrient enrichment: High (= 300 kg NPK * ha⁻¹ * yr⁻¹) and Low (= 65 kg NPK * ha⁻¹ * yr⁻¹), where the latter acts as the control. Lovofert NPK 15:15:15 (Lovochemie) fertilizer was used in this experiment. Nutrients were added every four weeks - twice in 2009 (on July 24 and August 26) and five times in 2010 (on April 27, June 4, July 6, August 2, and September 15) in a dose of 50 ml nutrient solution which was spread equally on the surface of each pot.

4.1.3 Water level regimes

We subjected individual tubs to one of three flooding regimes (constant flood, spring flood, and saturated), superimposed on the natural rainfall regime. As a consequence of the poor

condition of *P. arundinacea* plants after transplanting, the flood regime began on May 7, 2010. Constant flood treatments were flooded during the whole growing season until September 26. Spring flood treatments were flooded for four weeks during the growing season, from May 7 – June 4. When flooded, mesocosms contained standing water 10-12 cm above the sand surface. This water level is below the critical water depth of 40 cm estimated by Lavergne and Molofsky (2006). The standing water in the flooded mesocosms was drained every four weeks below the sand surface, in order to fertilize the pots and remove algae if needed, and then reflooded immediately.

4.1.4 Mesocosm maintenance

Due to an attack of aphids the plants were sprayed twice with a commercial preparation (Agrion Delta) on June 4 and July 13, 2010. During the winter, water from the tubs was drained and the plants were covered with dead leaves and mesh encumbered with stones as a protection against frost (Fig.6).



Fig. 6: Winter protection.

4.2 Data collection

Numbers of shoots per species per pot were counted and the height of the longest green leaf of the original four plants of each species was measured during both growing seasons. Furthermore, photos were taken of each pot to note the spread of each species during both seasons. At the end of the second growing season half of the pots (three pots from each tub)

were randomly chosen and harvested. Above- and belowground biomass of both species were collected at the end of August 2010 as well as sand samples for further analyses. Numbers of live and dead daughter plants of the original four plants were counted per each species. Biomass (aboveground with attached belowground structures) was sorted into species, washed carefully in a special tub with fresh water, and then the aboveground mass was separated from the belowground part with a knife (Fig. 7). All plant aboveground biomass fractions (live, dead, litter) and belowground biomass (roots and rhizomes together) were put into separately labeled paper bags (Fig. 8) and dried. All samples were placed into forced air ovens (Memmert) and dried at 68 - 70° C for 48 hours. The dry matter was then removed and weighed. Dry matter content was expressed as grams per square meter.

Plant biomass fractions - both aboveground and belowground - were ground with a mill to a 0.5 mm (#40) mesh size and then analyzed for total C and N by members of the Department of Ecosystem Biology, JCU. Total C and N (TC, TN) were analyzed using an elemental CN analyzer (ThermaQuest CN Analyzer, Italy). Standing stock [g/m^2] was calculated as % N, C multiplied by the dry weight of the biomass. The C: N ratio was then calculated from these data.



Fig. 7: *Carex acuta* biomass fractions



Fig. 8: Marked paper bags.

4.3 GIS

GIS methods were used to record and evaluate changes in area of the original four plants of each species in each pot. Photos of all tubs were taken at the end of both growing seasons (September 24, 2009 and August 20, 2010). However, due to the large number and height of plants, especially in the high fertilized treatments, photos from 2010 were not sufficient for

deciding where exactly a particular plant was rooted. Therefore, positions and numbers of plants were drawn manually in a 1:1 ratio in September 2010 (Fig. 9).

Photos and pictures were digitalized using ArcGIS 10 (Esri) in a coordinate system with orthographic projection “The World from space”. In order to estimate plant area, the function “Create Thiessen Polygons” was used. This tool divides the area covered by the point input features into Thiessen or proximal zones. These zones represent full areas where any location within the zone is closer to its associated input point than to any other input point. The arisen feature class was clipped to the real size of the pot and the area “sand”, where no plants grew, was omitted. Using the function “Update”, which computed a geometric intersection of the Input Features (feature class with Thiessen polygons clipped to the real size of the pot) and Update Features (area with no plants, only sand), a final feature class was created with particular areas of each plant species and sand.

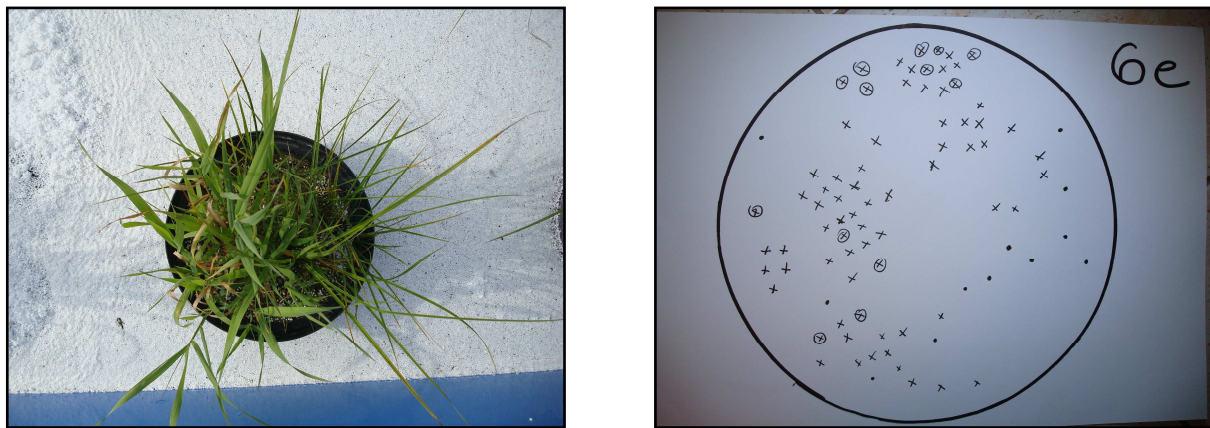


Fig. 9: Photo from 2009 and manually drawn picture from 2010 of the same pot “6e” (high flooded treatment).

4.4 Data evaluation

Factorial analyses of variance (ANOVAs) were used to analyze all of the data. In this, water level regime (“water level”), nutrient addition level (“fertilization”), tub effect (“tub”), and species were the independent variables and biomass (total, aboveground, and belowground), above to belowground ratio, stem height, numbers of shoots, nutrient contents in plants, and C: N ratio were the dependent variables. Cochran, Hartley, Bartlett tests of homogeneity of variances were performed first and, where needed, data were natural log transformed. Paired t-tests were used to compare shoot number, stem height, biomass (total,

aboveground, and belowground), above to belowground ratio, nutrient contents in plants, and C: N ratio in particular treatments between the two species (*Carex*, *Phalaris*). Alpha = 0, 05 was used for all statistical tests. All analyses were conducted using Statistica 9 (StatSoft, 2010).

Overall rate of shoot production (Mal *et al.*, 1997) was calculated by dividing the number of shoots found at the end of the second growing season 2010 by the initial number of shoots from the first growing season 2009.

Mean shoot size was calculated as the dry weight [g] of the live aboveground biomass for each species in each pot divided by the number of living plants in that particular pot.

5 Results

5.1 Shoot number and height

Both water level and fertilization treatment significantly affected shoot number (Table 1). Average shoot number per pot in the low fertilized treatments ranged from 8 to 11 shoots in *Carex* and from 21 to 29 shoots in *Phalaris*, while in the high nutrients levels it ranged from 15 to 23 shoots in *Carex* and from 59 to 69 shoots in *Phalaris*. Shoot number decreased with increased flooding duration for both species in both fertilizer treatments (Fig. 10). However, shoot number was higher in the high fertilized treatment, particularly for *Phalaris*, in contrast to the low treatment. The species significantly differed in their number of shoots ($p < 0,001$) with *Carex* having at least half the number of shoots compared to *Phalaris* in both nutrient enrichments. This resulted in a significant fertilization * species interaction, most likely due to fertilizing in both growing seasons in contrast to only one season of the flooding regime. Overall rate of shoot production in both fertilized treatments confirmed the decrease of shoots numbers with longer period of flooding in both species and fewer shoots in *Carex* (Table 2). *Phalaris* had almost twice as high shoot production in high fertilized + saturated treatment in contrast to *Carex*.

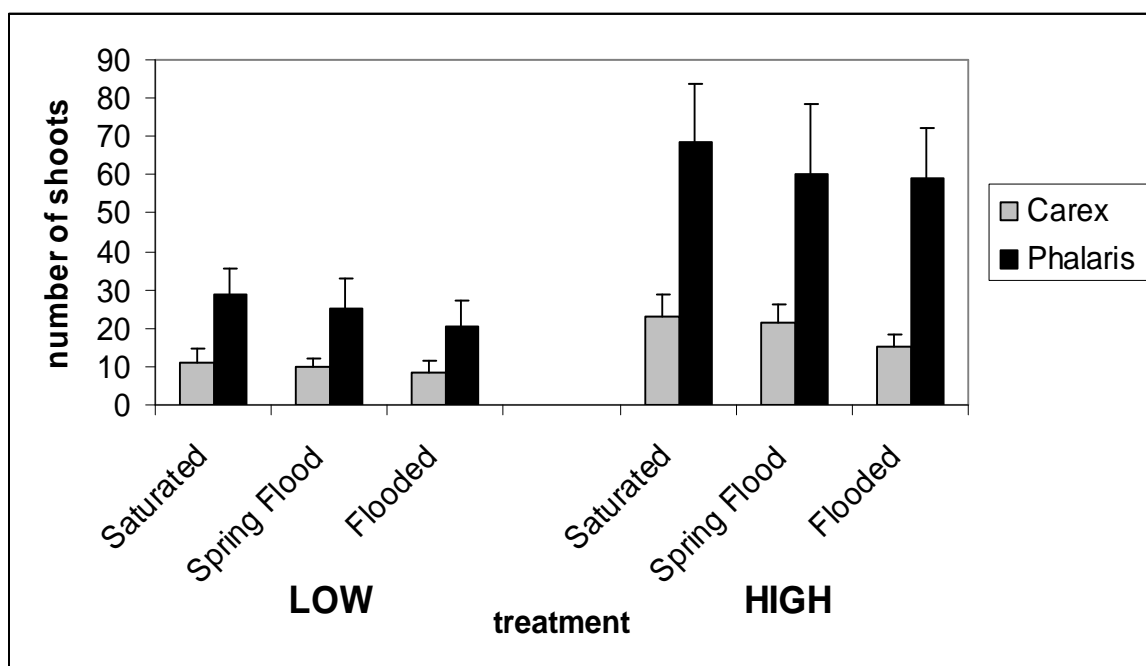


Fig. 10: Mean numbers of shoots of *C. acuta* and *P. arundinacea* in the fall 2010 ($p < 0,001$ in all treatments).

	df	F	p
water level	2	11,28	0,001
fertilization	1	316,48	0,001
tub	1	0,00	0,958
species	1	474,58	0,001
water level*tub	2	1,27	0,283
fertilization*tub	1	0,09	0,767
water level * fertilization	2	0,38	0,685
water level * species	2	1,59	0,208
fertilization * species	1	4,42	0,038
water level*fertilization*tub	2	3,17	0,056
water level * fertilization * species	2	1,87	0,158
Error	122		

Table 1: Results of factorial ANOVA for number of shoots between treatments. Significance for $\alpha = 0, 05$ is in bold.

a)	Carex	Phalaris
Saturated	1,10	1,85
Spring Flood	1,09	1,54
Flooded	1,06	1,45

b)	Carex	Phalaris
Saturated	1,72	2,31
Spring Flood	1,60	1,73
Flooded	1,14	1,65

Table 2: Overall rate of shoot production in low (a) and high (b) fertilized treatment.

Numbers of daughter plants were significantly affected by both water level and fertilization with there being significant differences between the two species ($p < 0,001$ for all). Both species had a larger number of daughters at the higher nutrient level (Table 3). For both species, total shoot number decreased while the number of dead shoots increased with increasing flood duration in the low nutrient treatment. Overall, *Phalaris* produced more daughter plants than *Carex*. Both species had the highest number of shoots under high + saturated conditions with *Phalaris* having more than three times the number of shoots than *Carex*.

Fertilization	Water level	<i>Carex</i>			<i>Phalaris</i>		
		Live	Dead	Total	Live	Dead	Total
Low	Saturated	6,9	2,7	9,6	24,7	6,1	30,8
	Spring Flood	5,9	2,7	8,6	21,3	3,1	24,3
	Flooded	4,2	3,0	7,2	16,6	7,3	23,8
High	Saturated	19,3	5,5	24,8	61,8	14,7	76,5
	Spring Flood	17,9	3,6	21,5	55,1	13,2	68,3
	Flooded	11,7	4,6	16,3	56,8	13,6	70,4

Table 3: Mean numbers of daughter plants per species and treatment.

Stem height significantly differed between the species as well as among the water regime and rate of fertilization (Table 4). Under low nutrient conditions plant height increased in both species with increased flood duration (Fig. 11). The height of *Carex* plants was similar to *Phalaris* in the low fertilized treatments. *Carex* stems had similar heights in all water regimes in the high fertilized treatments. On the contrary, *Phalaris* plants achieved the highest stem height under high fertilized + saturated conditions, but then decreased with greater flooding duration. Average stem height in the low nutrient levels ranged from 34,9 cm to 50,7 cm in *Carex* and from 36,1 cm to 46,1 cm in *Phalaris*, while in the high fertilization treatment it ranged from 56,7 cm to 59,1 cm in *Carex* and from 51,5 cm to 59,7 cm in *Phalaris*. The two species significantly differed between each other under low + flooded and high + spring flood conditions ($p < 0,001$ and $p = 0,012$, respectively).

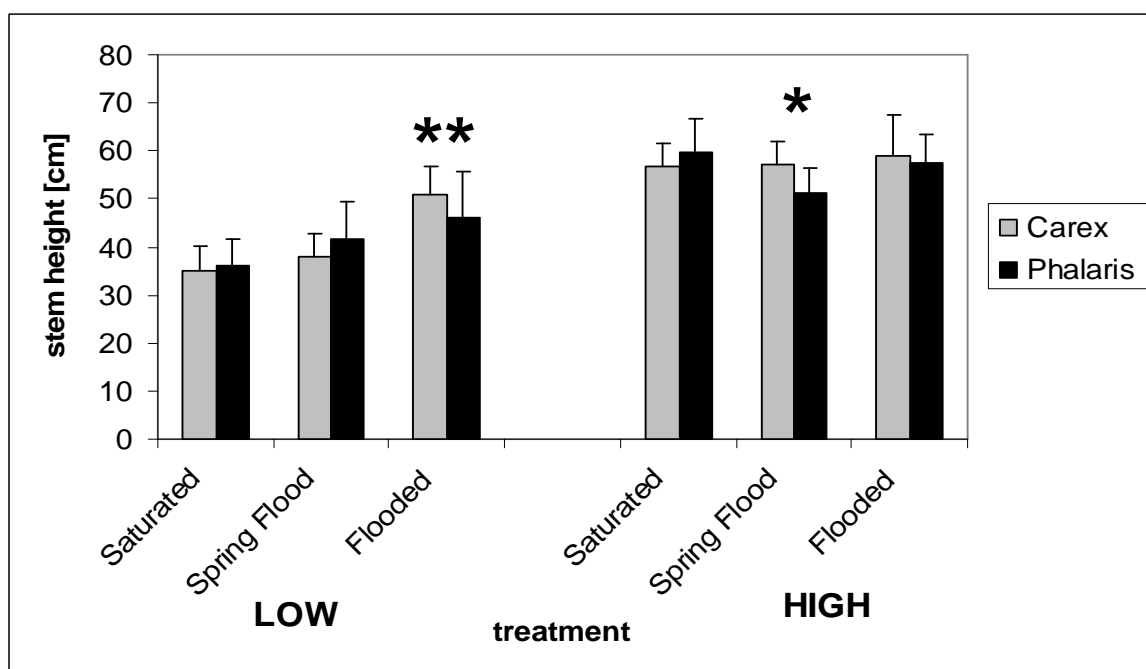


Fig. 11: Mean stem height of *C. acuta* and *P. arundinacea* (* = $p < 0,05$; ** = $p < 0,001$).

	df	F	p
water level	2	19,2	0,001
fertilization	1	512,6	0,001
tub	1	24,0	0,001
species	1	7,5	0,007
water level*tub	2	10,6	0,001
fertilization*tub	1	22,9	0,001
water level * fertilization	2	14,9	0,001
water level * species	2	2,1	0,128
fertilization * species	1	0,9	0,336
water level*fertilization*tub	2	1,6	0,213
water level * fertilization * species	2	6,5	0,002
Error	122		

Table 4: Results of factorial ANOVA for stem height between treatments.

5.2 Biomass

5.2.1 Aboveground biomass

Aboveground biomass ranged from 72,8 g/m² to 104,6 g/m² in *Carex* and from 84,3 g/m² to 107,4 g/m² in *Phalaris* in the low nutrient levels, while in the high fertilized treatment it ranged from 299,1 g/m² to 360,5 g/m² in *Carex* and from 391,2 g/m² to 554,4 g/m² in

Phalaris. *Phalaris* had significantly higher aboveground biomass than *Carex*, especially in the nutrient richer treatment (Fig. 12), but only in the saturated and spring flood conditions ($p = 0,011$ and $p = 0,028$, respectively). *Phalaris* had less aboveground biomass than *Carex* only in the low fertilized + flooded treatment, but the difference was not significant. *Carex* increased its biomass in both flooded treatments reflecting a possible better adaptation to flooded conditions. Aboveground biomass was significantly influenced by fertilization and both species significantly differed in their aboveground biomass (Table 5). Water regime did not significantly affect biomass. The weaker influence of water level can be due to only one growing season with that treatment in contrast to two seasons for the fertilization treatment. However, the water level * species interaction was significant due to the great increase in *Carex* biomass under flooded conditions (Fig. 13).

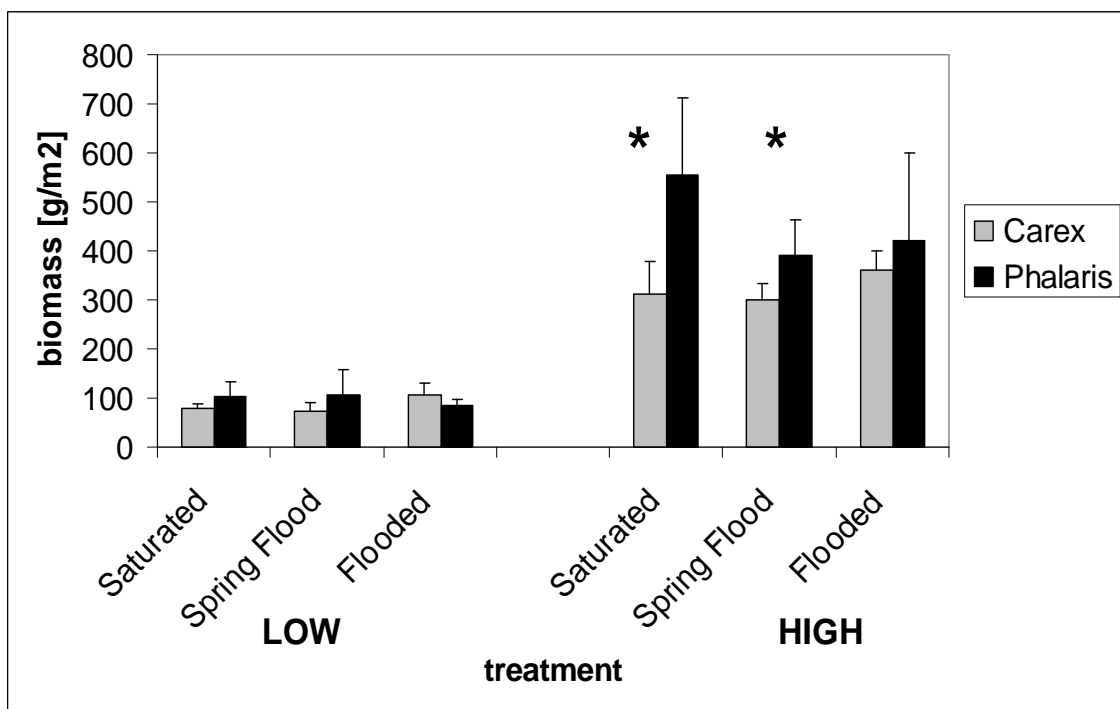


Fig. 12: Aboveground biomass of *C. acuta* and *P. arundinacea* in particular treatments (* = $p < 0, 05$).

	df	F	p
water level	2	1,8	0,181
fertilization	1	692,0	0,001
tub	1	6,4	0,015
species	1	12,4	0,001
water level*tub	2	4,8	0,012
fertilization*tub	1	21,4	0,001
water level * fertilization	2	0,6	0,579
water level * species	2	6,1	0,004
fertilization * species	1	2,7	0,108
water level*fertilization*tub	2	1,5	0,230
water level * fertilization * species	2	1,0	0,359
Error	50		

Table 5: Results of Factorial ANOVA for aboveground biomass between treatments.

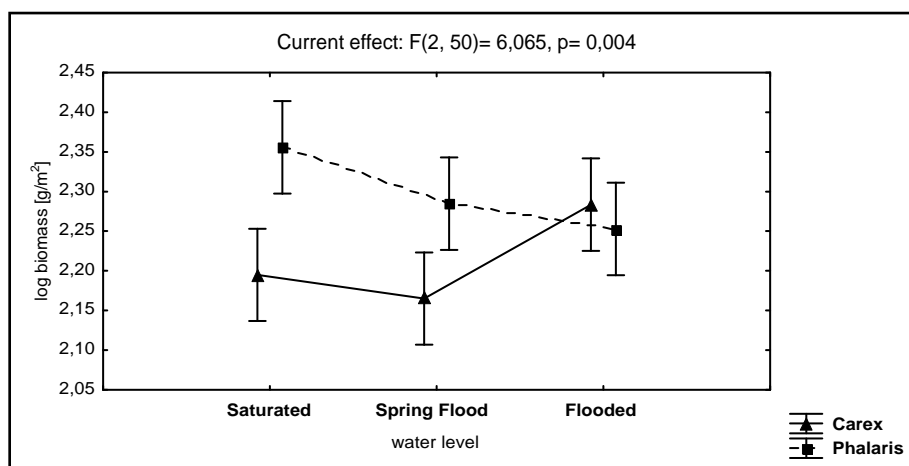


Fig. 13: Significant water level * species effect on the aboveground biomass.

The average shoot size for each species was calculated by dividing the live aboveground DW in each pot by the number of live shoots. This parameter was significantly ($p < 0,001$) affected by both water level and fertilization treatments, as well as there being a significant difference between the species. *Phalaris* had greater shoot numbers in all treatments (see above), but with smaller mean shoot size (Table 6). For example, there were increased shoot numbers for *Phalaris* in the high nutrient and flooded treatment, but these shoots were very thin with almost four times lower mean shoot size compared to *Carex*. On the contrary, *Carex* increased shoot size with longer flooding period.

Fertilization	Water level	Mean shoot size [g]	
		<i>Carex</i>	<i>Phalaris</i>
Low	Saturated	0,48	0,23
	Spring Flood	0,50	0,31
	Flooded	0,94	0,24
High	Saturated	0,86	0,52
	Spring Flood	0,88	0,45
	Flooded	1,67	0,43

Table 6: Mean shoot size of each species in each treatment.

5.2.2 Belowground biomass

Belowground biomass ranged from 362,5 g/m² to 607,8 g/m² in *Carex* and from 181 g/m² to 480,6 g/m² in *Phalaris* in the low fertilized treatments, while in the high nutrient levels it ranged from 1366,1 g/m² to 1671,7 g/m² in *Carex* and from 819,4 g/m² to 1913,3 g/m² in *Phalaris*. Both water level and fertilization significantly affected belowground biomass (Table 7). Both species also differed significantly in their production of belowground biomass. *Carex* allocated more biomass to belowground structures compared to *Phalaris* in all low fertilized treatments and the high fertilized + flooded treatment (Fig. 14). Also *Carex* had significantly higher belowground biomass in both flooded treatments ($p < 0,001$; $p = 0,022$ respectively). This resulted in there being significant water level * species and fertilization * species interactions (Figs. 15 and 16).

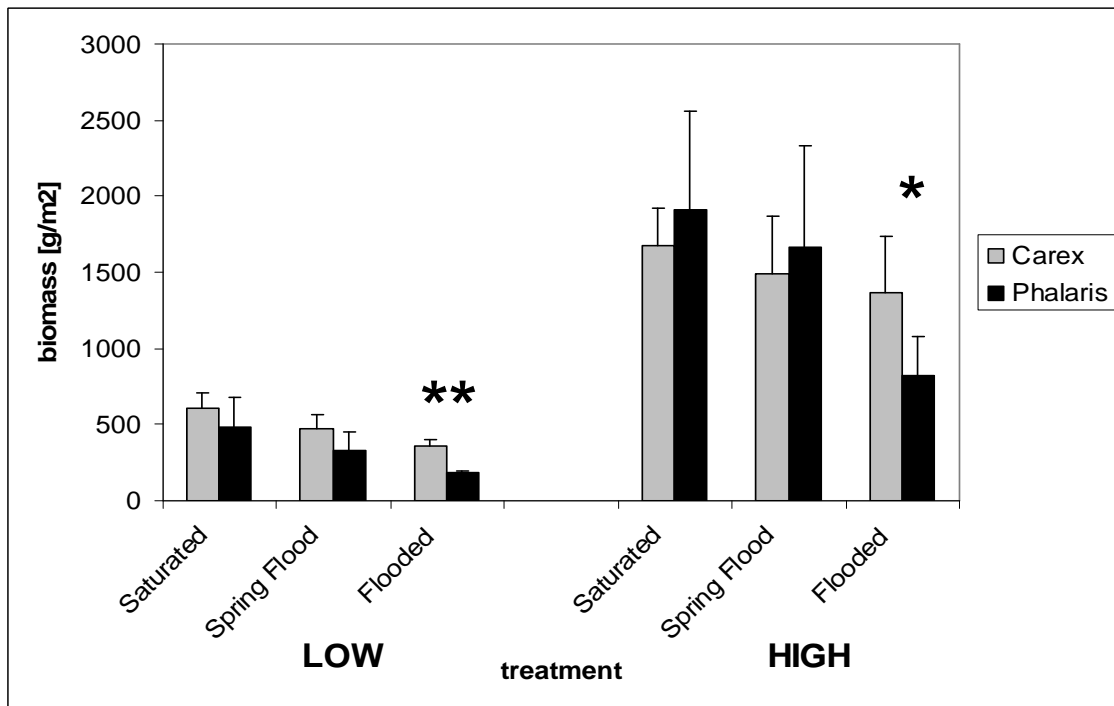


Fig. 14: Belowground biomass of *C. acuta* and *P. arundinacea* in particular treatments (* = $p < 0,05$; ** = $p < 0,001$).

	df	F	p
water level	2	26,2	0,001
fertilization	1	355,9	0,001
tub	1	0,4	0,554
species	1	16,1	0,001
water level*tub	2	1,2	0,304
fertilization*tub	1	13,8	0,001
water level * fertilization	2	0,9	0,417
water level * species	2	5,8	0,005
fertilization * species	1	7,3	0,001
water level*fertilization*tub	2	0,4	0,667
water level * fertilization * species	2	0,5	0,603
Error	49		

Table 7: Factorial ANOVA results for the belowground biomass.

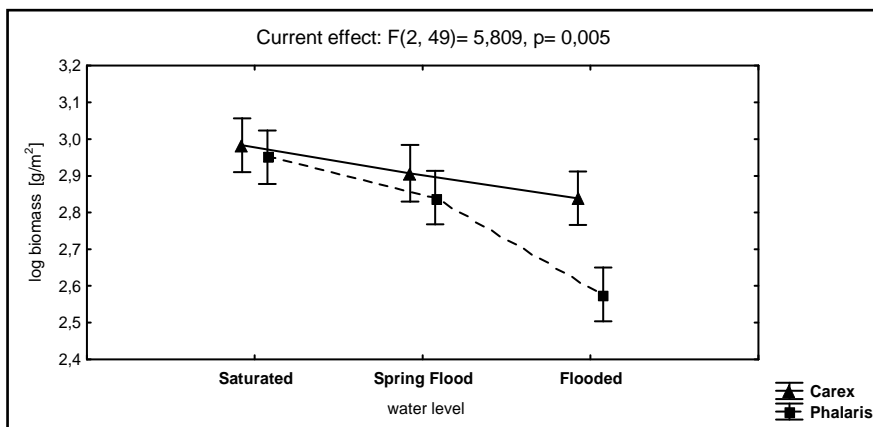


Fig. 15: Significant water level * species effect on belowground biomass.

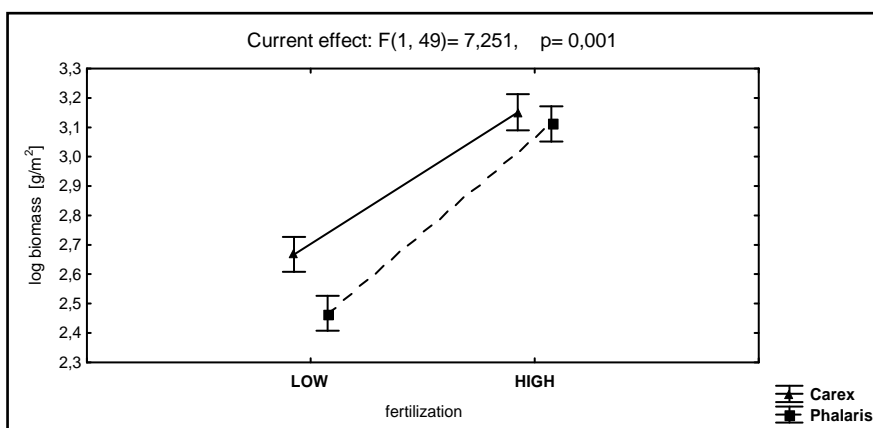


Fig. 16: Significant fertilization * species effect.

5.2.3 Total biomass

As with belowground biomass, both of the water level and fertilization treatments significantly affected total biomass for both species (Table 8). There were also significant differences between species. *Phalaris* had lower total biomass than *Carex* in the lower fertilized treatments, but with the same decreasing trend with a longer flooding period (Fig. 17). On the other hand, *Phalaris* plants were larger in the higher fertilized treatments under saturated and spring flood conditions. Only in high fertilized + flooded regime did *Phalaris* plants have lower biomass than *Carex*. It appears that *Carex* plants may be less stressed the flooded condition than *Phalaris* resulting in higher total biomass, especially in the low fertilized conditions. There were significant water level * species and fertilization * species interactions (Figs. 18 and 19), but the three way interaction among these factors was not significant. Still, *Phalaris* showed a negative response to prolonged flooding even under

nutrient richer conditions. Total biomass ranged from 467,1 g/m² to 687,1 g/m² in *Carex* and from 265,3 g/m² to 583,1 g/m² in *Phalaris* in the low nutrient levels, while in the high nutrient levels it ranged from 1726,6 g/m² to 1984,8 g/m² in *Carex* and from 1239,5 g/m² to 2467,7 g/m² in *Phalaris*.

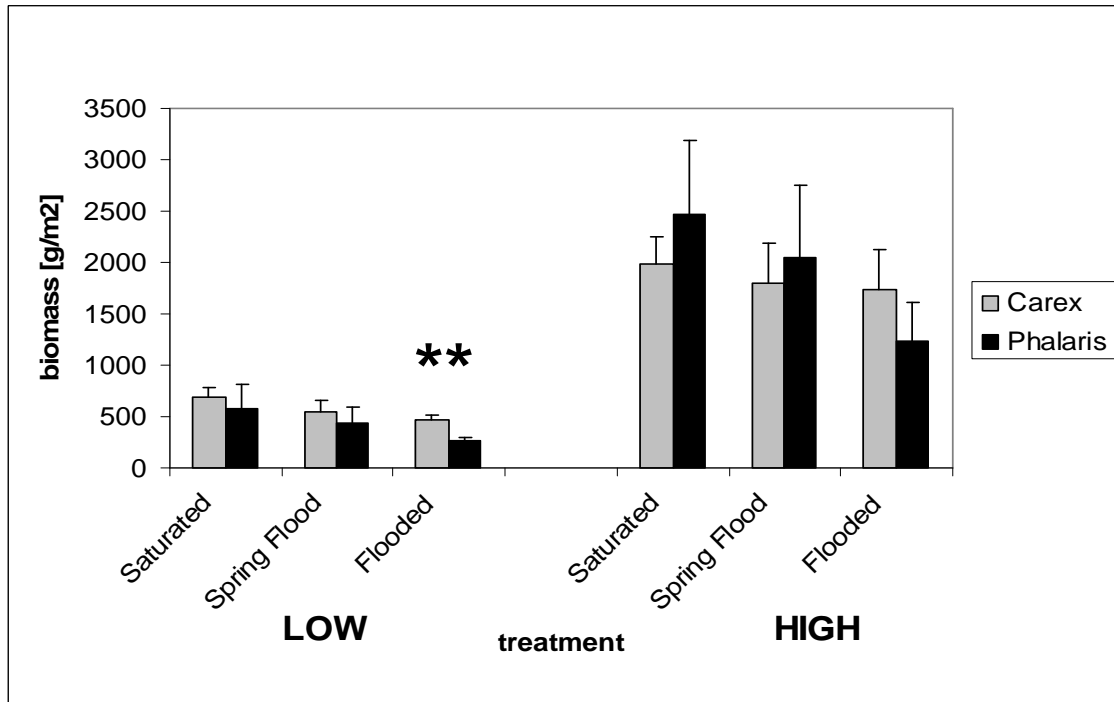


Fig. 17: Total biomass of *C. acuta* and *P. arundinacea* in particular treatments (** = p < 0,001).

	df	F	p
water level	2	19,6	0,001
fertilization	1	460,8	0,001
tub	1	0,0	0,903
species	1	7,9	0,007
water level*tub	2	2,0	0,143
fertilization*tub	1	18,5	0,001
water level * fertilization	2	0,6	0,542
water level * species	2	5,3	0,008
fertilization * species	1	8,2	0,006
water level*fertilization*tub	2	0,1	0,940
water level * fertilization * species	2	0,3	0,712
Error	49		

Table 8: Results of Factorial ANOVA for the total biomass.

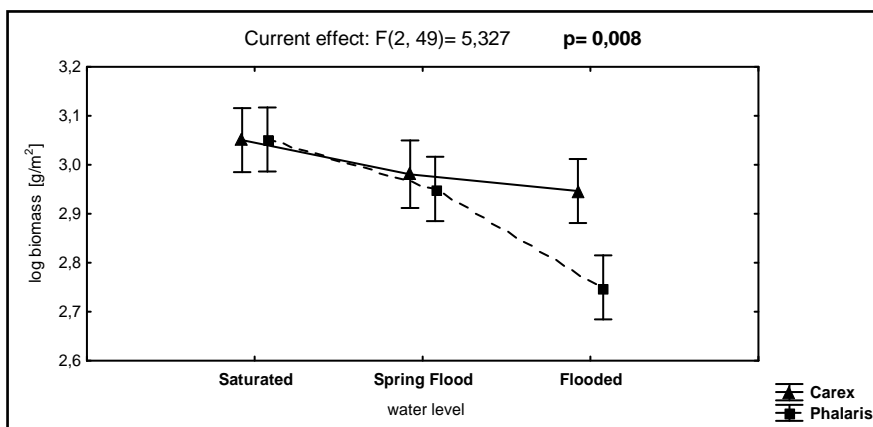


Fig. 18: Significant influence of water level * species with decrease of *Phalaris* biomass in flooded treatment.

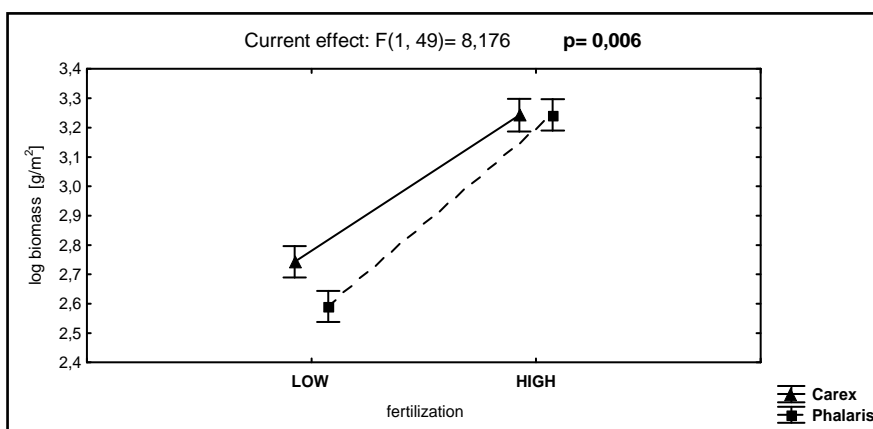


Fig. 19: Significant fertilization * species effect.

5.2.4 Above to belowground ratio

Carex allocated more biomass belowground compared to *Phalaris* in all treatments except for the high fertilized + spring flood, where both species behaved the same way (Fig. 20). The A: B ratio ranged from 0,13 to 0,29 in *Carex* and from 0,21 to 0,47 in *Phalaris* in the low nutrient conditions, while it ranged from 0,19 to 0,26 in *Carex* and from 0,24 to 0,51 in *Phalaris* in the high nutrient treatments. *Carex* significantly allocated more biomass to belowground under all low fertilized treatments ($p= 0,004$, $p< 0,001$, and $p= 0,014$; respectively) and in the high fertilized + flooded treatment ($p= 0,040$). Water level and fertilization significantly affected the biomass allocation patterns, as well as their interaction (Table 9; Figs. 21, 22). Both species showed increasing biomass allocation to aboveground

structures with flooding duration in the low fertilized treatment, but this relationship was not as clear under high fertilization.

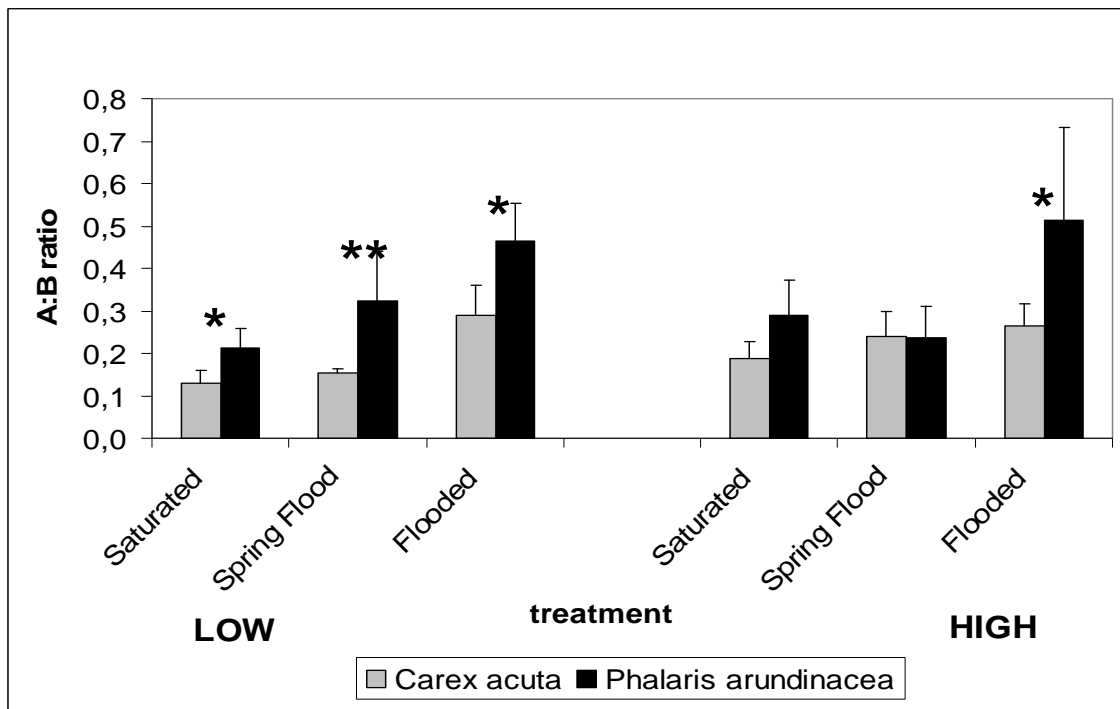


Fig. 20: Above to belowground ratio in particular treatments (* = $p < 0, 05$; ** = $p < 0,001$).

	df	F	p
water level	2	28,6	0,001
fertilization	1	7,8	0,007
tub	1	9,8	0,003
species	1	50,8	0,001
water level*tub	2	0,5	0,635
fertilization*tub	1	0,4	0,518
water level * fertilization	2	4,7	0,013
water level * species	2	1,0	0,386
fertilization * species	1	7,1	0,010
water level*fertilization*tub	2	1,8	0,181
water level * fertilization * species	2	1,9	0,158
Error	49		

Table 9: Results of Factorial ANOVA for above to belowground ratio.

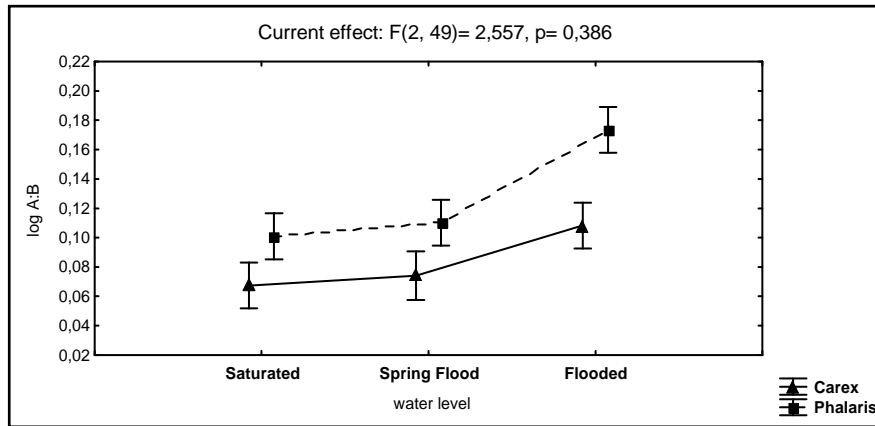


Fig. 21: Water level * species effect for the aboveground: belowground biomass ratio.

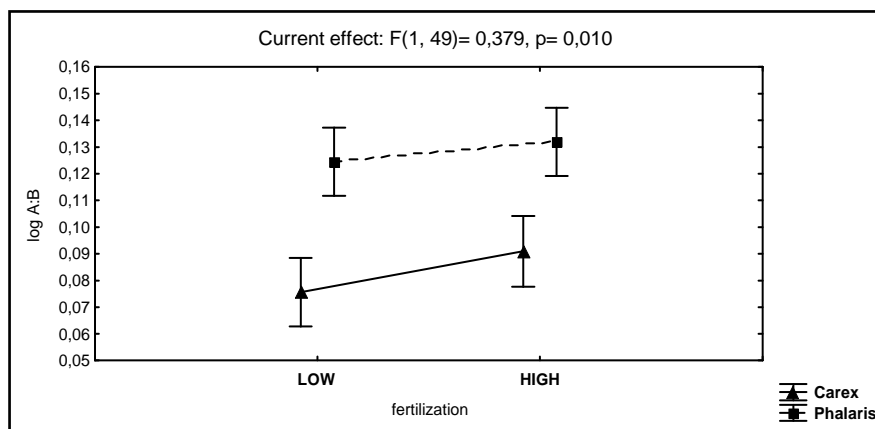


Fig. 22: Fertilization * species effect for the aboveground: belowground biomass ratio.

5.3 Nutrient contents in plants

5.3.1 Nitrogen

As expected, there was increased N% in aboveground plant structures with greater fertilization (Fig. 23). There was also a significant difference between species (Table 10). Percentage of TN per gram of aboveground material was greater in *Carex* in all treatments except the low fertilized + spring flood treatment, where both species had almost similar amounts. TN in the aboveground biomass ranged from 0,75% to 0,84% in *Carex* and from 0,67% to 0,80% in *Phalaris* in the low fertilized treatments, while in the high nutrients levels it ranged from 1,04% to 1,11% in *Carex* and from 0,86% to 0,91% in *Phalaris*.

On the contrary, *Carex* had lower content of TN in the belowground material than *Phalaris*. There were significant differences between the two species (Table 11). Under flooded conditions, *Phalaris* plants had significantly more nitrogen in belowground structures than

Carex (Fig. 24). Both treatment factors (water level, fertilization) significantly affected the % of total nitrogen in belowground biomass as well as their interaction. There were also significant water and fertilization by species interactions. Thus, the influence of water level and fertilization on how TN was allocated to belowground structures differed between the species. TN in the belowground biomass ranged from 0,32% to 0,35% in *Carex* and from 0,47% to 0,56% in *Phalaris* in the low fertilized treatments, while in the high nutrient levels it ranged from 0,32% to 0,39% in *Carex* and from 0,37% to 0,60% in *Phalaris*.

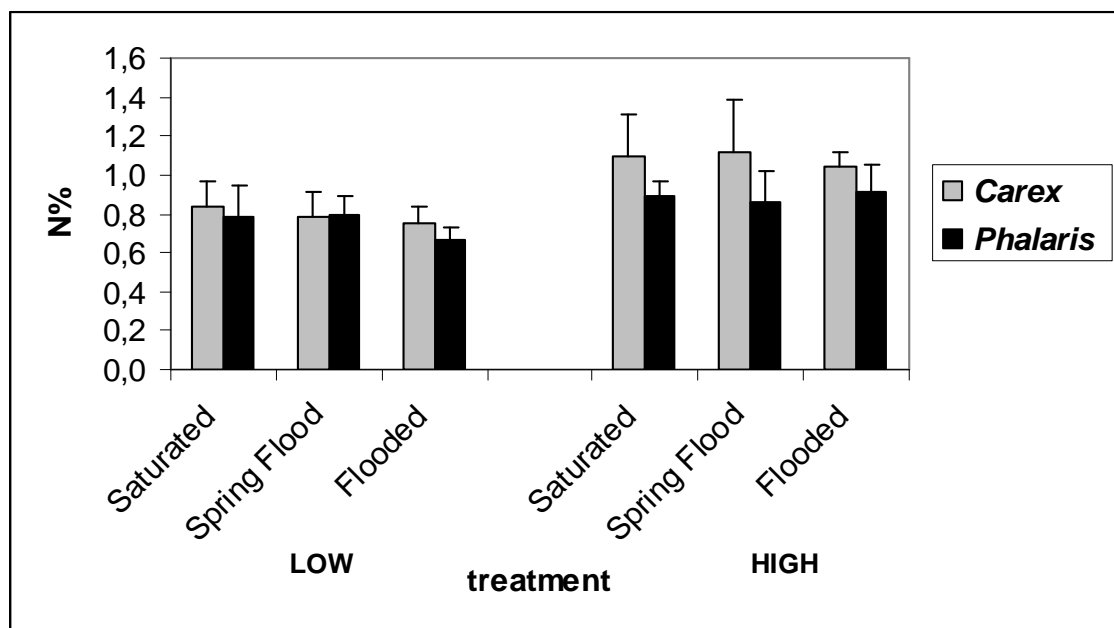


Fig. 23: Percentage of total nitrogen in **aboveground** biomass.

	df	F	p
water level	2	1,0	0,385
fertilization	1	34,0	0,001
tub	1	7,4	0,009
species	1	9,3	0,004
water level*tub	2	0,0	0,987
fertilization*tub	1	1,7	0,198
water level * fertilization	2	0,8	0,435
water level * species	2	0,0	0,983
fertilization * species	1	3,4	0,070
water level*fertilization*tub	2	1,1	0,346
water level * fertilization * species	2	0,7	0,521
Error	50		

Table 10: Results of Factorial ANOVA for percentage of total nitrogen in **aboveground** biomass.

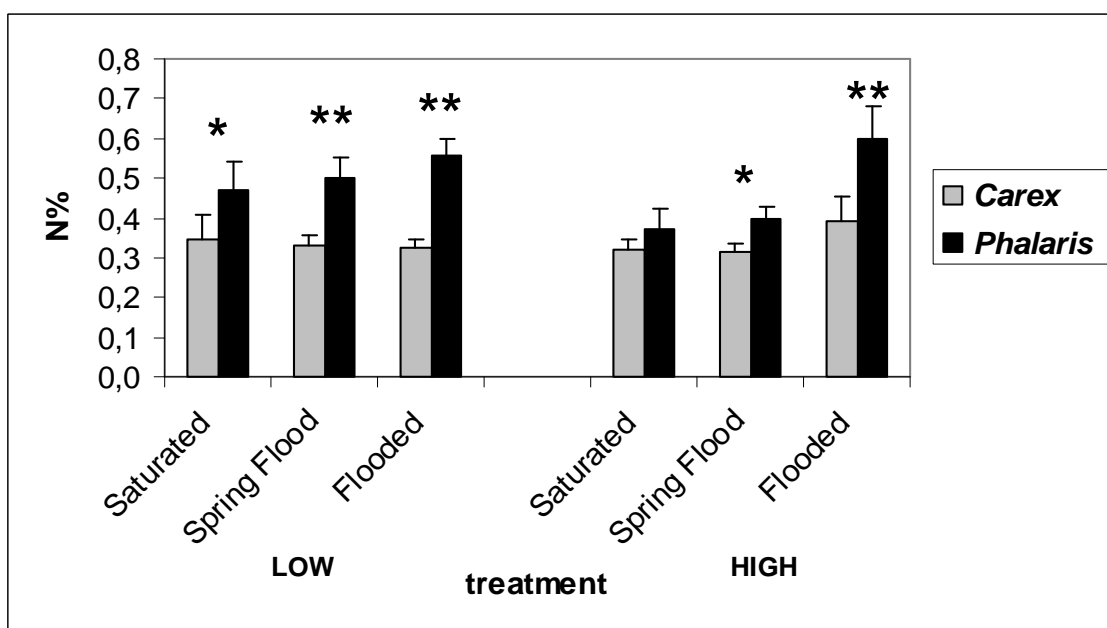


Fig. 24: Percentage of total nitrogen in **belowground** biomass (* = $p < 0, 05$; ** = $p < 0,001$).

	df	F	p
water level	2	23,8	0,001
fertilization	1	4,1	0,048
tub	1	0,0	0,915
species	1	153,8	0,001
water level*tub	2	2,9	0,064
fertilization*tub	1	4,0	0,051
water level * fertilization	2	10,8	0,001
water level * species	2	10,5	0,001
fertilization * species	1	7,7	0,010
water level*fertilization*tub	2	5,9	0,051
water level * fertilization * species	2	0,5	0,638
Error	49		

Table 11: Results of Factorial ANOVA for percentage of total nitrogen in **belowground** biomass.

Nitrogen standing stock [g/m^2] in aboveground biomass was significantly affected by fertilization (Table 12). Both species had almost the same contents in all treatments, except for the high fertilized + saturated treatment in which *Phalaris* had greater nitrogen content in the aboveground biomass compared to *Carex* (Fig. 25), but this difference was not significant. *Carex* had significantly higher nitrogen content under low fertilized + flooded conditions ($p = 0,010$). Nitrogen standing stock in the aboveground structures ranged from $0,57 \text{ g/m}^2$ to $0,78 \text{ g/m}^2$ in *Carex* and from $0,56 \text{ g/m}^2$ to $0,86 \text{ g/m}^2$ in *Phalaris* in the low nutrient levels, while in

the high nutrient levels it ranged from 3,33 g/m² to 3,76 g/m² in *Carex* and from 3,38 g/m² to 4,94 g/m² in *Phalaris*.

Both water level and fertilization treatments significantly affected TN standing stock in belowground structures (Table 13). *Phalaris* had higher amounts of nitrogen contents in belowground biomass in all treatments except for the flooded ones, but these were not significantly different (Fig. 26). Nitrogen standing stock in the belowground structures ranged from 1,18 g/m² to 2,12 g/m² in *Carex* and from 1,01 g/m² to 2,25 g/m² in *Phalaris* in the low fertilized treatments, while in the high nutrient levels it ranged from 4,70 g/m² to 5,36 g/m² in *Carex* and from 4,89 g/m² to 7,14 g/m² in *Phalaris*.

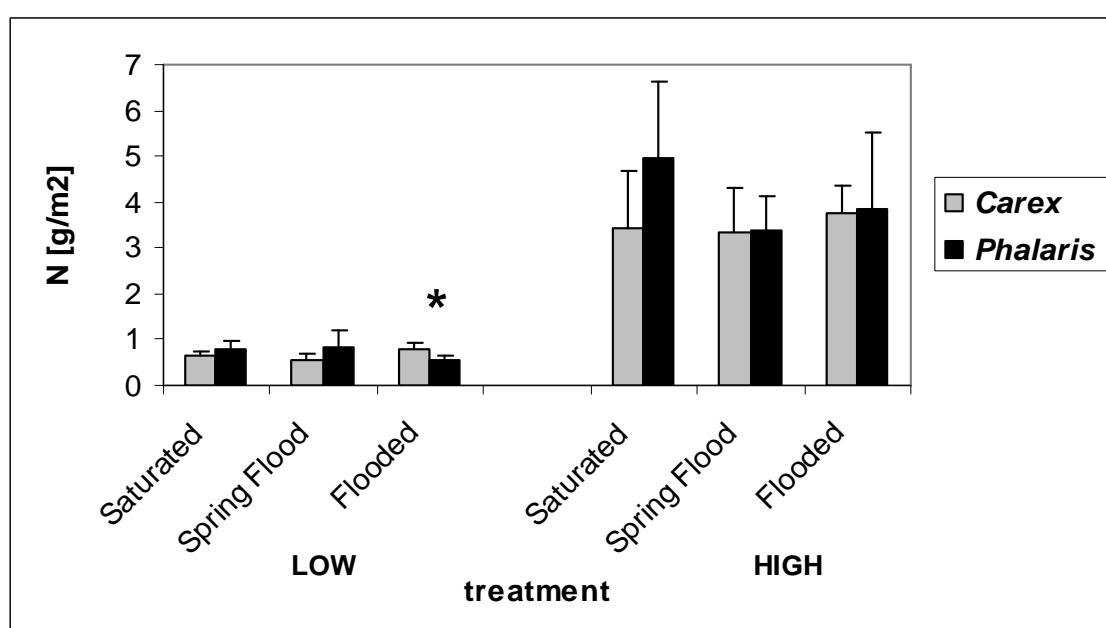


Fig. 25: Nitrogen contents [g/m²] in **aboveground** biomass (* = p < 0,05).

	df	F	p
water level	2	1,5	0,240
fertilization	1	550,3	0,001
tub	1	0,9	0,361
species	1	1,6	0,212
water level*tub	2	3,3	0,044
fertilization*tub	1	15,6	0,001
water level * fertilization	2	0,9	0,402
water level * species	2	3,0	0,060
fertilization * species	1	0,4	0,531
water level*fertilization*tub	2	1,4	0,259
water level * fertilization * species	2	1,4	0,245
Error	50		

Table 12: Factorial ANOVA results for nitrogen contents in **aboveground** biomass.

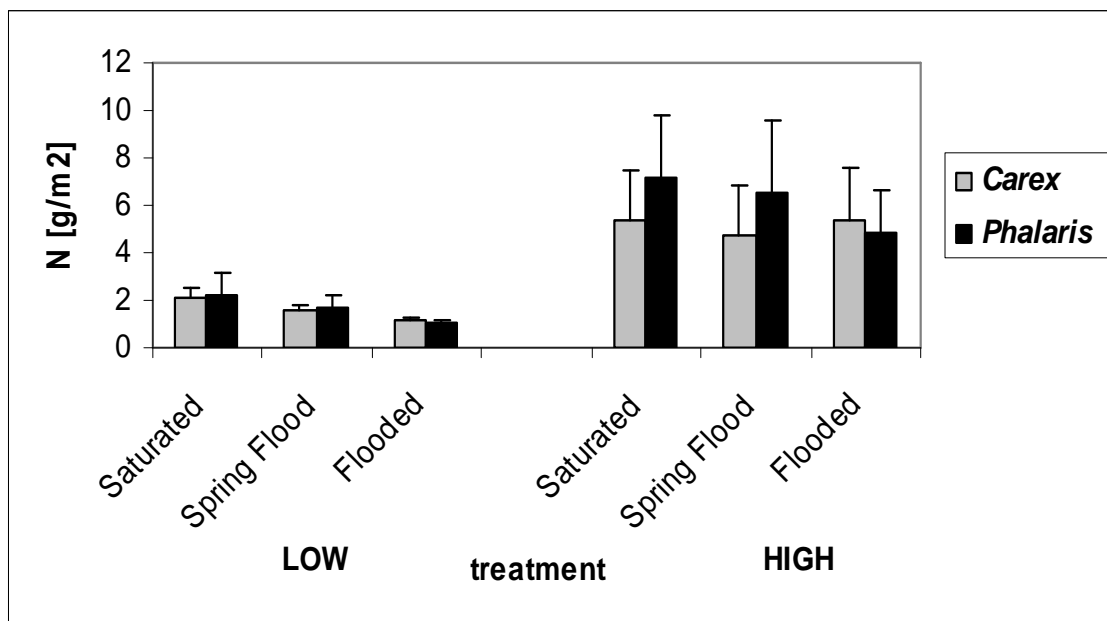


Fig. 26: Nitrogen contents [g/m²] in **belowground** biomass.

	df	F	p
water level	2	6,8	0,002
fertilization	1	236,6	0,001
tub	1	1,0	0,316
species	1	1,3	0,256
water level*tub	2	2,0	0,140
fertilization*tub	1	15,2	0,001
water level * fertilization	2	1,7	0,202
water level * species	2	1,6	0,219
fertilization * species	1	1,9	0,174
water level*fertilization*tub	2	0,8	0,442
water level * fertilization * species	2	0,5	0,605
Error	49		

Table 13: Factorial ANOVA results for nitrogen contents in **belowground** biomass.

5.1.1 Carbon

Percentage of total carbon in aboveground biomass was significantly higher in *Carex* in all treatments except for the high fertilized + spring flood treatment (Fig. 27). TC % decreased with longer flooding period in both species, except again for the high + spring flood. TC % in the aboveground biomass was significantly affected by water level, fertilization, and species (Table 14). There were no significant interactions. TC in the aboveground structures ranged from 44% to 48% in *Carex* and from 42,9% to 43,2% in *Phalaris* in the low fertilized

treatments, while in the high nutrient levels it ranged from 44,6% to 45,8% in *Carex* and from 43,6% to 44,3% in *Phalaris*.

No significant effects were found for % TC in belowground biomass (Table 15). *Carex* seemed to have similar % TC in all treatments in belowground material, but the results were quite variable (Fig. 28). This was also the case for *Phalaris*, except that there was a nonsignificant increase in % TC with flooding duration under high fertilization levels. TC in the belowground structures ranged from 41,2% to 41,5% in *Carex* and from 41,3% to 42,3% in *Phalaris* in the low nutrients levels, while in the high fertilized treatments it ranged from 41% to 42,3% in *Carex* and from 39,5% to 42,5% in *Phalaris*.

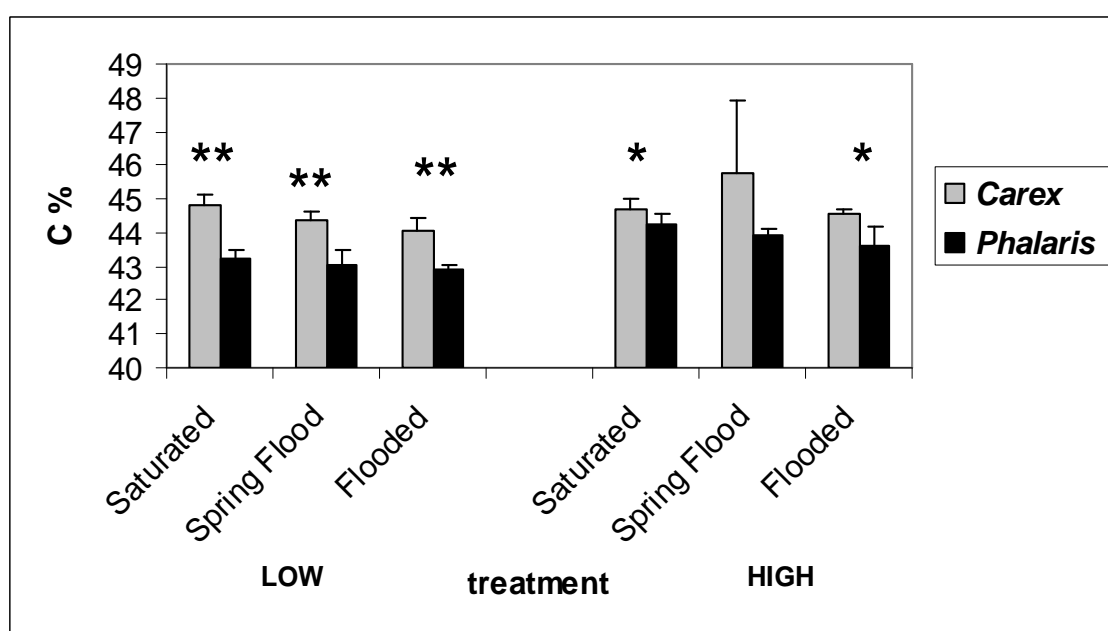


Fig. 27: Percentage of total carbon in **aboveground** biomass (* = $p < 0,05$; ** = $p < 0,001$).

	df	F	p
water level	2	3,9	0,026
fertilization	1	20,3	0,001
tub	1	2,5	0,122
species	1	56,1	0,001
water level*tub	2	0,0	0,955
fertilization*tub	1	3,3	0,077
water level * fertilization	2	1,5	0,237
water level * species	2	1,1	0,325
fertilization * species	1	0,9	0,337
water level*fertilization*tub	2	1,3	0,289
water level * fertilization * species	2	2,0	0,150
Error	50		

Table 14: Factorial ANOVA results for percentage of total carbon in **aboveground** biomass.

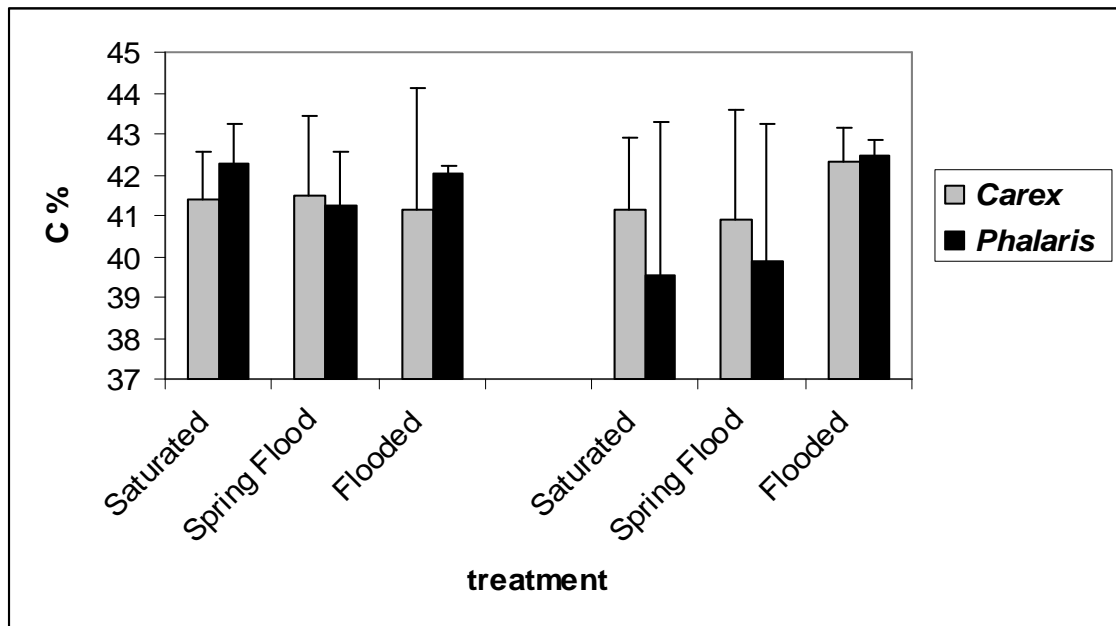


Fig. 28: Percentage of total carbon in **belowground** biomass.

	df	F	p
water level	2	1,3	0,280
fertilization	1	1,0	0,334
tub	1	0,4	0,532
species	1	0,1	0,712
water level*tub	2	0,4	0,676
fertilization*tub	1	1,9	0,169
water level * fertilization	2	1,5	0,226
water level * species	2	0,4	0,654
fertilization * species	1	1,6	0,210
water level*fertilization*tub	2	1,0	0,393
water level * fertilization * species	2	0,2	0,789
Error	49		

Table 15: Factorial ANOVA results for percentage of total carbon in **belowground** biomass with no significant effects.

Carbon standing stock [g/m^2] in aboveground biomass significantly differed between the nutrient treatments and the two species (Table 16). Moreover, there was a significant water level * species interaction, as shown by the slight increase of carbon in the aboveground biomass of *Carex* with a longer flooding period (Fig 29). On the contrary, C content in the aboveground biomass of *Phalaris* seemingly decreased with longer flooding, but this species still had higher C content than *Carex*, being significantly higher in the high fertilized + saturated treatment ($p= 0,011$). Carbon standing stock in the aboveground biomass ranged

from 32,3 g/m² to 46,1 g/m² in *Carex* and from 36,2 g/m² to 46,2g/m² in *Phalaris* in the low nutrient levels. In the high nutrient levels, it6 ranged from 137 g/m² to 160,7 g/m² in *Carex* and from 171,9 g/m² to 245,3 g/m² in *Phalaris*.

Belowground C content in the low fertilization treatments ranged from 148,2 g/m² to 251,7 g/m² in *Carex* and from 76 g/m² to 203,1 g/m² in *Phalaris*. In the high fertilization treatments ranged from 578 g/m² to 688,1 g/m² in *Carex* and from 347,8 g/m² to 756,1 g/m² in *Phalaris*. Carbon contents in belowground biomass were significantly affected by the fertilization and water level treatments and also between species (Table 17). C content in *Carex* belowground was greater than *Phalaris* under nutrient poorer conditions, with decreasing C content with increased flood duration. However, only in the low nutrient + flooded treatment did belowground C content differ significantly between the species (p<0,001). Belowground C content also decreased with greater flood duration in the high nutrient conditions, but the change was greater for *Phalaris* than *Carex* (Fig. 30), probably resulting in there being significant fertilizer * species and water level * species interactions. Still, only for the high nutrient + flooded treatment, was there a significant difference between the species (p= 0,019).

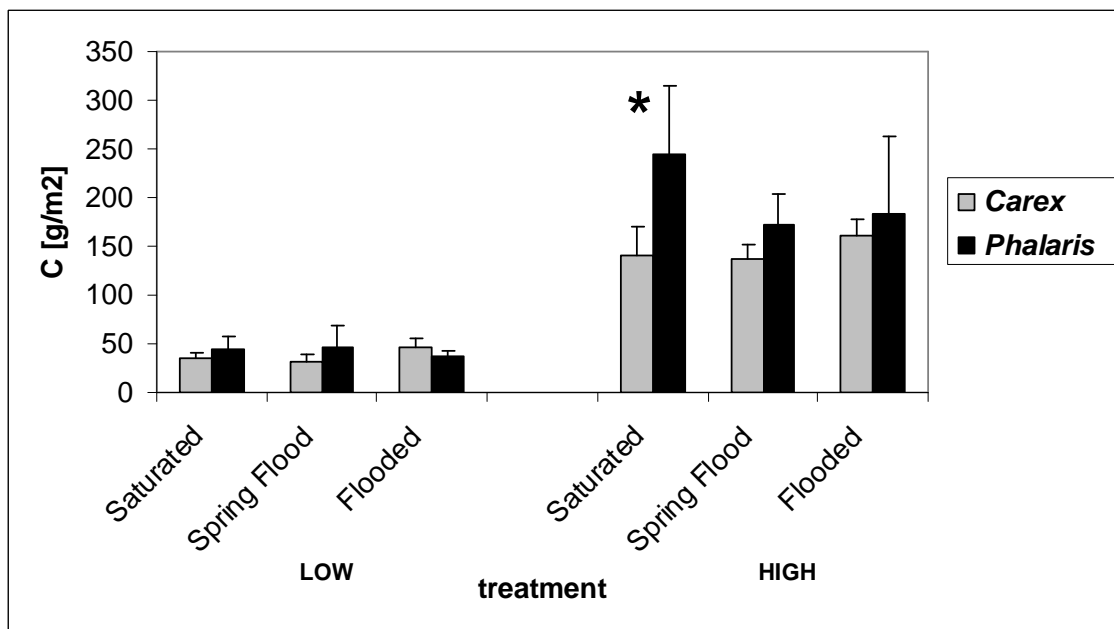


Fig. 29: Carbon contents [g/m²] in **aboveground** biomass (* = p< 0, 05).

	df	F	p
water level	2	1,6	0,206
fertilization	1	707,7	0,001
tub	1	5,7	0,021
species	1	9,2	0,004
water level*tub	2	4,9	0,012
fertilization*tub	1	22,3	0,001
water level * fertilization	2	0,5	0,611
water level * species	2	6,0	0,005
fertilization * species	1	2,9	0,093
water level*fertilization*tub	2	1,5	0,243
water level * fertilization * species	2	1,2	0,301
Error	50		

Table 16: Factorial ANOVA results for carbon contents in **aboveground** biomass.

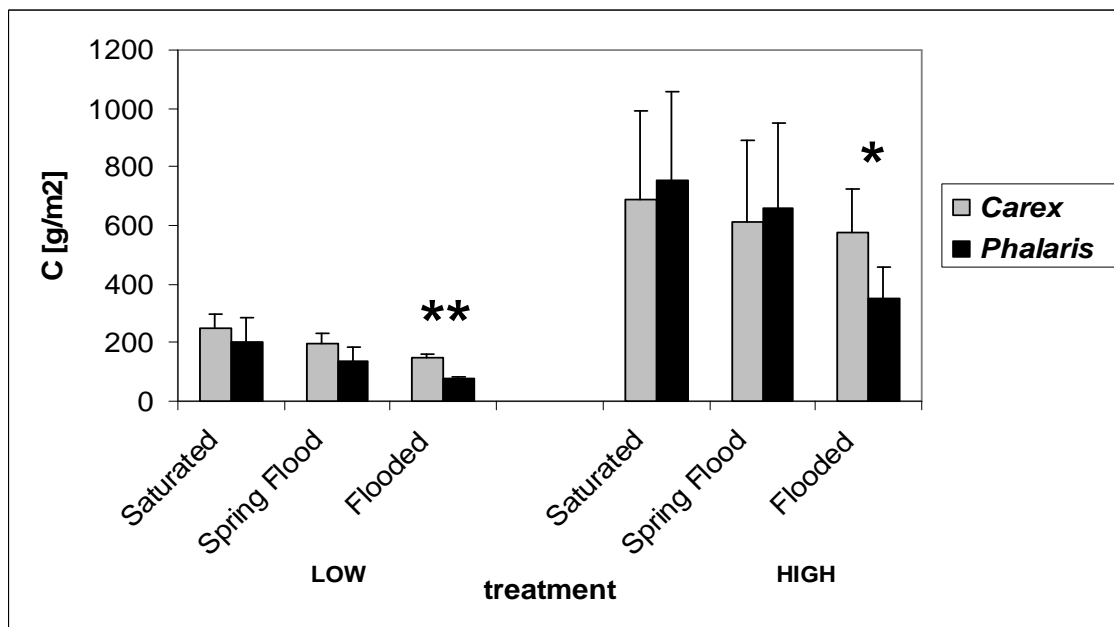


Fig. 30: Carbon contents [g/m²] in **belowground** biomass (* = p < 0, 05; ** = p < 0,001).

	df	F	p
water level	2	19,8	0,001
fertilization	1	285,8	0,001
tub	1	0,2	0,673
species	1	13,7	0,001
water level*tub	2	0,8	0,453
fertilization*tub	1	9,6	0,003
water level * fertilization	2	1,1	0,340
water level * species	2	4,3	0,020
fertilization * species	1	4,8	0,033
water level*fertilization*tub	2	0,2	0,844
water level * fertilization * species	2	0,4	0,698
Error	49		

Table 17: Factorial ANOVA results for carbon contents in **belowground** biomass.

5.3.3 C: N ratio

Aboveground C: N ratio was higher in *Phalaris* in all treatments in contrast to *Carex*, except for the low fertilized + spring flood (Fig. 31). However, none of the between species differences were significant. Nutrient level significantly affected aboveground CN, with both species having higher C: N ratios under the low nutrient conditions than the high nutrient treatments (Table 18). No other factors significantly influenced aboveground CN. Aboveground CN in the low nutrient levels ranged from 54 to 60 in *Carex* and from 55 to 65 in *Phalaris*, while in the high nutrient enrichment it ranged from 43 to 45 in *Carex* and from 50 to 53 in *Phalaris*.

On the other hand, C: N ratio of belowground biomass was very similar in *Carex* among all treatments (CN ranged from 123 to 130), except for the high nutrient + flooded treatment (CN = 111). The C: N ratio in belowground structures of *Phalaris* ranged from 76 to 93 in the low nutrient conditions and from 73 to 107 in the high nutrient treatments, decreasing in both with greater flood duration (Fig. 32). These differences resulted in there being significant effects of water level and species on belowground CN (Table 19). *Carex* had significantly higher C: N ratio than *Phalaris* in all treatments.

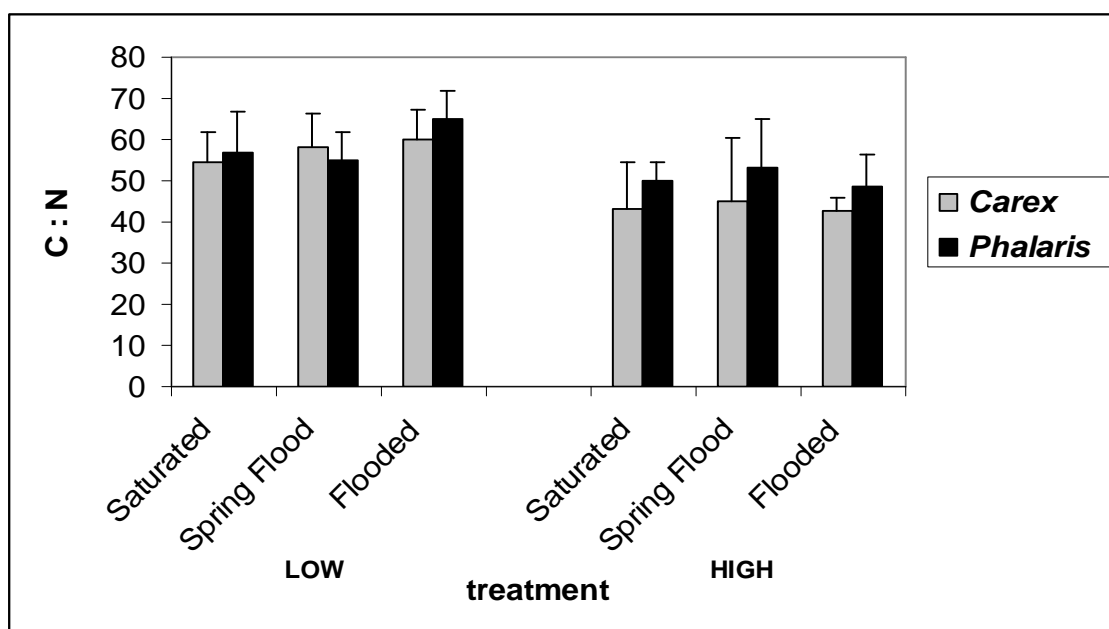


Fig. 31: C: N ratio of aboveground biomass.

	df	F	p
water level	2	0,6	0,536
fertilization	1	23,8	0,001
tub	1	7,5	0,009
species	1	3,5	0,067
water level*tub	2	0,0	0,971
fertilization*tub	1	0,6	0,454
water level * fertilization	2	1,6	0,216
water level * species	2	0,2	0,849
fertilization * species	1	1,5	0,230
water level*fertilization*tub	2	1,4	0,253
water level * fertilization * species	2	0,5	0,631
Error	50		

Table 18: Factorial ANOVA results for C: N ratio of **aboveground** biomass.

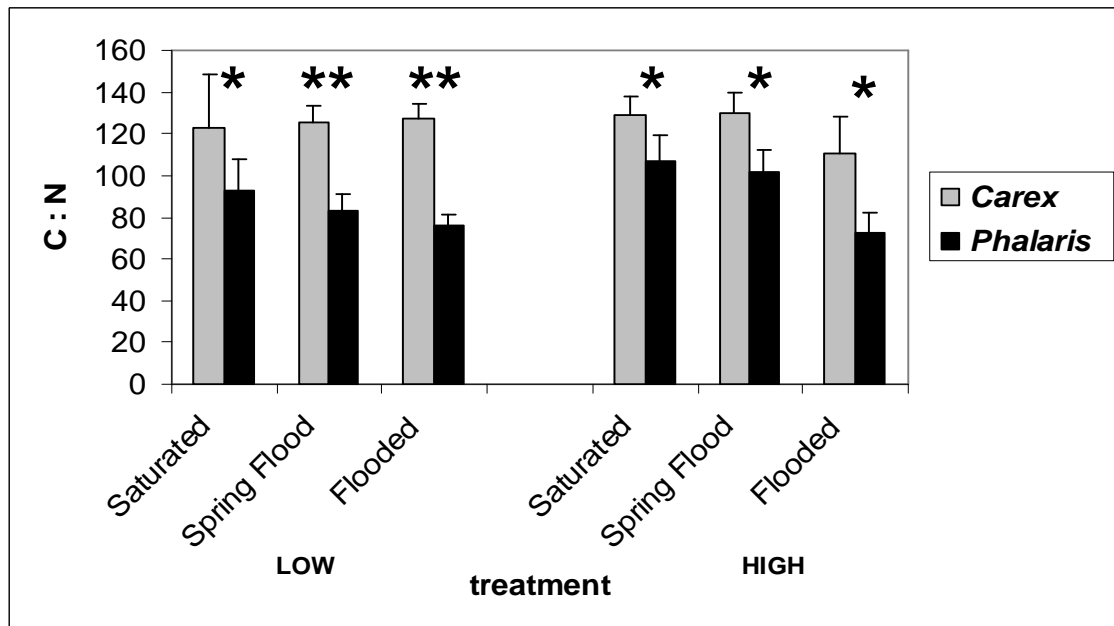


Fig. 32: C: N ratio of **belowground** biomass (* = $p < 0,05$; ** = $p < 0,001$).

	df	F	p
water level	2	11,9	0,001
fertilization	1	1,8	0,180
tub	1	0,0	0,934
species	1	141,8	0,001
water level*tub	2	3,0	0,057
fertilization*tub	1	5,4	0,025
water level * fertilization	2	5,5	0,007
water level * species	2	3,2	0,048
fertilization * species	1	3,9	0,053
water level*fertilization*tub	2	4,3	0,019
water level * fertilization * species	2	0,1	0,908
Error	49		

Table 19: Factorial ANOVA results for C: N ratio of belowground biomass.

5.4 GIS

Changes in cover differed significantly between the two species (Table 20), but water level and fertilization treatment did not have any significant effects, which may be due to the high variability of the data.

	df	F	p
water level	2	2,5	0,093
fertilization	1	1,2	0,288
tub	1	1,2	0,282
species	1	13,3	0,001
water level*tub	2	1,6	0,207
fertilization*tub	1	0,9	0,337
water level * fertilization	2	0,6	0,544
water level * species	2	1,1	0,333
fertilization * species	1	0,1	0,803
water level*fertilization*tub	2	3,5	0,038
water level * fertilization * species	2	1,5	0,237
Error	50		

Table 20: Factorial ANOVA results for differences in plants areas.

Pictures from the GIS (Appendix 1) give an approximate insight into the fate of plants in each tub after one growing season with both effects (water regime and nutrient enrichment). The pictures are representatives of each treatment chosen by the closest proximity to the average results per particular treatment. Under low fertilized + saturated conditions, *Phalaris* increased its area by about 79 cm² and had 18 more shoots, of which 4 were dead. On the other hand, *Carex* increased in area by about 48 cm², but it had only dead shoots, no living ones. In the low fertilized + spring flood treatment, *Phalaris* increased its area by 103 cm² with 15 new living shoots, while *Carex* increased in area by about 43 cm² with again only dead shoots. Low fertilized + flooded conditions caused the most considerable decrease in *Phalaris* area by about 30 cm² and a loss of 1 shoot, while *Carex* gained 24 cm² in area with no changes in shoot numbers. The high fertilized + saturated treatment was the one with the highest plant numbers with both species (especially *Phalaris*) increasing their area: *Phalaris* by about 238 cm² and 35 new shoots, of which 10 were dead, and *Carex* by about 94 cm² and 9 new shoots, of which 6 were already dead. On the contrary, *Carex* thrived greatly under high fertilized + spring flood conditions, where especially its area increased by 236 cm² with 13 new shoots (of which 6 were already dead), while *Phalaris* gained only 86 cm² with also 13 new shoots, but 7 of them were dead. High fertilized + flooded conditions were also

negative for *Phalaris*, but due to the higher nutrient level, were not as detrimental as was the low fertilized + flooded treatment. *Phalaris* gained only 3 cm² in area, but had 28 new shoots, which were quite thin and small with 6 of them being dead. *Carex*, on the contrary, increased its area by about 75 cm² and gained only 8 new shoots, 2 of which were dead.

6 Discussion

The effects of two nutrient and three flooding regimes were investigated on *C. acuta* and *P. arundinacea* plants. Both species are perennials and therefore two growing seasons of different nutrient enrichment and one season of water level treatment can only give a preliminary insight into the influence of particular treatments on these plants. As suggested by Green and Galatowitsch (2002), long-term research (e.g. greater than three years) is critical for understanding plant community dynamics, and the outcomes of interspecific competition may in fact be substantially different over varying time frames. Even though our results seem to outline at least some trends of the possible reaction of these species, they must be interpreted with care.

Both species had decreasing shoot numbers with a longer period of flooding in both nutrient treatments. *Phalaris* had at least twice the number of shoots under both fertilized conditions, but with a steeper decrease of the overall rate of shoot production with prolonged flooding in the low fertilized treatments as compared to *Carex*. This may show a slightly better adaptation of *Carex* to low nutrients conditions, but it needs a longer-term experiment to prove it. Reduction of tillering was found as the main response of *Phalaris* to submersion (Klimešová, 1994; Salo, 1989; Conchou and Fustec, 1988). Also, flooding reduced the growth of *Phalaris* in comparison to water-saturated soil in a mesocosm experiment (Miller and Zedler, 2003). As presented in Mal *et al.* (1997), the rate of shoot production may differ among years of an experiment demonstrating temporal development in competitive behavior. In their experiment, for instance, overall shoot production in *Typha angustifolia* was greater than that of *Lythrum salicaria* in the first year. However, from the second year onward, the situation was reversed and *Typha* had a much lower rate of shoot production than *Lythrum*. Therefore, our results may change with a longer experiment time; it is too early to forecast the long-term outcome of competition between these species under the particular experimental conditions.

Both species showed a similar trend in plant height under low nutrient conditions: plants were taller with longer flooding periods, which is an obvious plant reaction to flooding (Miller and Zedler, 2003). Shoot internode elongation is a response to flooding that has been observed in many species (Armstrong *et al.*, 1994). On the contrary, *Carex* had almost the same plant height under high nutrient conditions with no reaction to flooding, whereas *Phalaris* plants were the tallest in the saturated treatment, but were significantly smaller than *Carex* in both flooding regimes. This may indicate a possible competitive disadvantage of *Phalaris* to longer periods of oxygen deficiency compared to *Carex*. Greater allocation to stems and thus greater height result in increased competitive ability for light (Tilman, 1988; Givnish, 1982). However, only the four original plants of each species were measured, which resulted in a high variance with little explanatory or useful effect. Measuring all of the plants would provide more useful information with reduced variation due to greater sample size.

Aboveground biomass was significantly affected only by nutrient enrichment, not water regime. As mentioned before, this lack of a water level effect may be the result of this treatment only being applied for one growing season. Still, some factors were influenced by water level. For instance, *Carex* responded to prolonged flooding by increasing its biomass in both nutrient levels. *Carex* aboveground biomass was 72,8 g/m² in the spring flood regime, 79,3 g/m² in the saturated and 104,6 g/m² in the flooded conditions of the low nutrient treatments and from 299,1 g/m² in the spring flood, 313,1 g/m² in the saturated, to 360,5 g/m² in the flooded regime of the high nutrient levels. This is in agreement with Kuncová (2007), who reported the highest value of live biomass of *C. acuta* at 244,1 g/m² in 2006, but a higher value of 550,8 g/m² in 2008 (Kuncová, 2009), in an unmown and wet site of Mokrý Louky (Třeboň Basin Biosphere Reserve, Czech Republic). Maximum seasonal biomass of *C. acuta* was 414 g/m² in 2006, when there were three floods (in April, July, and August). Water level was almost 2 meters above the soil in the spring and first summer floods, which caused delayed plant growth in spring and early death of leaves and tillers at the beginning of summer. On the contrary, the limiting factor for biomass production in 2007 was the lack of rainfall, which resulted in a similar maximum biomass of 423 g/m². The best conditions occurred in 2008, when there were fluctuating water levels during the growing season without any long dry period or long-term flooding, which resulted in the highest seasonal biomass of 618 g/m² (Kuncová, 2009). Other studies from Mokrý Louky calculated aboveground biomass of *Carex acuta* at 390,4 g/m² (Lukavská, 1988) and 277,7 g/m² (Filipová, 2006), which are similar to our high fertilized treatments.

Phalaris aboveground biomass was 84,3 g/m² in the flooded regime, 102,5 g/m² in the saturated and 107,4 g/m² in the spring flood conditions of the low nutrient levels and 391,2 g/m² in the spring flood, 420,1 g/m² in the flooded, to 554,4 g/m² in the saturated conditions of the high fertilized treatments. A positive effect of water and nutrient supply in spring was noted by Květ *et al.* (1996) on a community dominated by *Phalaris*, with net aboveground production of 1259 g.m⁻² of dry mass in 1985, which was a year with two spring floods. On the contrary, in the following year (1986) with summer floods that mechanically damaged the *Phalaris* stands, the production was only 645 g.m⁻². *Phalaris* aboveground biomass estimated on Mokré Louky (Třeboň Basin Biosphere Reserve, Czech Republic) by Káplová (2009) was 268 g/m² in the low nutrient site and 616,7 g/m² in the high nutrient site in August 2007. This year was drier compared to 2008, in which the aboveground biomass in August was higher: 438 g/m² in the low site and 947,6 g/m² in the high site. The lower biomass recorded in our mesocosm experiment may indicate that even the high fertilized conditions of our mesocosm experiment were not as eutrophicated as the high nutrient site in Mokré Louky, especially when water supply was not limiting. This was also the case when comparing other studies of mown stands of *Phalaris* on Mokré Louky, which measured higher aboveground biomass production, from 941 g/m² to 1478 g/m² (Květ, 1983) and 1078,1 g/m² (Lukavská, 1988), and 1407,6 g/m² on an unmown stand in Mokré Louky (Rychterová, 2007). The aboveground biomass of *Phalaris* of 465,9 g/m² in August 2006 (Rychterová, 2007) is similar to our results; slightly higher than in the flooded conditions and lower than in the saturated conditions of the high fertilized treatments. .

There were significant water level and fertilization effects on belowground biomass, which was higher in *Carex* compared to *Phalaris* in all low nutrient treatments and significantly higher in both flooded treatments. Overall, belowground biomass decreased in both species with flooding duration. Similarly, total biomass was higher in *Carex* in all low fertilized treatments and both flooded water regimes, where again the flooding caused a steeper decrease in *Phalaris* compared to *Carex*. The higher total biomass of *Carex* compared to *Phalaris* under lower nutrient conditions is in agreement with Perry *et al.* (2004), who found that *Phalaris* was at a competitive disadvantage under N-poor conditions. In their experiment using *Carex hystericina*, this species outcompeted *Phalaris* and had higher total biomass when soil N was immobilized by incorporating a high carbon amendment (saw dust) in their experiment, thereby increasing the C: N ratio. These authors noted that under these nutrient-poorer conditions, *C. hystericina* was more efficient in taking up N than *Phalaris*. On the contrary, the steep decrease of *Phalaris* biomass in the flooded water regimes in both nutrient

levels is in conflict with Kercher *et al.* (2007), who found that *Phalaris* biomass increased 35% when low levels of nutrients coincided with prolonged floods compared to intermittent flooding. These authors showed that the absolute increase (12 times greater) in *Phalaris* biomass was in treatments with high nutrient inputs and floods lasting 14 weeks compared to intermittent flooding. Our results also do not agree with those of Herr-Turoff and Zedler (2007), who found that *Phalaris* aboveground biomass was 200–900% larger under constant flooding than under early-season or intermittent flooding in a wet prairie mesocosm study. However, our results agree with these two studies in terms of nutrient addition effects. For instance, *Phalaris* biomass increased >100% with high vs. low nutrient addition (Herr-Turoff and Zedler, 2007) while aboveground biomass was more than five times greater in the high than the low saturated treatments in our experiment. In contrast to our results, Kercher and Zedler (2004a) noted a reduced dominance of *Phalaris* under intermittent flooding (flooded two days every two weeks), while floods lasting four weeks or longer allowed *Phalaris* plants to grow and spread rapidly. In their study, *Phalaris* grew in competition with 15 herbaceous native North American species and, because several of them declined with prolonged flooding, it enabled *Phalaris* to spread into the large gaps created during the dieoff. However, in our experiment, *Phalaris* grew only with *Carex acuta*, a species which tolerates high water levels and the associated oxygen deprivation quite effectively (Klimeš, 1996).

Miller and Zedler (2003) found that flooding reduced belowground biomass and increased total shoot length and shoot: root biomass of *Phalaris*, which is in agreement with our results. In their experiment, *Phalaris* grew in competition with *Spartina pectinata* and produced the most biomass, the highest number of shoots, and total shoot length when wetter and drier conditions alternated weekly, while *Spartina* grew best with prolonged (4-week) inundation. Moreover, Lavergne and Molofsky (2006) demonstrated that high water levels exceeding 40 cm, and long term flooding up to 10 weeks, significantly reduced *Phalaris* growth.

Carex allocated significantly more biomass to belowground structures than *Phalaris* in both flooded treatments and under low nutrient conditions. Higher allocation to roots was found as a trait that would lead to a species superior competitive ability on nutrient poor soils as it increases nutrient uptake ability (Tilman, 1988). Moreover, both species increased allocation to aboveground structures with higher water levels and flooding duration; many plants decrease their biomass allocation to belowground structures when water supply or nutrients is increased (Lavergne and Molofsky, 2004). A similar biomass allocation pattern for *Phalaris*, producing higher above: belowground ratios with increased flooding and

nutrients, was observed in other studies (Miller and Zedler, 2003; Kercher and Zedler, 2004b; Maurer and Zedler, 2002; Tilman and Cowan, 1989).

It is likely that nutrient enrichment is the dominant effect influencing plant biomass, allocation patterns, and reproduction ability (Miller and Zedler, 2003; Kercher and Zedler, 2004a; Lavergne and Molofsky, 2004). High nutrient levels especially help *Phalaris* to survive unfavorable conditions such as oxygen deficiency when subjected to prolonged flooding. *Phalaris* was more opportunistic under high-nutrient conditions and increased nutrients in water appeared to be more influential than altered hydrologic regimes (Miller and Zedler, 2003). However, Klimešová and Čížková (1996) found greater tolerance of *Carex acuta* to flooding compared to *Phalaris*. In their experiment, increased soil organic matter content resulted in increased respiratory oxygen demand of the interstitial water. *Phalaris* responded to this by decreasing root porosity and biomass production. On the contrary, root porosity in *Carex acuta* did not change in a similar experiment when organic matter was added alone. But *Carex* decreased its root porosity when additions of organic matter were combined with a high nitrogen supply. Therefore, better adaptation to low oxygen conditions could explain the higher total biomass of *Carex* compared to *Phalaris* in the flooded treatments of our mesocosm experiment.

Both studied species grow best in wet meadows with high nutrient levels, but can survive in low nutrient conditions (Hroudová *et al.*, 1988). The use of sand as the growing medium, in combination with short-term nutrient addition, most likely was the cause of the small nitrogen contents in the plant structures. The nutrients in the fertilizer were the only ones they received and could use. *Carex* did have a higher percentage of total nitrogen in aboveground material than *Phalaris*. Herr-Turoff and Zedler (2005) also found higher amounts of nitrogen in the aboveground tissues of native species stands without *Phalaris* compared to the ones with *Phalaris* in a wet prairie, which did not support the presumption of *Phalaris* retaining more N than native plant assemblages. Otherwise, *Phalaris* had significantly higher content of total nitrogen in belowground biomass than *Carex*. Nitrogen standing stocks in above- and belowground plant structures were significantly positively affected by fertilization. *Phalaris* had higher nitrogen standing stock in the aboveground biomass than *Carex* in all water regimes in both nutrient levels, except for the low, flooded treatment. A similar trend was found in the belowground plant material with *Phalaris* having higher nitrogen standing stock especially in high fertilized treatments, except for both flooded water regimes. Low nutrient and especially low oxygen conditions seem to favor *Carex* being a better competitor for nitrogen due to higher root porosity and adaptability to oxygen deficiency (Klimešová and

Čížková, 1996). Comparison of the total nitrogen content from August in *Phalaris* plants of the mesocosm and a field study (Káplová, 2009) showed that, at the time of maximum biomass, the plants from the mesocosm had lower amounts of N% and N standing stock. N% in *Phalaris* ranged between 2,4 – 3,3% and 4,1 – 4,5 % in the low and high sites of Mokré Louky respectively in 2007, while in the mesocosm it ranged from 0,7-0,8 % and around 0,9% in the low and high fertilized treatments, respectively. The N standing stock was lower in the mesocosm experiment as well, ranging from 0,6 to 0,9 g/m² in the low and from 3,4 to 4,9 g/m² in the high fertilized treatments, while it was 7-12 g/m² in the low and 24-35 g/m² in the high fertilized sites in Mokré Louky. The evident difference between the field and mesocosm studies is in the age of the plants. The plants on Mokré Louky are much older and have received nutrients for a longer time compared to the experimental plants. They may also have received different amounts of nutrients through run off from the still fertilized field (pig sewage). The amount of nutrients in the sand of our experiment was too low to be detected on the CN analyzer indicating that the duration of the experiment was too short for a build up of soil nutrients.

Carbon concentrations were between 43-45% for both nutrient levels, which is a standard range of carbon concentration in plant tissues (Procházka *et al.*, 1998). Even so, *Carex* had a significantly higher percentage of total carbon in the aboveground biomass than *Phalaris* with a slightly decreasing trend with higher water levels and prolonged flooding in both species. *Carex* had almost the same amounts of carbon percentage in belowground biomass in all treatments, while *Phalaris* had the lowest concentration in the high saturated and high spring flood treatments. The high variation in the results can be caused by the fact that samples were made from a mixture of belowground structures of all shoots of the species from a particular pot and not just one shoot. On the other hand, carbon standing stock was higher in *Phalaris* than in *Carex* for the aboveground biomass, while *Carex* had higher carbon content than *Phalaris* for belowground biomass in all low fertilized treatments and the high, flooded one. This may indicate a better adaptation of *Carex* to low oxygen conditions as well as being a superior competitor for nutrients due to better absorption capacity under nutrient poorer conditions (Perry *et al.*, 2004). Kuncová (2009) calculated the total carbon in aboveground biomass of *Carex acuta* to be 186 g/m² in 2006, 190 g/m² in 2007, and 278 g/m² in 2008 in an unmown and wet site of Mokré Louky (Třeboň Basin Biosphere Reserve, Czech Republic). The increasing amounts of carbon among the years are due to there being higher biomass due to better conditions as already discussed above. These numbers are higher compared to our results (137 g/m² to 160,7 g/m² in high fertilized treatments), but that is because the plants in

the field were older. Comparison of total carbon in *Phalaris* plants of the experiment to the results from Mokré Louky in August 2007 (Káplová, 2009) showed a lower C standing stock in the experimental plants of the low fertilized treatments (36,2 to 46,2 g/m²) and the low nutrient site of Mokré Louky (110 to 160 g/m²), while higher in the high fertilized treatments and the high nutrient site (347-756 g/m² in mesocosm; 260-370 g/m² in Mokré Louky). This may be due to a greater photosynthetic rate of plants in the mesocosm, especially the high nutrient treatments. The mesocosm plants were not as tall or dense as those in Mokré Louky, which would have more likely suffered from shading (Perry and Galatowitsch, 2003; Lavergne and Molofsky, 2006). Unfortunately, we did not measure photosynthesis in our plants, but this may be an interesting parameter that should be included in future research.

Phalaris had higher aboveground C: N ratios in almost all treatments. This ratio was higher for both species in the low nutrient conditions than in the high treatments. This indicates greater N availability and plant uptake under the high nutrient conditions, which would be expected (Lambers *et al.*, 1998). On the contrary, the belowground C: N ratio was significantly higher in *Carex* in all treatments, with little variation among the treatments. However, the ratio decreased in *Phalaris* with higher water levels and longer flooding periods. This may be due to several different factors. For instance, if the *Phalaris* plants are more stressed under flooded condition than *Carex* plants, they may have a higher respiration rate with higher loss of carbon. Or, they may have lower storage of carbon under stressful conditions. Unfortunately, we were not able to determine total nonstructural carbohydrates (Smith, 1981) due to time and health reasons. Such measurements may help us to better explain the differences in belowground C: N as well as providing a qualitative measure of plant stress.

Higher belowground biomass and greater nitrogen content in the belowground biomass could contribute to the better growth of *Carex* than in *Phalaris* under both flooded conditions. Greater allocation to belowground structures could help *Carex* to take up more space than *Phalaris* (Perry *et al.*, 2004), which is in agreement with the GIS results, where *Carex* increased in area more than *Phalaris* in both flooded conditions. Even though *Phalaris* had higher shoot and daughter numbers under both flooded conditions, its shoots were tiny and smaller, with a lower probability of survival, than shoots of *Carex*. This visual evidence was supported by the mean shoot size results. On the contrary, *Phalaris* thrived best in the high nutrient and saturated treatment, which seems to be the optimal condition for it. *Phalaris* had its greatest spread in this treatment, with the highest shoot number, longest stem height, highest aboveground, belowground and total biomass, and highest nitrogen and carbon

standing stock in above- and belowground biomass as well. Although the GIS results differed significantly only between the species, visual inspection seemed to show that the differences were based on the water level effect. The weak statistical effect ($p = 0,09$) is most likely a reflection of the low sample sizes. To our knowledge, there is not any other study using GIS methods for similar purpose.

Our results, along with those of other studies, indicate a better adaptation of *Carex* to low oxygen conditions and greater nutrient uptake under nutrient poorer conditions. *Carex* predominated over *Phalaris* under lower nutrient enrichments and/or flooded water regimes in our experiment. This may explain its spontaneous return to the low nutrient site in Mokré Louky, where it is now a co-dominant species to *Phalaris*, which was the dominant species five years ago (Káplová *et al.*, 2011).

Our data suffer from high variability, which may be caused by several factors. For instance, our experiment was originally planned for both water and nutrient treatments to be applied over two growing seasons with harvesting of all samples at the end of the second season. Due to high mortality of transplanted *Phalaris* plants, as well as the length of time it took for the transplanted plants to adapt to their new conditions, we could not begin the flooding treatments in the first growing season. Also, we decided to harvest only half of the samples to let the plants grow one more season. Therefore, not only the short time, but also the small number of samples could affect the results. Moreover, genetic differences between plants could play an important role in the variation of the data, connected with different photosynthetic rates among genotypes (Brodersen *et al.*, 2008) and hence increased variation in total carbon contents in plants. We did not test for genetic variation between plants, which was not a central interest of our experiment. However, this would be an important factor to consider in future studies. The significant tub effect in some of our results could also be caused by algal growth in the high fertilized treatments especially. Even though both tubs of the high fertilized + flooded regime were treated in the same manner, there was greater algal growth in one of those tubs and therefore the water in that tub had to be changed more often.

7 Conclusion

Our results support some, but not all, of our initial hypotheses. We predicted that *Phalaris* would be taller and with greater biomass in the high nutrient treatments compared to *Carex*.

However, both species did well in these treatments. *Carex* had similar results as *Phalaris* and, moreover, prevailed over *Phalaris* with a longer period of flooding.

Our results did support our second hypothesis, that *Phalaris* would be negatively affected by long-term flooded conditions. This is seen in the lower belowground and total biomass, lower nitrogen contents and C % in the aboveground biomass, lower carbon contents in the belowground biomass, and decreased plants areas with smaller mean shoot sizes as well.

Our third hypothesis was that changes in the species biomass allocation pattern as well as the ability to spread vegetatively are the two factors determining which species may become a dominant, depending upon the particular environment conditions. *Carex* allocated more biomass to belowground structures than *Phalaris* and, similarly, had higher amounts of belowground biomass, with higher total nitrogen and carbon contents in belowground structures. Also, its spreading ability was less limited by the long flooded water regime than *Phalaris*, especially in the nutrient poorer conditions. This may reflect its greater nutrient uptake and better adaptation to low fertilized and flooded conditions compared to *Phalaris*. On the contrary, *Phalaris* grew better and with the greatest spread in high nutrient and water saturated conditions, in which it had the longest stems, highest amounts of above- and belowground biomass, and the highest total nitrogen and carbon contents in above- and belowground structures. Conditions with sufficient water and especially high nutrient amounts enable *Phalaris* to grow rapidly, suppress other wetland species, and change species rich wetland habitats into monotonous stands with decreased plant and animal biodiversity. Under such circumstances, these wetlands lose some of their valuable ecological functions as well.

8 References

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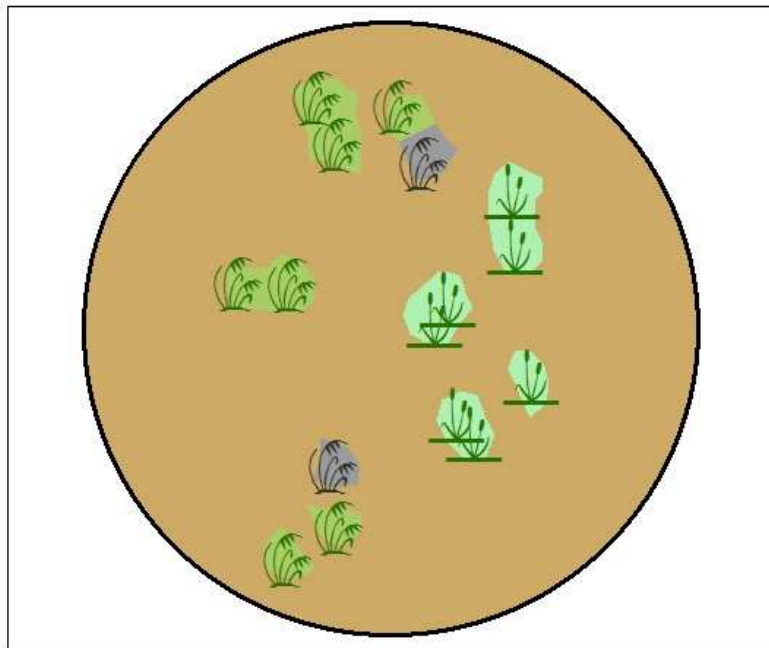
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9 Appendix

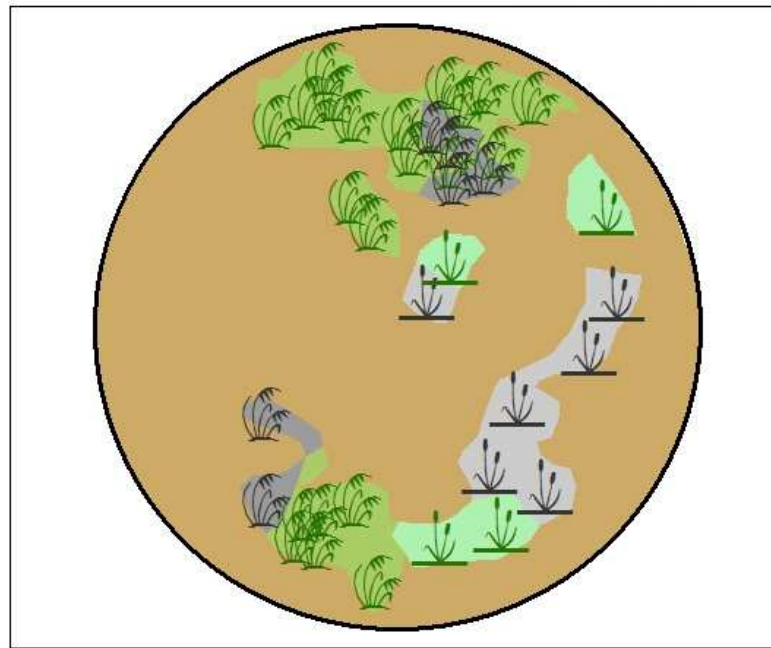
Appendix 1: Pictures from GIS showing the numbers and positions of shoots (live and dead) and area [m²] of each species in each treatment. Also shown are the differences in the measured parameters of the same sample (pot) between the ends of the 2009 (left) and 2010 (right) growing seasons.

Low Saturated

11b 2009



11b 2010



2009

Species	Number of shoots	Area [m ²]
Carex Live	7	0.0032
Carex Dead	0	0.0000
Phalaris Live	7	0.0034
Phalaris Dead	2	0.0009

Differences

Species	Number of shoots	Area [m ²]
Carex Live	-3	0.0001
Carex Dead	6	0.0047
Phalaris Live	14	0.0064
Phalaris Dead	4	0.0015

2010

Species	Number of shoots	Area [m ²]
Carex Live	4	0.0033
Carex Dead	6	0.0047
Phalaris Live	21	0.0098
Phalaris Dead	6	0.0025

Species

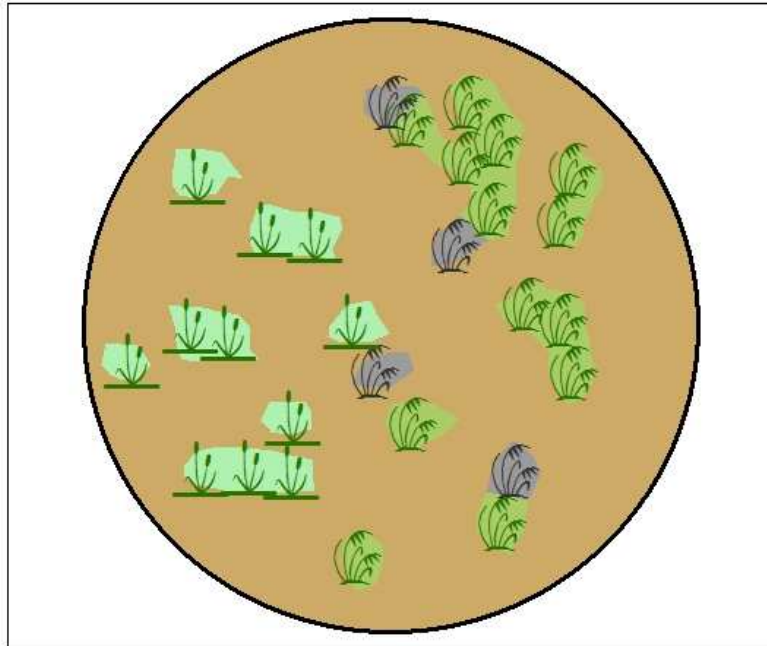


Area

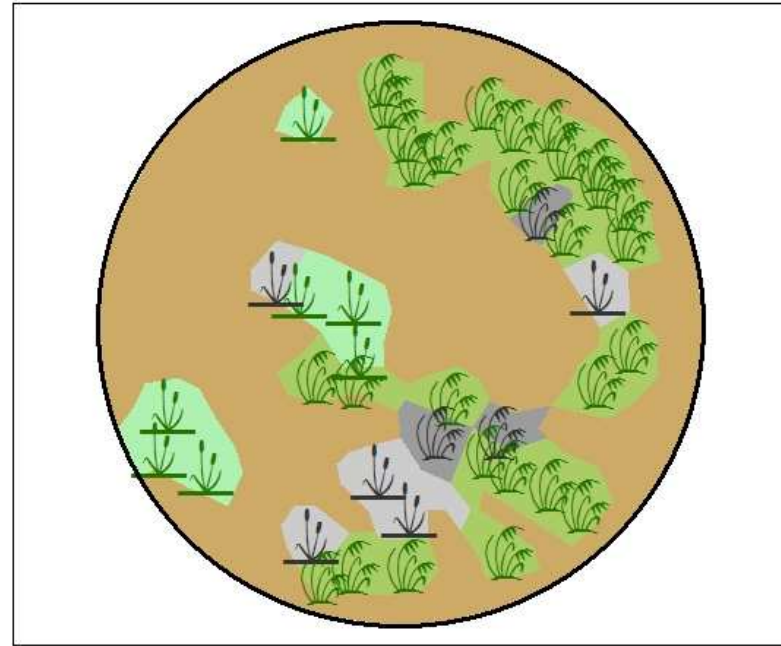


Low Spring Flood

7a 2009



7a 2010



2009

Species	Number of shoots	Area [m2]
Carex Live	11	0.0050
Carex Dead	0	0.0000
Phalaris Live	13	0.0068
Phalaris Dead	4	0.0018

Differences

Species	Number of shoots	Area [m2]
Carex Live	-4	0.0002
Carex Dead	5	0.0041
Phalaris Live	15	0.0100
Phalaris Dead	-1	0.0003

2010

Species	Number of shoots	Area [m2]
Carex Live	7	0.0052
Carex Dead	5	0.0041
Phalaris Live	28	0.0168
Phalaris Dead	3	0.0021

Species

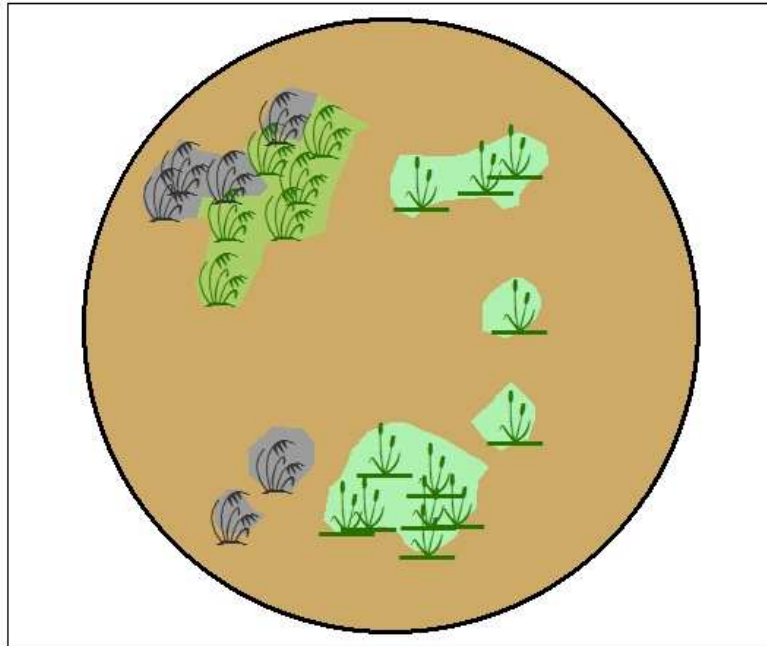


Area

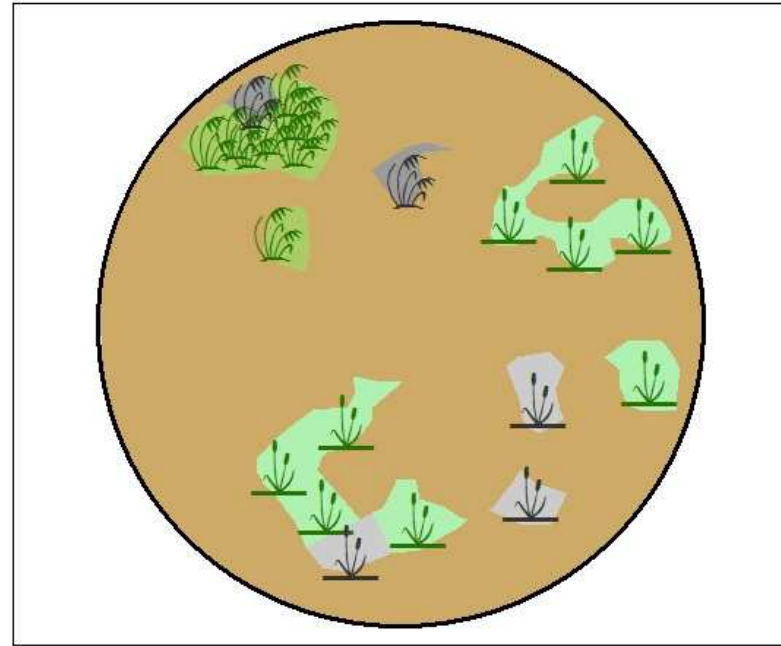


Low Flooded

12d 2009



12d 2010



2009

Species	Number of shoots	Area [m2]
Carex Live	12	0.0070
Carex Dead	0	0.0000
Phalaris Live	6	0.0040
Phalaris Dead	6	0.0033

Differences

Species	Number of shoots	Area [m2]
Carex Live	-3	0.0002
Carex Dead	3	0.0022
Phalaris Live	3	-0.0007
Phalaris Dead	-4	-0.0023

2010

Species	Number of shoots	Area [m2]
Carex Live	9	0.0072
Carex Dead	3	0.0022
Phalaris Live	9	0.0033
Phalaris Dead	2	0.0010

Species

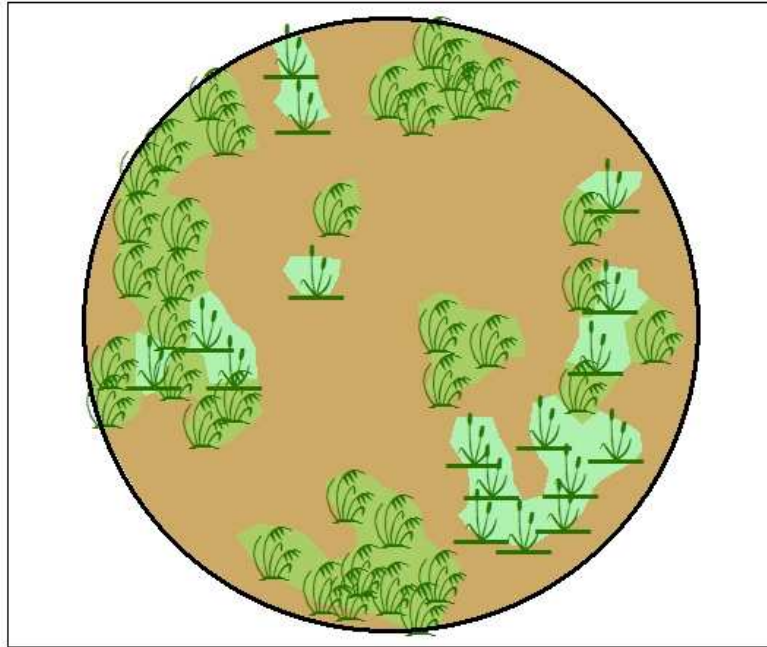


Area

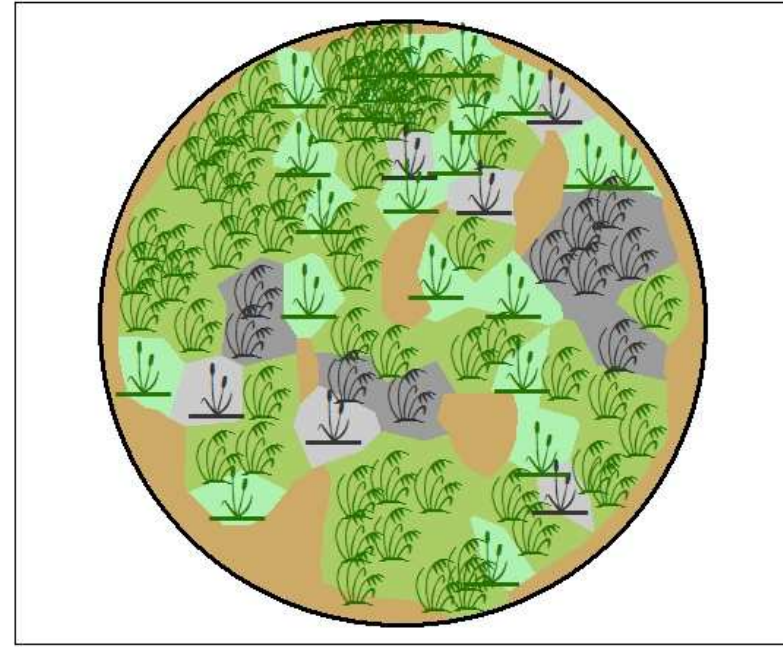


High Saturated

10e 2009



10e 2010



2009

Species	Number of shoots	Area [m ²]
Carex Live	17	0.0084
Carex Dead	0	0.0000
Phalaris Live	37	0.0190
Phalaris Dead	0	0.0000

Differences

Species	Number of shoots	Area [m ²]
Carex Live	3	0.0046
Carex Dead	6	0.0048
Phalaris Live	25	0.0157
Phalaris Dead	10	0.0081

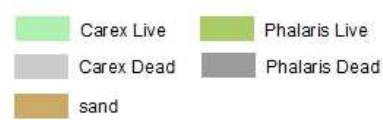
2010

Species	Number of shoots	Area [m ²]
Carex Live	20	0.0130
Carex Dead	6	0.0048
Phalaris Live	62	0.0347
Phalaris Dead	10	0.0081

Species

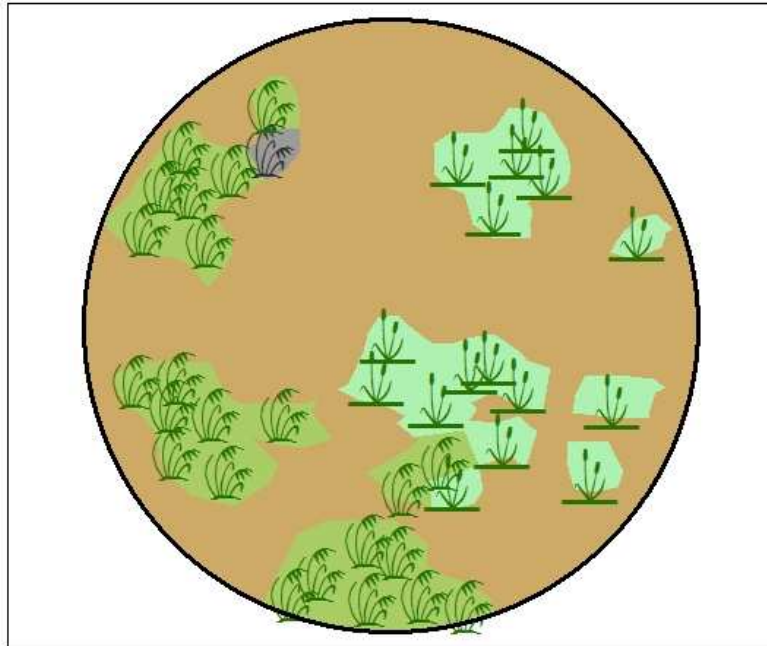


Area

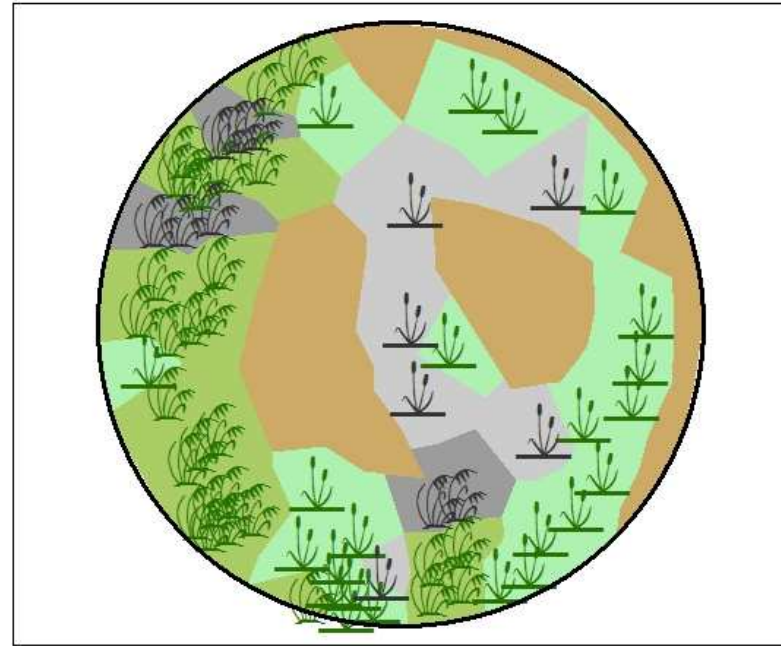


High Spring Flood

3f 2009



3f 2010



2009

Species	Number of shoots	Area [m ²]
Carex Live	16	0.0096
Carex Dead	0	0.0000
Phalaris Live	23	0.0139
Phalaris Dead	1	0.0005

Differences

Species	Number of shoots	Area [m ²]
Carex Live	7	0.0123
Carex Dead	6	0.0113
Phalaris Live	6	0.0037
Phalaris Dead	7	0.0049

2010

Species	Number of shoots	Area [m ²]
Carex Live	23	0.0219
Carex Dead	6	0.0113
Phalaris Live	29	0.0176
Phalaris Dead	8	0.0054

Species



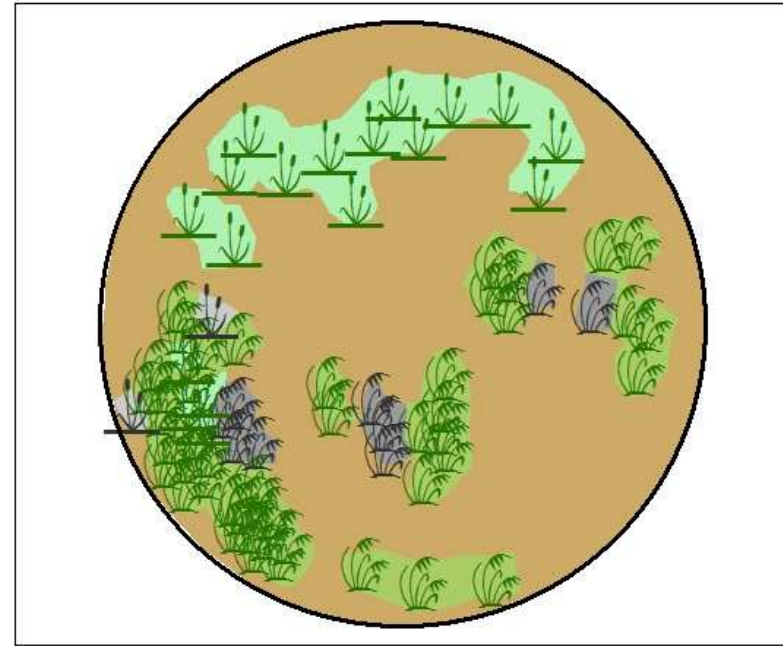
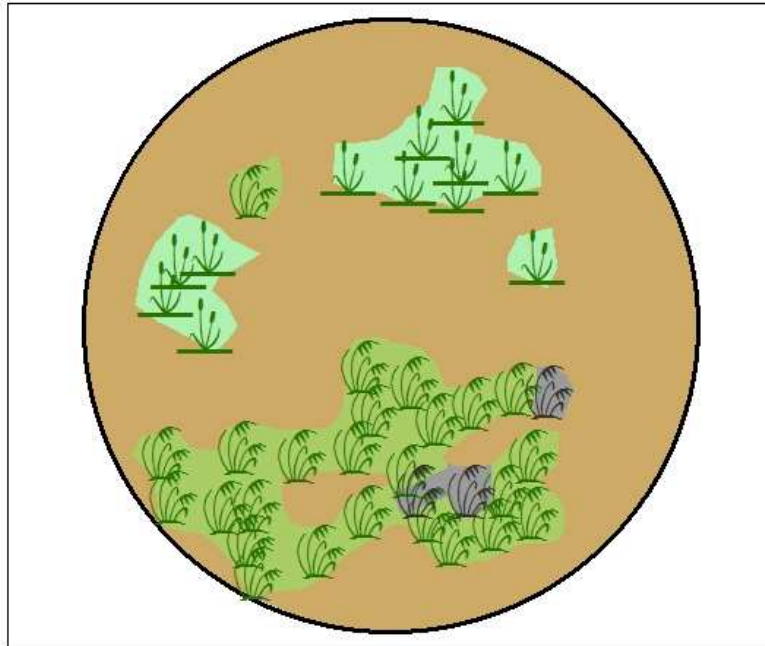
Area



6b 2009

High Flooded

6b 2010



2009

Species	Number of shoots	Area [m ²]
Carex Live	12	0.0069
Carex Dead	0	0.0000
Phalaris Live	25	0.0143
Phalaris Dead	3	0.0012

Differences

Species	Number of shoots	Area [m ²]
Carex Live	6	0.0025
Carex Dead	2	0.0050
Phalaris Live	22	-0.0008
Phalaris Dead	6	0.0011

2010

Species	Number of shoots	Area [m ²]
Carex Live	18	0.0095
Carex Dead	2	0.0005
Phalaris Live	47	0.0135
Phalaris Dead	9	0.0024

Species



Area

