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Bachelor thesis

**Comparing aboveground primary production in areas of
low and high nutrient levels in Mokr  Louky, Třebon 
Basin Biosphere Reserve**



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Annotation

Aboveground primary production differs depending on nutrient levels. This thesis compares net annual aboveground production and biomass levels in high and low areas of Mokré Louky. Aboveground plant biomass was collected from particular quadrats over two growing seasons, from April to September 2007 and April to October 2008. Samples were separated into species, dried and weighed.

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České Budějovice 22.12.2008

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1 Introduction

Natural and semi-natural grasslands represented a dominant part of agricultural land in the Czech Republic after WW II. Their area decreased over time and, in the 1980s, was less than one fourth of its previous extent (Balátová-Tuláčková, 1982). Wet grasslands, with an area of 379 891 ha, account for almost half of the grassland sites (Klesnil, 1978). These wet ecosystems perform many important functions and, as wetlands, are some of the most important ecosystems on Earth. Wetlands are a transition biotope between aquatic and terrestrial ecosystems. Wet grasslands are an important “stability item in the landscape”, because of the many valuable functions that occur in these systems. These include: (i) protecting soil from water erosion, (ii) filtering nutrients and pollution which would endanger surface and subterranean waters, and (iii) are a valuable gene pool for plants and animals (Rychnovská *et al.*, 1985). Moreover, their unique habitats have considerable aesthetic and recreational qualities.

The loss of wet grasslands has been an on-going problem for several decades. In recent times, especially the 1970s and 1980s, most marshes and wet grassland ecosystems in the Czech Republic have undergone rapid changes, being mostly converted into arable land either directly or due to drainage. The abandonment of traditional management regimes (little fertilization, mowing one to two times per year) led to the loss of large areas of wet grasslands in the Czech Republic. Current management is much more intensive, with greater use of fertilizers and increased mowing frequency than in the past. A consequence of eutrophication, caused by high nutrient inputs from direct fertilization and manuring, or polluted flood or ground water from adjacent areas (Prach and Soukupová, 2002), has been the expansion of several competitively strong species. This has led to a large decrease in biodiversity, together with perturbations in ecological functioning of many wet meadows (Benstead *et al.*, 1999).

This work compared current vegetation composition and production in a wet grassland, Mokrý Louky near Třeboň, Czech Republic, to historical records. Historically, the grassland area was dominated by sedges (*Carex gracilis*) and grasses (*Alopecurus pratensis*). Due to intensive management actions and the 2002 floods, the grassland became dominated by *Phalaris arundinacea*. Cessation of fertilization and mowing, starting in 2005, has led to the re-establishment of *C. gracilis* in parts of the grassland. These results indicate that restoration of historical wet grassland areas may be quite rapid once disturbances have been removed.

2 Objectives

Objective 1: Determine net annual aboveground production and biomass levels in high vs low nutrient areas in a wet grassland.

Objective 2: Compare current aboveground plant biomass and production levels to those of 30 years ago to determine the effects of increased fertilization of the wet grasslands over time.

3 Literature review

3.1 Wetlands – General Description

Wetlands are among the most important ecosystems on the Earth. They are a major feature of the landscape in almost all parts of the world. Wetlands are sometimes described as "the kidneys of the landscape" for the functions they perform (Mitsch and Gosselink, 1986). They work as a buffer and filter zone which entraps heavily eutrophicated runoff from surrounding soils (Závodská, 1990).

Inland aquatic ecosystems comprise less than 1% of the Earth's surface, but often are among the most productive areas (Likens, 1975). The character of aquatic systems at the primary producer level is dependent upon a variety of changing environmental factors but also on biological factors, e.g. grazing (Vollenwieder, 1969). Many of them have undergone dramatic changes in recent years as a result of human activities. In most cases the change has been beneficial to short-term human desires and requirements. These changes have mostly been detrimental. Nowadays freshwater marshes and swamps comprise an area of about 2.10^6 km² (Likens, 1975).

3.1.1 Definition of wetlands

It is quite difficult to define wetlands because there are several types of wetlands, including swamps, bogs, marshes, mires, fens and other wet ecosystems, found throughout the world and named differently in different places. Nevertheless it is possible to find some common key characteristics. They all have shallow water or saturated soil, all accumulate plant organic materials that decompose slowly, and all support a variety of plants and animals adapted to saturated conditions. Three main components are often included in that definition: 1) wetlands are distinguished by the presence of water; 2) they often have unique soils that differ from adjacent uplands; and 3) they support vegetation adapted to wet conditions without flood-intolerant vegetation (Mitsch and Gosselink, 1986).

Wetlands have numerous other characteristics that distinguish them from other ecosystems yet make them less easily definable (Zinn and Copeland, 1982). The presence of water is for at least part of the time yet the depth and duration of flooding varies considerably from wetland to wetland. Wetlands vary widely in size and location, from inland to coastal wetlands and from rural to urban areas. Similarly the degree to which a wetland is influenced by humans varies from region to region and from wetland to wetland.

Wetland soils, known as hydric soils, are formed when oxygen is cut off due to the presence of water, causing reduced conditions. They are both the medium in which many of the wetland chemical transformations take place and the primary storage of available chemicals for most wetland plants. They can be generally classified into two types: (i) organic or peat soil or (ii) mineral soil which contains less than 20% to 35% organic matter on a dry weight basis. Where mineral soils occur in wetlands, such as in some freshwater marshes or riparian forests, they generally have a soil profile made up of horizons, or layers. The upper layer of wetland mineral soils is often organic peat composed of partially decayed plant materials (Mitsch and Gosselink, 2000). Wetland soils, when submerged, are usually anoxic, except for a thin surface layer (Čížková *et al.*, 1996). They can be high- or low- nutrient.

Wetlands have unique biogeochemical cycles with many chemical transformations and chemical transport processes that are not shared by many other ecosystems. Storage in water reservoirs or other types of wetlands may be the most natural and effective mechanism for removing nitrogen from water (Simmons *et al.*, 1992).

At the level of the whole ecosystem, wetlands have value to the public for flood mitigation, aquifer recharge, water quality improvement, and aesthetic qualities (Mitsch and Gosselink, 1986). Wetlands can provide a direct utilization for human society through the

“energetic biomass”. Specific production and consequent processing of harvested mass of some suitable plants, e.g. willows and some species of grasses (*Phalaris arundinacea*, *Phragmites sp.*, etc.), can be used for fuel production or construction material. That could be very important in these days of finding alternative sources of energy (Rychterová, 2007). Their abilities are being used in “root waste-water treatment systems” too (Vymazal, 2001).

3.1.2 Nutrient contents & effects of eutrophication

Batzer *et al.* (2006) evaluated the most limiting nutrients in wetlands. Species diversity is frequently greater in undisturbed wetlands, with the greater diversity being associated with a somewhat lower nutrient status. These more species-rich wetlands typically have moderate productivity and standing crop (Bedford *et al.*, 1999; Úlehlová and Rychnovská, 1982). Declines in species diversity are associated with nutrient increases, especially increases in nitrogen from atmospheric deposition or agricultural and urban runoff waters. Numerous studies have reported changes in species composition, declines in overall plant species diversity, loss of rare and uncommon species, and replacement of native species by exotics when nutrient enrichment occurs (Bedford *et al.*, 1999).

In terrestrial ecosystems, plant growth is often limited by low nitrogen availability (Schlesinger, 1977), partly as a result of limited storage in soil and litter. In freshwater wetlands, where organic matter and nitrogen accumulate in the soil, plant growth is often limited by phosphorus or co-limited by both (Shaver, 1998). Nitrogen: phosphorus (N: P) ratios in plant tissues and soils have been used to identify thresholds of nutrient limitation in wetlands. Sites with plant live tissue N: P < 14 are N limited, sites with N: P > 16 are P limited and sites with N: P between 14 and 16 are co-limited by N and P (Shaver, 1998).

3.1.3 Species diversity

The number of species in any ecological system depends on the particular habitat conditions. Fewer species are found when the conditions are optimal or extreme. Species diversity is reduced while dominants and co-dominants exceed due to their ability of faster growth under these conditions and better competitive abilities. For example, increasing nutrient contents due to fertilization can lead to morphological and functional monospecific stands. On the contrary, suboptimal habitat conditions lead to a rich floristic composition

(Úlehlová and Rychnovská, 1982). Associations with strong dominants seem to have higher primary productivity than associations with higher species richness. This could be caused by the ecological dominants being best adapted to the habitat and hence their higher biomass productivity (Slavíková, 1982).

The rate of succession in terms of species turnover is generally expected to be positively related to site fertility (Prach *et al.*, 1993). The higher the level of resources, the greater is their consumption by plants. This results in faster growth and a faster exchange of species under higher competitive pressure than in nutrient-poor sites. In less eutrophicated floodplains, both processes, i.e. degradation and restoration, are slower (Bakker *et al.*, 2002). During spontaneous succession, i.e. after abandonment, available light decreases inside a stand, while nutrients increase due to litter accumulation and no export by cutting (Prach, 2007).

3.1.4 Production

3.1.4.1 What is production

Biomass productivity and nutrient content in biomass portions reflect the fertility of a site and help to demonstrate the fate of nutrients in an ecosystem. Study of these ecosystem characteristics can provide accurate figures for possible economic exploitation of the productive potential of an ecosystem as well as generally illustrate ecological functioning of a system (Šmilauer *et al.*, 1996).

Net primary production is that part of total or gross primary production of photosynthetic plants that remains after some of this material is used for respiration. The remaining portion, net production, is available for use by heterotrophic consumers and reduction by saprobes. Net primary production provides the energetic and material basis for the life of all organisms besides the plants themselves.

Net primary production is most commonly measured as dry organic matter synthesized per unit area of the Earth's surface per unit time, and is expressed as grams per square meter per year. Biomass is the dry matter of living organisms present at a given time per unit of the Earth's surface, and may be expressed as grams or kilograms per square meter (Lieth and Whittaker, 1975).

3.1.4.2 Examples in relation to other habitats

Net primary production is a key index of ecosystem function. Mean values of primary production for some ecosystem types are shown in Table 1A, with swamps and marshes being the most productive type of habitat (Lieth and Whittaker, 1975). Mean values for different wetland ecosystem types (Table 1B) are usually in the range from 600 to 2000 g m⁻² yr⁻¹, from which inland freshwater marshes are one of the most productive ecosystems (Mitsch and Gosselink, 2000).

Table 1. Examples of primary production in different ecosystem types –**A** (Lieth and Whittaker, 1975), and among different wetland types- **B** (Mitsch and Gosselink, 2000).

A		B	
Ecosystem	Primary production [g m⁻² yr⁻¹]	Wetland type	Primary production [g m⁻² yr⁻¹]
swamp and marsh	3000	fresh marshes	1980
tropical rain forest	2200	salt marshes	1950
temperate forest: evergreen	1300	mangroves	1500
temperate forest: deciduous	1200	tidal fresh marshes	1370
savanna	900	riparian forests	1040
boreal forest	800	swamp forests	870
temperate grassland	600	northern bogs	560
tundra and alpine	140		
desert and semidesert scrub	90		
open ocean	125		

3.2 Wet Grasslands

3.2.1 General Description

Wet grasslands play a very important role among wetlands. They are stable habitats, whose main profit used to be mainly in production. They are a primary source of fodder and the basis of livestock production (Melčáková, 1993). As a consequence of industrial expansion also into agriculture, particularly in the three decades before the Velvet revolution, interest in these areas was reduced. Many of them, where it was possible, were changed into arable land; others became abandoned without any interventions. Grassland degradation is a result of two possible extremes - i) too intensive or ii) no management while there is an enormous input of nutrients into the whole landscape (Prach, 2000). Wet grasslands have

considerably higher primary production with a lot less energy supply than arable areas. This is due to the sufficiency of soil moisture supported by running surface or ground water, bringing continually nutrients into the wetlands and sediments from floods.

The unique importance of grasslands is not just in production but in them being considered as more ecologically well-balanced and stable landscape, with higher aesthetic and recreational values (Melčáková, 1993). Wet grasslands along streams have the ability to filter water, which runs off through soil from neighbouring agriculturally used areas (Rychterová, 2007). Nevertheless, for good-working of this filter, it is necessary to mow them at least once a year, otherwise they will accumulate nutrients returned back to the soil due to decomposition. Lastly, wet grasslands act as stabilizing factors of the local climate. Hamadejová (2001) showed that 1 m³ of air is cooled 1° C by the evaporation of 0,5 g of water in middle and lower positions. Wet grasslands transpire about 4 liters of water from 1 m² in summer; 0,7 kWh of energy is needed for evaporation of 1 liter of water. As a result of the consequent cooling, water vapours condense as dew or precipitation. The place where the condensation occurs is being warmed (Larcher, 1988). Although the importance of grasslands has been studied and mentioned several times (see for example Rychnovská, 1985; Lukavská, 1988), these unique functions of grasslands have not been generally appreciated.

3.2.2 Phalaris arundinacea: syn. Baldingera arundinacea

3.2.2.1 Species description

Phalaris arundinacea is a typical species of lowland river floodplains and can potentially grow along the whole topographic/ moisture gradient in a floodplain (Prach, 1992). Nevertheless it grows also in mountainous regions at high altitudes (Klimešová and Čížková, 1996). *Phalaris arundinacea* grows very quickly in the spring. Its ability to overgrow other species places this plant among the most efficient grasses. Production of dry biomass varies between 5 to 11 t . ha⁻¹, and rarely can be 12-13 t . ha⁻¹ (Rychterová, 2007). It can have 4-5 cuts under optimal conditions. Due to intensive vegetative propagation, *P. arundinacea* is a very persistent plant. But, if it is mown systematically 6-7 times per year, it will disappear from the herbage (Klapp, 1956). The best areas for *P. arundinacea* growth are when ground water is between 30-40 cm (Melčáková, 1993), due to its requirement for a large amount of water for aboveground biomass production. On average, it needs about 700-800 liters of water for 1 kilogram of dry matter. Therefore, it is used in places where biological drainage is

needed (Klesnil *et al.*, 1973). It is also used successfully in vegetating fertilized peats and bogs (Hron, 1979).

Mature *P. arundinacea* flowering culms can be as tall as 3 m. In floodplain habitats, mature plants benefit from an extensive rhizome system adapted to low oxygen conditions in the soil (Shiple *et al.*, 1989). Spring emergence of new shoots occurs at the expense of reserve carbohydrate stored in the rhizomes (Čížková- Končalová *et al.*, 1992). However, in dry periods, oxygen is not limiting and species with deep rhizomes may be at a competitive disadvantage to species with a shallow rhizome system, because their shoots will emerge earlier in spring (Crawford *et al.*, 1989).

Phalaris arundinacea caryopses can germinate both in light and dark conditions (Vose, 1962); the latter is an advantage in habitats where sediments are deposited. The primary culm of the seedling remains relatively small compared to its offspring tillers, which are slightly thicker and taller. Tillers produce short rhizomes which bear several thicker and taller culms. By tillering young clones, *P. arundinacea* can cover an area of one square meter and will consist of 100 tillers by the end of the first growing season. The smallest primary culm is in the centre of the clone, with culm size increasing towards the periphery of the clone. Flowering tillers arise from rhizome tips in the second growing season. Culm growth rates depend on habitat conditions. In a floodplain, for example, seedling growth is slower because of intraspecific competition from mature plants or by seedling crowding (Klimešová and Čížková, 1996).

3.2.2.2 Spread and characteristics in wet grasslands

Phalaris arundinacea has recently expanded into wet wastelands (Prach and Wade, 1992). The species withstands both trampling and intensive mowing; on nutrient rich wet localities with a fluctuating ground water table it may be used as forage and for bedding. The presence of *P. arundinacea* causes increased sedimentation and protects the substrate against erosion when growing on sandy deposits in river beds and along river banks (Conchou and Patou, 1987). The ability of *P. arundinacea* to concentrate large amounts of nutrients in its aboveground biomass makes it suitable for waste-water treatment systems (Dubois, 1994).

Species diversity in stands dominated by *P. arundinacea* is obviously quite low (Hamadejová, 2001). The occurrence of *P. arundinacea* can be restricted by three types of floodplain habitats: (i) in the driest parts of abandoned meadows, (ii) on drier parts of regularly mown meadows, or (iii) in the littoral of permanent pools. *Phalaris arundinacea*-dominated meadows should be harvested three times per year under optimal nutrient

conditions (Lawrence and Ashford, 1969; Horrocks and Washko, 1971). However, if nutrient inputs do not cover demands, mowing may cause nutrient limitations (Klimešová and Čížková, 1996). Replacement of *P. arundinacea* is caused by its morphology. The plants have tall leafy culms without rosette leaves. A characteristic feature of this species is its inability to flower after mowing, because of the loss of its apical meristems. New tillers which emerge from the bud pool after decapitation do not flower.

Phalaris arundinacea seedlings were more frequent in unmown meadows along the whole topographic/moisture gradient in a floodplain (Klimešová and Čížková, 1996). Seedlings were absent in bare patches created by physical disturbances of heavy mowing machinery. The presence of *P. arundinacea* seedlings throughout the floodplain suggests that suitable conditions for emergence occur in all floodplain habitats except for the driest parts of meadows, especially when the plant cover is disturbed. Mature plants of *P. arundinacea* occur mainly in unmown grasslands. In managed meadows, *P. arundinacea* occurs mostly in the wetter parts of the topographic/moisture gradient (Šrůtek *et al.*, 1988) because mowing has less of an effect on growth when nutrients and water are not limiting growth. *Alopecurus pratensis* can replace *P. arundinacea* in mown meadows of the river floodplain, because mowing does not affect the vegetative spreading nor generative reproduction of *A. pratensis* as much as it does in *P. arundinacea*. Therefore *A. pratensis* is more successful in managed meadows. On the other hand, when a meadow is abandoned, *A. pratensis* is outcompeted by tall leafy tillers of *P. arundinacea*; this species replacement occurs quickly because of increased growth and regeneration of *P. arundinacea* relative to *A. pratensis* (Klimešová and Čížková, 1996). *Alopecurus pratensis* also replaces *P. arundinacea* in the drier parts of regularly mown meadows.

In the littoral of permanent pools, *P. arundinacea* is replaced by *Carex gracilis*, which is better adapted to the low oxygen conditions associated with standing waters and soils with high organic matter content. Root porosity of *C. gracilis* decreases, however, when additions of organic matter are combined with high nitrogen supply (Klimešová and Čížková, 1996). Similarly, root porosity was reduced in three *Carex* species subjected to flooding with diluted piggery sewage (Končalová *et al.*, 1993).

Prach and Straškrabová (1996) estimated that it usually takes two decades for *P. arundinacea* to overgrow meadows. They also addressed the question of how long the opposite process takes, if a previously abandoned meadow is started to be cut again. *Phalaris arundinacea* dominated over most of a meadow which had been left without mowing for ca. 20 years, together with *Urtica dioica* in the most elevated parts. Restoration of the cutting

regime immediately induced fast changes in vegetation cover. Dominant species typical for abandoned meadows, such as *P. arundinacea* and *U. dioica*, dramatically decreased during the observed time. On the contrary, species typical for regularly managed meadows in that area started to increase. Sedges (*Carex sp.*) increased in their occurrence in the lowest part of the moisture gradient. After five years of the studied period, the species composition was comparable to that of cut meadows (Prach and Straškrabová, 1996).

Significant changes in productivity also occurred during the study period and are well recognizable by comparing biomass of the mown and unmown treatments. Biomass of the mown variant was 190% greater than that of the unmown one in the first cut after four years of cutting. Total productivity was evidently higher in the mown variant as a result of changed species composition: earlier growth of *Alopecurus pratensis* in comparison with *P. arundinacea* (Rychnovská, 1985). *Alopecurus pratensis* is a more palatable species than *P. arundinacea*, because it is the most productive species in the area (Prach and Straškrabová, 1996).

3.3 Study Site – Mokré Louky (Wet Meadows)

3.3.1 Site Description

Mokré Louky (Wet Meadows) is an area adjacent to Rožmberk fishpond. According to the Catalogue of Biotopes in the Czech Republic (Chytrý *et al.*, 2001), this area belongs to class M1.4 Riverine reed vegetation, while the phytosociological association is Phalaridion arundinacea. More characteristics of the studied locality are given in the Methods.

3.3.2 Historical Data

Two main sources of data about Mokré Louky from the second half of the 20th century are Holubičková (1959) for the 1950's and Prach (1993) for the 1980's.

The first phytosociological description of Mokré Louky was made in 1956 (Holubičková, 1959). The vegetation pattern of 1956 still reflected the former traditional management pattern that had been carried out for centuries. This consisted of (i) regular mowing, usually three times a year; (ii) maintenance of a sophisticated drainage system with numerous open ditches; and (iii) amelioration of the ancient fen with mineral earth layers (Holubičková, 1959). Only the wettest northernmost part in the outer littoral zone of Rožmberk fishpond was

virtually untouched by human impact, being left without external mineral input and cut only once a year (Prach and Soukupová, 2002).

Management of Mokrý Louky substantially changed, beginning in 1956. In the 1960s, hay was harvested only once or twice a year, and collection of litter for bedding near Rožmberk Pond ceased completely. The drainage system was neglected, and only the main canals were occasionally cleaned. At the end of the 1970s, heavy degradation of the meadows started. Drastic amelioration started with excessive application of slurry from a nearby pig farm and a water-treatment station, and rebuilding of the previous fine channel system into a coarse system with deep transverse ditches. A part of the meadows close to the fishpond remained abandoned, while others were cut three or even four times a year (Prach, 1993). Degradation seemed to have stopped in the 1990s and some slow recovery was expected. However, the distinct increase of ruderal species between 2001 and 2006 indicates continuing deterioration of the natural quality of the meadows.

It is evident that the diversified mosaic of seminatural vegetation types found in 1956 mostly changed into monospecific stands (Prach and Soukupová, 2002). While there were no ruderal or segetal species in 1956, in 2006 there were 22 species belonging to this category. The number of meadow and marsh species was reduced by more than one third (Prach, 2008).

Previous differences in vegetation, as a result of fine differences in moisture and soil conditions, were overwhelmed by uniformly intensive agricultural practices, especially manuring. Cleaning and deepening of the drainage system also contributed to vegetation changes, together with the fact that the water table in the Rožmberk fishpond has been lower since 1981. Large patches and strips of short sedge communities of the alliance *Caricion fuscae* have almost disappeared and been replaced by stands of more robust plant species, enhanced by the large nutrient input. Along the ditches and channels, *Phalaris arundinacea* has expanded, because of increased nutrient supply, mechanical disturbances during cleaning of ditches, or lack of mowing. The obvious increase in the importance of robust wetland species, such as *Phalaris arundinacea*, *Glyceria aquatica*, and *Carex gracilis*, is probably a consequence of wet years at the beginning of the present century (Prach, 2008).

Mokrý Louky was an example of a peaty sedge meadow, particularly of *Carex gracilis*, *Carex vesicaria* and *Calamagrostis canescens* (Lukavská, 1988). On the contrary, this site has recently had a massive increase in *Phalaris arundinacea*, which, in some places, has repressed those other species and become the dominant species of the site.

A vegetation and habitat survey of the Rožmberk fishpond littoral was conducted mainly in 1981-83 (Hroudová, 1988). It found that the presence of *Phalaris arundinacea* indicated

soil containing a large portion of mineral particles, which therefore dries out more readily than that of surrounding stands of *Carex gracilis*. The whole association of this site was very poor in species; the dominant *Phalaris arundinacea* is accompanied occasionally by species of the alliance *Caricion gracilis* or reed-belt species. Its most common contact association is the *Caricetum gracilis* or, sometimes, the *Glyceritetum maximae*. In some places, *Phalaris arundinacea* forms mixed stands either with *Carex gracilis* or *Glyceria maxima*.

This survey also summarized that vegetation development is dependent upon a combination of two groups of factors: natural changes in habitat factors and human impact. Progressive land-formation, in addition to changes in the water table, influences the groundwater level in littoral communities. According to long-term averages, the height of the water table in littoral stands is dependent upon the rate of silting of bays and accumulation of plant detritus, resulting in a stable littoral zonation. Short or medium-term changes in the water table, brought about by floods or drought, can have a temporary effect both on the composition and floristic homogeneity of littoral communities, or can be responsible for the predominance of several species (Hroudová, 1988).

Another study done by Prach (2007) addressed the question concerning rate of degradation if traditional or restoration management is stopped or interrupted for any reason. That study described a successful restoration being followed again by degradation, when restoration management was abolished. A strip 150 m long and 5 m wide was cut three times, later only twice a year, for 5 years. Successful restoration of the meadow was more or less completed after only four years of the experiment. Subsequent degradation took approximately 7 years to reach the stage that was similar in cover of constituent species and species number to that before the experiment started. Very fast changes in species composition and cover of constituent species were observed following both the re-establishment of regular mowing and its ceasing. *Phalaris arundinacea*, the dominant species at the beginning of the experiment, slightly increased in its dominance after the first season of cutting, but then decreased very rapidly. However, after the cessation of mowing, *P. arundinacea* was able to attain its previous dominance also very quickly (Prach, 2007).

Nowadays, nearly the whole floodplain is left without management, which has resulted in the rapid expansion of *P. arundinacea*. In such conditions, *P. arundinacea* would be expected to expand, becoming dominant 5-10 years after the cessation of cutting (Guth and Prach, 1996). Then restoration will be less probable than now (Zobel *et al.*, 1998). However, resumption of a more traditional management regime should lead to the almost complete disappearance of *P. arundinacea* (Guth and Prach, 1996). Therefore, regular management

should be of interest for both nature conservancy and farmers. The management must be regular; if interrupted for even a few years, a fast degradation can be expected again (Prach, 2007). Traditional land use, which consisted usually of three cuts a year (Prach *et al.*, 1996), maximizes plant diversity (Bakker, 1989).

3.3.3 Production examples

Aboveground biomass production ranged from 625 g.m⁻² - 1800 g.m⁻² and 941 g.m⁻² - 1478 g.m⁻² for unmown and mown stands, respectively, in Mokré Louky in the early 1980s (Květ, 1983). A few years later (1985-86), Lukavská (1988) estimated aboveground primary production in Mokré Louky at 1676, 2 g.m⁻² for a mown stand and 1577,4 g.m⁻² for an unmown one in 1985. These values decreased in the following year to 1015, 2 g.m⁻² and 1498 g.m⁻² for the mown and unmown stands, respectively. The mown stand was dominated by *Carex gracilis* and *C. vesicaria*, while the unmown stand was dominated by *Calamagrostis canescens*. Kuncová (2007) reported much lower primary production, 352 g.m⁻², in a site dominated by *Carex vesicaria*. Rychterová (2007) estimated aboveground primary production at 1407,6 g.m⁻² and Filipová (2006) at 1459,3 g.m⁻² in a stand dominated by *Phalaris arundinacea*.

4 Methods

4.1 Study Site

Třeboňsko is an area situated in South Bohemia near the town of Třeboň and is composed of a cultural landscape in which natural, semi-natural, and anthropogenic ecosystems are represented. This area is of national and international importance. Therefore, Třeboň was duly proclaimed as a city reservation in 1976. In addition, UNESCO designated Třeboňsko as a biosphere reservation in 1977 and in 1979 the Protected Landscape Area Třeboňsko was established (Jeník, 1983).

Wetlands are an important component of this particular area. Our locality, Mokré Louky (Wet Meadows), is situated on the eastern edge of Třeboň, in a wide zone from the Zámecké forest district to Rožmberk fishpond. Mokré Louky is the northern part of the wide complex of peat-bogs in the Zámecký and Cepský forest districts (Jeník, 1983).

The study site is in the northernmost part of Mokré Louky at 14°46' E and 49° 01' N and 427 m a.s.l (Fig.1). The macroclimate of Třeboňsko is suboceanic with moderate winters and temperate summer maxima (long-term measurements from the Třeboň weather station). The average temperature is 7, 4 °C with maximum rainfall in the growing season (Jeník, 1983).

The area is influenced by the fluctuating water table of the nearby Rožmberk fishpond, the largest fishpond in the Czech Republic (500ha). Occasionally, the wet meadows are flooded. The meadows in this area are subdivided into nearly regular strips of about 500 x 100m in size, separated by ditches which are perpendicular to a central canal going to the fishpond (Prach, 2008).

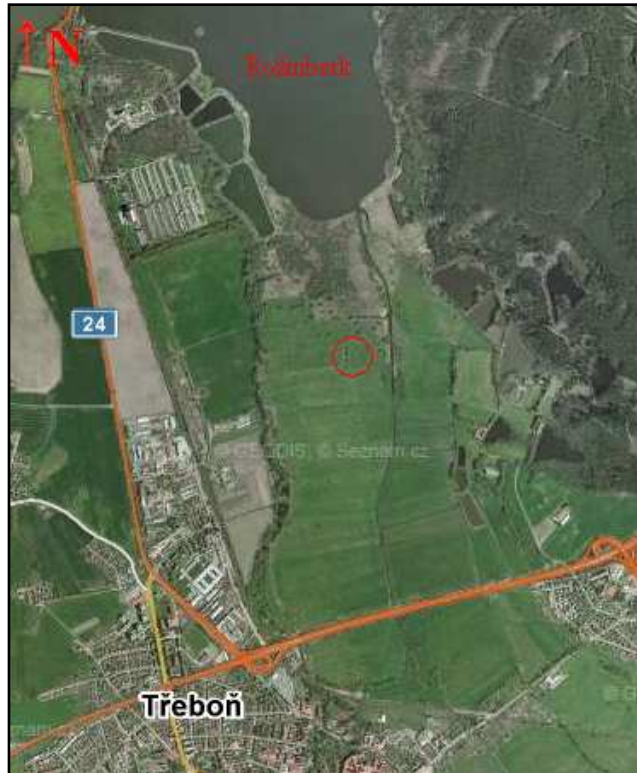


Fig.1: Location of the study site, as shown by the red circle. To the north is Rožmberk fishpond and to the south is Třeboň.



Fig.2: Aerial photo of the site, showing the two study areas, A (low nutrients) and B (high nutrients).

The study site has not been mown since 2005. The site was dominated by *Phalaris arundinacea* at the beginning of the study. Our experimental area is divided into two parts- part A and part B (Fig.2) - which have significant differences in nutrient levels. Site B is closer to a still fertilized field and probably receives more nutrients through run-off (Fig.3).

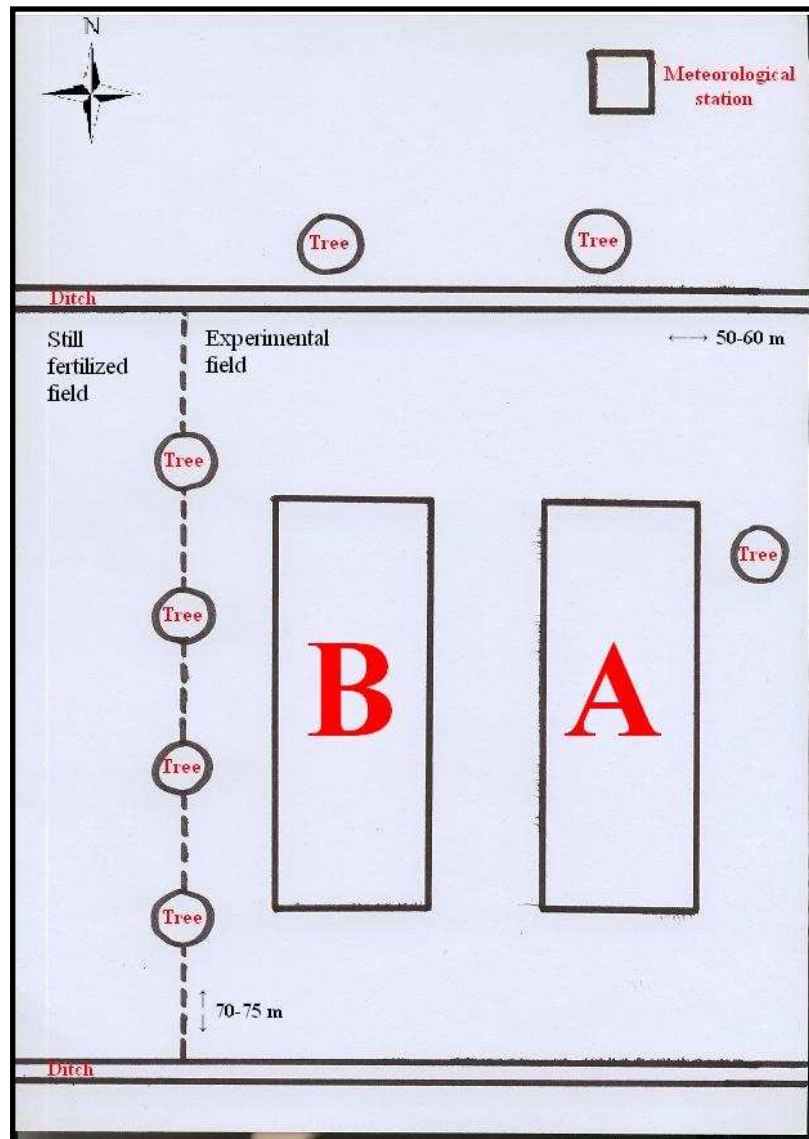


Fig. 3: Schematic of the experimental area showing parts A and B.

4.2 Methodology

4.2.1 NAPP (net aboveground plant production)

Dry weight was used as the main measure of biomass in this study. Biomass was collected using the direct destructive harvesting method (Dykyjová, 1989). The sampling technique is based on harvesting the whole aboveground stand in quadrats for investigating primary production during the growing season. Direct harvesting can be particularly difficult in wetlands (Westlake *et al.*, 1998), partly because of difficulties of access (neither dry land nor deep enough for diving), but also because populations are subject to several environmental gradients as well as having clumped distributions, which give high variances. Therefore, it is necessary to consider the size of the quadrats and the sampling pattern very carefully.

The destructive harvesting method allows for the recognition of plant structure, not only of the stand but also for individuals and populations with minimal technical equipment. For these reasons, this has become the most popular and used method for production ecology (Rychnovská, 1987).

Biomass will vary with time and the determination should be made at the time of seasonal maximum biomass, which is often near the time of flowering (Vollenweider, 1969). It is necessary to decide which plants to be harvested. For this study, plants that were rooted within a 50 x 50 cm quadrat were removed by hand (Fig.4). This has been found to be an ideal size for wetland vegetation such as *P. arundinacea* (Rychnovská, 1987).

Monthly samplings occurred in sites A and B from April until September during the 2007 growing season. Four quadrats were sampled from each site in each sampling time. In 2008, sites A and B were again sampled six times, with sampling again starting in April. However due to circumstances beyond our control, the second sampling was conducted in early June instead of the end of May, while the last sampling was in October instead of the end of September. Again, four samples were taken from each site.

Shoots were cut at ground level. We divided the LIVE part from the LITTER part into separate polythene bags (Fig. 5). The plants were then taken back to the University of South Bohemia where they were kept in polythene bags in cold storage until they were processed. If this could not be done on the same day; processing of the plant material always occurred within one week of harvesting.



Fig. 4: A square 50x50 cm frame



Fig. 5: A harvested plot with biomass in polyethylene bags

Biomass was removed from the polythene bags and the STANDING DEAD part was separated from the LIVE part. The LIVE fraction was sorted into different species (Fig. 6), except for *Carex*, which was only labeled as *Carex* spp. Each species was put into a marked paper bag (Fig. 7). All plant biomass fractions (LIVE, STANDING DEAD and LITTER) were put into separately labeled paper bags and dried. All samples were placed into forced air ovens (Memmert) and dried at 70° C for at least 48 hours (Fig. 8). The dry matter was then removed and weighed.



Fig. 6: Sorting into species

Dry matter content was expressed as grams per square meter. Net annual aboveground production was calculated as grams per square meter per year (Lieth and Whittaker, 1975). Mean net annual aboveground plant production (NAPP; $\text{g DW} * \text{m}^{-2} * \text{yr}^{-1}$) was calculated from the dried living, standing dead and litter material in each site. Production of live material was determined as the maximum DW during the growing season. In addition, production of dead material was determined by adding the standing dead and litter DWs collected in each quadrat and calculating the mean dead DW for each site. Differences in mean dead DW were calculated between subsequent sampling dates. Only differences resulting in positive numbers were included in estimating NAPP. NAPP for each site was finally calculated by adding together the total live production (LIVEPROD) with those positive differences in dead matter ($\text{NAPP} = \text{LIVEPROD} + \Sigma \text{DEAD}_{\text{Positive}}$).

Statistica 7 was used for data evaluation. Analysis of Variance (ANOVA) for repeated measures was used to determine if there were significant differences in biomass production between sites A and B. Post-hoc Tukey HSD test was done for multiple comparisons in the case of significant differences. Moreover, t-tests were run to compare site A to site B in each sampling time. The 2008 data were naturally logged transformed in order to achieve homogeneity of variance; no such data transformation was needed for the 2007 data.



Fig. 7: Marked paper bags



Fig. 8: Samples drying in the oven

4.2.2 Belowground production (NBPP) and above-to-belowground ratios

Net belowground primary production (NBPP) was measured using the in-growth core bag method in 2007 (Steen, 1984; Vogt *et al.*, 1998). Three points were selected within each site for placement of the core bags. Two bags (7 cm diameter x 15 cm depth), and filled with soil from the site, were placed into each sampling point on 30 April 2007. They were left in place until collected on 21 September 2007. Keeping the core bags in the soils over most of the growing season allowed for adequate root growth into the bags without significant root mortality (Steingrobe *et al.*, 2000). The removed cores were taken to the laboratory where they were carefully cleaned of soil and the root mass dried in a convection oven at 70° C for 72 hours. The resulting dry weight mass was then weighed. The ensuing dry weight equals the net belowground primary production (NBPP) for the growing period. The dry weights (and NBPP) were calculated to a m² basis.

Above-to-belowground production (A: B) ratios were determined for each site by dividing mean NAPP by mean NBPP. The results were then shown graphically.

4.2.3 Nutrient content in plants

Plant samples, after grinding, were analyzed for total C, N and P by members of the Department of Ecosystem Biology, JCU. Total C and N (TC, TN) were analyzed using an elemental CN analyzer. Total P was determined by a semi-micro modification of the perchloric acid digestion method (Kopáček and Hejzlar, 1995).

4.2.4 Line intercepts

In order to obtain more detailed information about plant species composition and dominance in our sites, line intercepts were established in A site in late August 2007 and in both sites (A and B) in early September 2008. Three 30 m long transects were established randomly in each site; the distance between neighboring transects was 4 m in site A, and 5 m in B (Fig. 9). Each transect began at a distance of 16 m from the side ditch. We noted the particular species which was dominant or co-dominant within a 1 m strip on each side of the transect and for a particular length along the intercept. From those data, frequency of *P. arundinacea* was calculated. This was done by determining the total distance along each transect in which *P. arundinacea* was the dominant or co-dominant species (in the case of co-dominance, the the length was divided by the number of co-dominant species). The percent

frequency was calculated by dividing the total length when *P. arundinacea* was dominant by the total length of the transect, multiplied by 100 (% Phalaris = (length on each transect where *Phalaris* was dominant / total transect length) * 100). The average cover of *Phalaris* for each site was then determined by taking the mean of the percent covers for each transect.

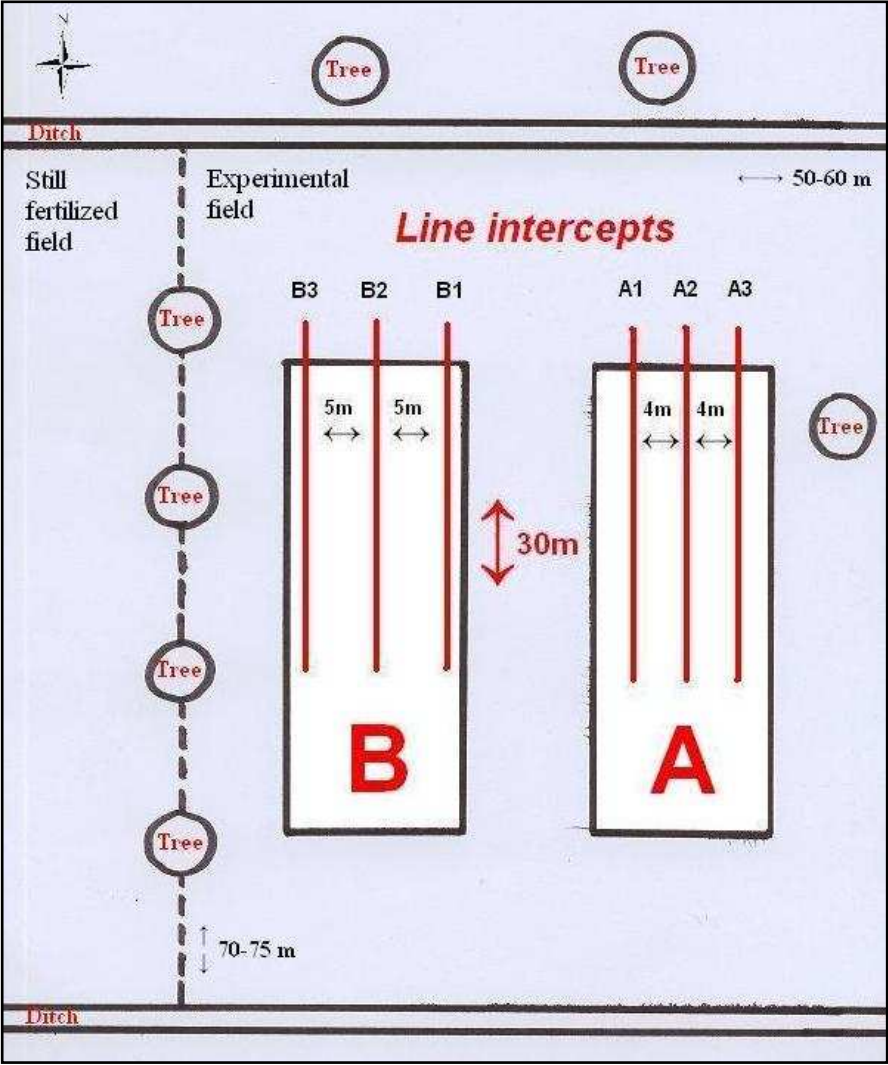


Fig. 9: Schematic showing the location of the line intercepts to determine percent cover of *Phalaris arundinacea* on a site basis

5 Results

5.1 NAPP 2007

Aboveground biomass ($\text{g DW} \cdot \text{m}^{-2}$) increased from the start of the growing season in April to mid-summer, at which time the maximum biomass value was found for site A (Fig. 10). There was then a sharp decrease in biomass levels for this site, while the graph for site B shows that biomass levels remained at this high level for the rest of the growing season. There were significant between-site differences in biomass production over time in 2007 (repeated measures ANOVA, $p < 0,001$; Fig. 10), with site B having more living aboveground biomass than in site A. Mean biomass levels also differed significantly in the two sites within each sampling period ($B > A$), except for June and July.

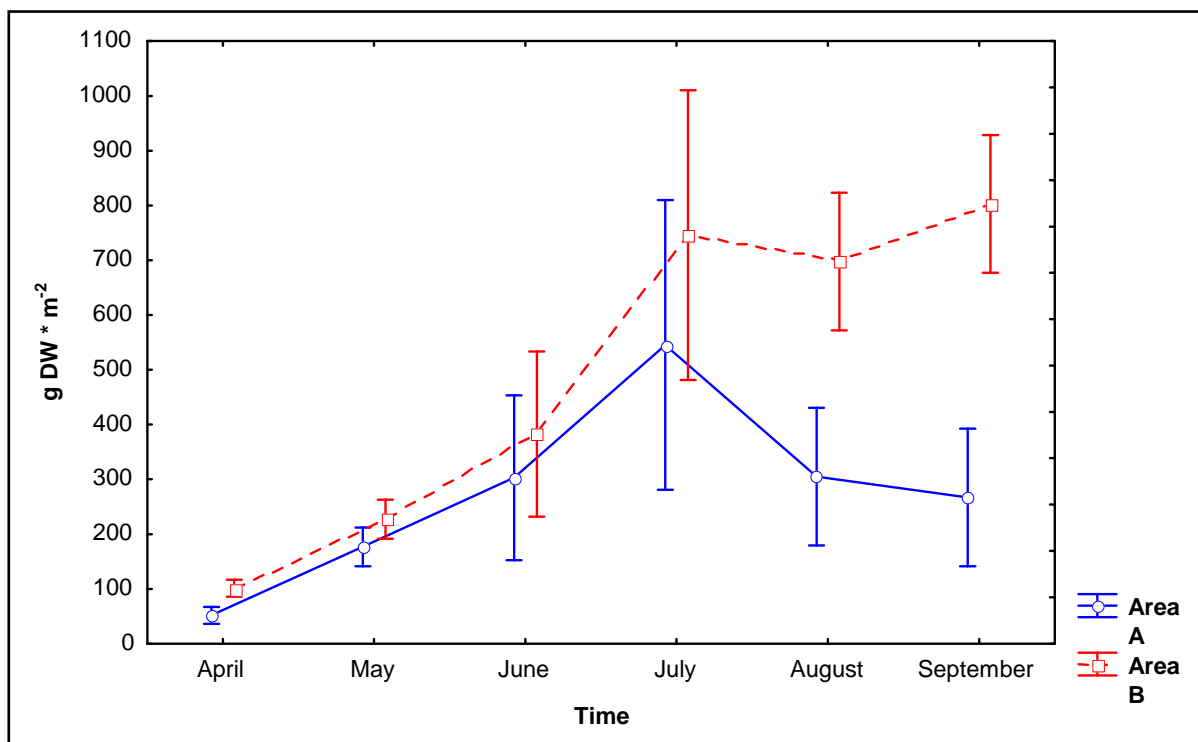


Fig. 10: Mean biomass levels (bars for each point are 95% confidence intervals) for the two study areas over the 2007 growing season.

The amount of dead material (litter + standing dead) was also greater in site B than for A throughout the 2007 growing season (Fig. 11), although the variation was not as large as for the live material. The amount of dead material found in the site A plots decreased throughout

the growing season from its maximum in May. This resulted in the small contribution of dead material to the overall NAPP for this site (Table 2). The maximum amount of dead biomass in site B was found in the August sampling date and represents a change in stems moving from the living to the standing dead categories. Decreasing levels of dead material during the growing season probably represent the amount of material lost to decomposition.

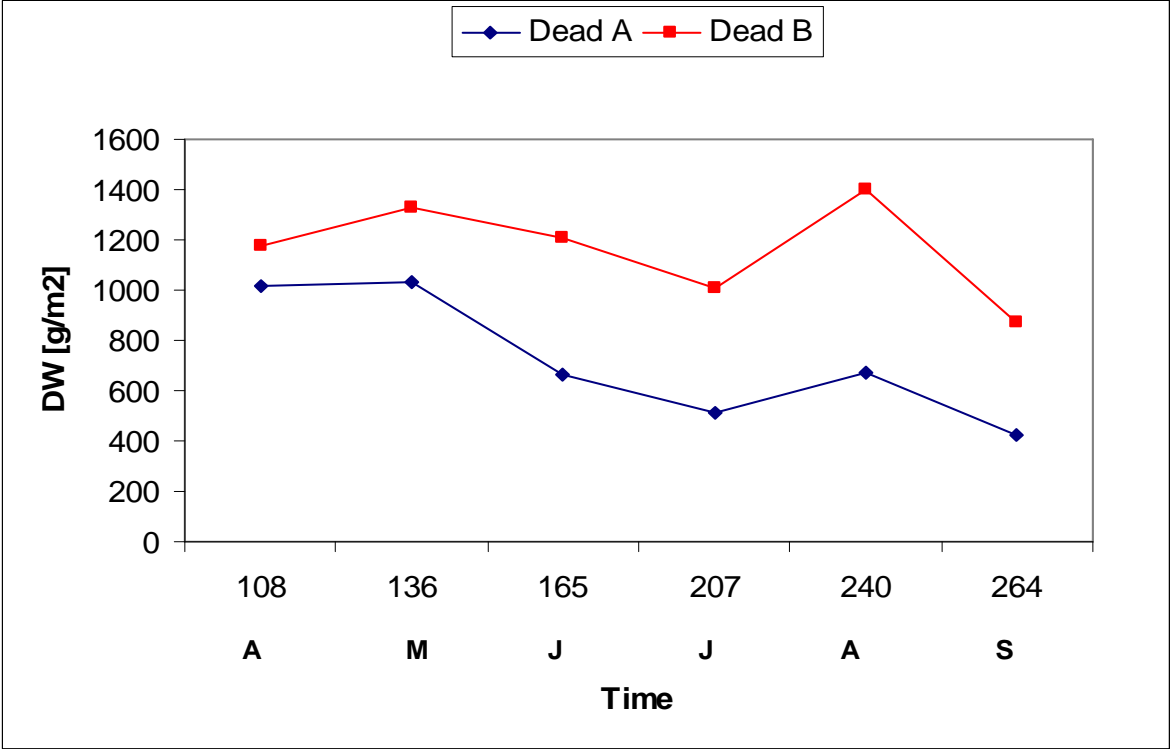


Fig. 11: Biomass of dead material for the two study areas over the 2007 growing season.

Table 2: NAPP for the two study areas for the 2007 growing season.

Area	Living Production [g/m ²]	Dead Production [g/m ²]	Total Production [g/m ²]
A	529,20	179,40	708,60
B	782,50	540,65	1323,15

Overall, NAPP was almost twice as large in site B compared to site A (Table 2), reflecting the differences in live aboveground biomass (Fig. 12, $p < 0,004$).

Belowground production (NBPP) was greater in site A than in B (1017, 2 and 730, 4 $\text{g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$, respectively), but these values were not significantly different ($t = 0.61$, $p = 0.561$). However, aboveground – to – belowground production ratio (A: B) was twice as large in site B compared to site A (Fig. 13). This reflects the greater aboveground biomass, and thus production levels in site B compared to site A.

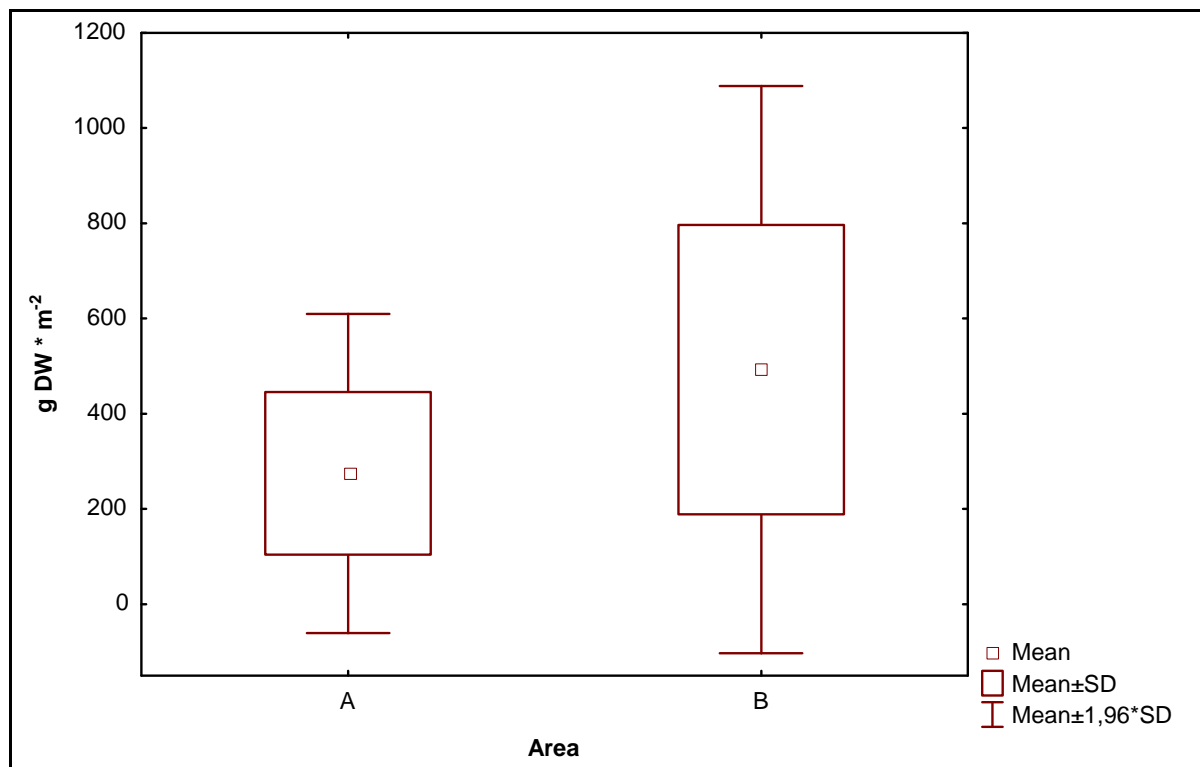


Fig. 12: Box and whiskers plot showing mean and standard deviations (SD) of aboveground biomass in sites A and B for the Mokré Louky study area in 2007.

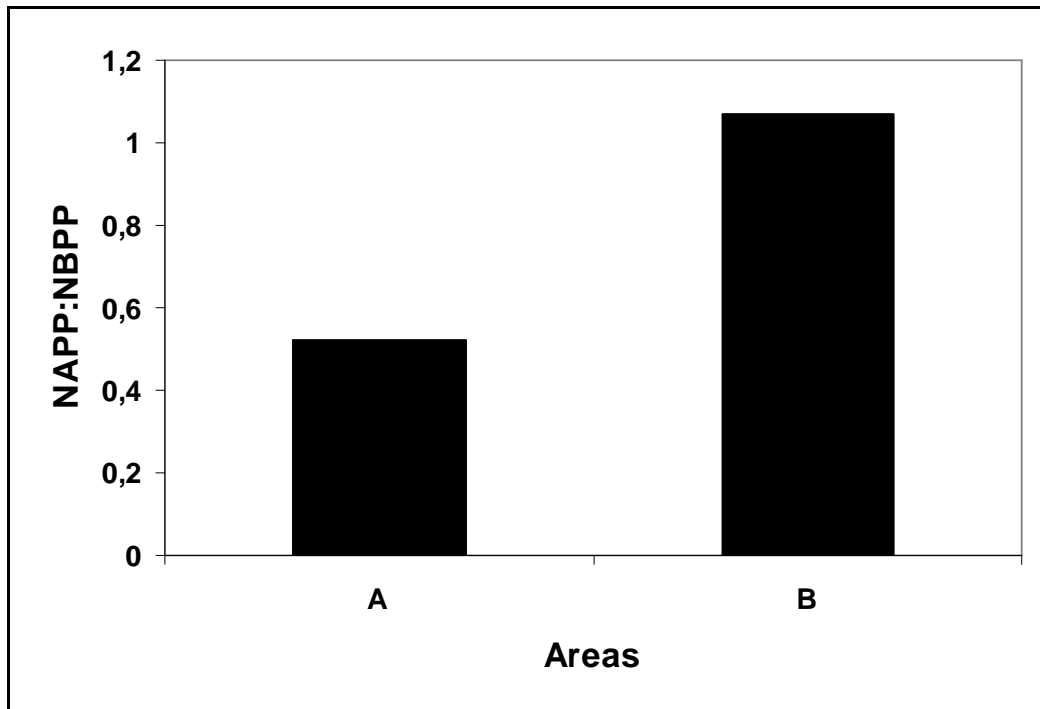


Fig.13: Above to belowground production ratios for the two study sites in 2007.

5.2 NAPP 2008

Aboveground biomass in 2008 was higher and with higher variations than in the previous year. Again, living biomass levels increased from the beginning of the growing season in April to the maximum amount in July; unlike in 2007, a clear maximum in July was seen in both sites (Fig. 14). The decreasing biomass levels later in the growing season were connected to increasing levels of dead biomass material (standing dead + litter) in that time (Fig. 15). Same as the previous year, there were significant between-site differences in biomass production over time in 2008 (repeated measures ANOVA, $p < 0,004$; Fig. 14), with site B having more living aboveground biomass than in site A. Mean biomass levels also differed significantly in the two sites within each sampling period ($B > A$), except for July and October. Still, the overall comparison in the differences in live aboveground biomass between sites A and B (Fig. 16) were again significantly higher for site B in 2008.

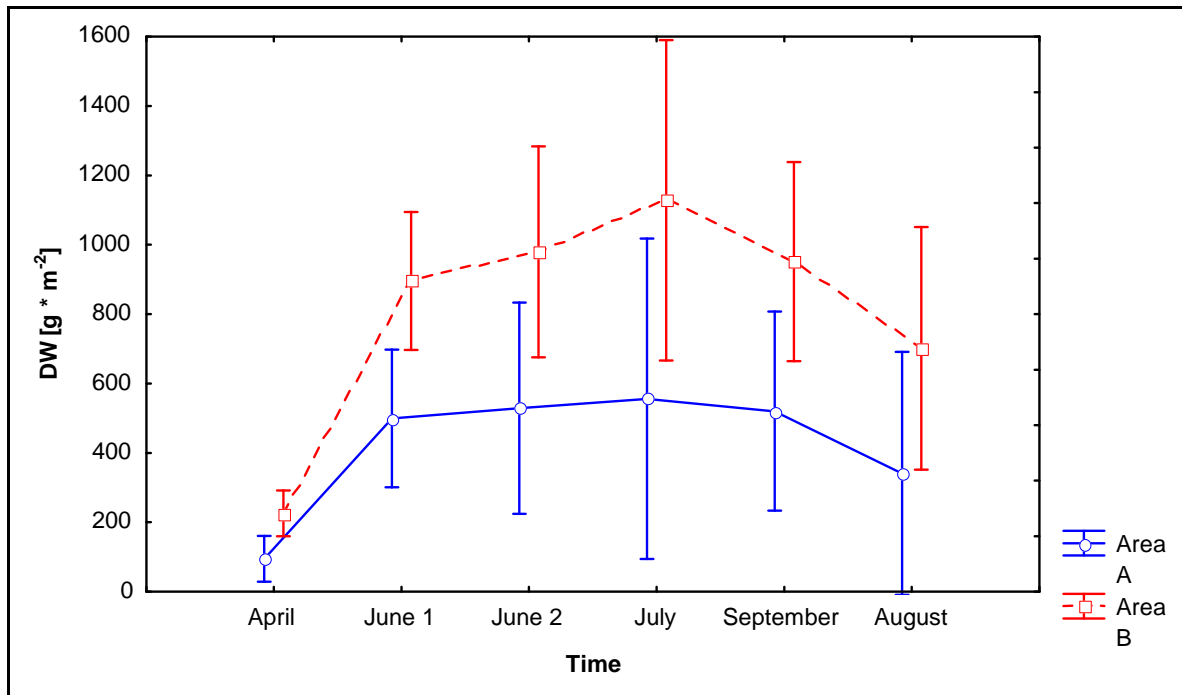


Fig. 14: Mean biomass levels (bars for each point are 95% confidence intervals) for the two study areas over the 2008 growing season. Analyses were conducted on natural log transformations of the data (see text).

Table 3: NAPP for the two study areas for the 2008 growing season.

Area	Living Production [g/m ²]	Dead Production [g/m ²]	Total Production [g/m ²]
A	461,3	413,2	874,4
B	902,8	786,8	1689,5

The last sampling occurred in October 2008 (versus September in 2007). This resulted in an increase in dead material (litter + standing dead) at the end of growing season (Fig. 15). This was caused by the senescence of the plants at that time.

Similar to 2007, NAPP was significantly greater in site B compared to site A ($p < 0,001$) in the 2008 growing season, again being almost twice as large (Table 3).

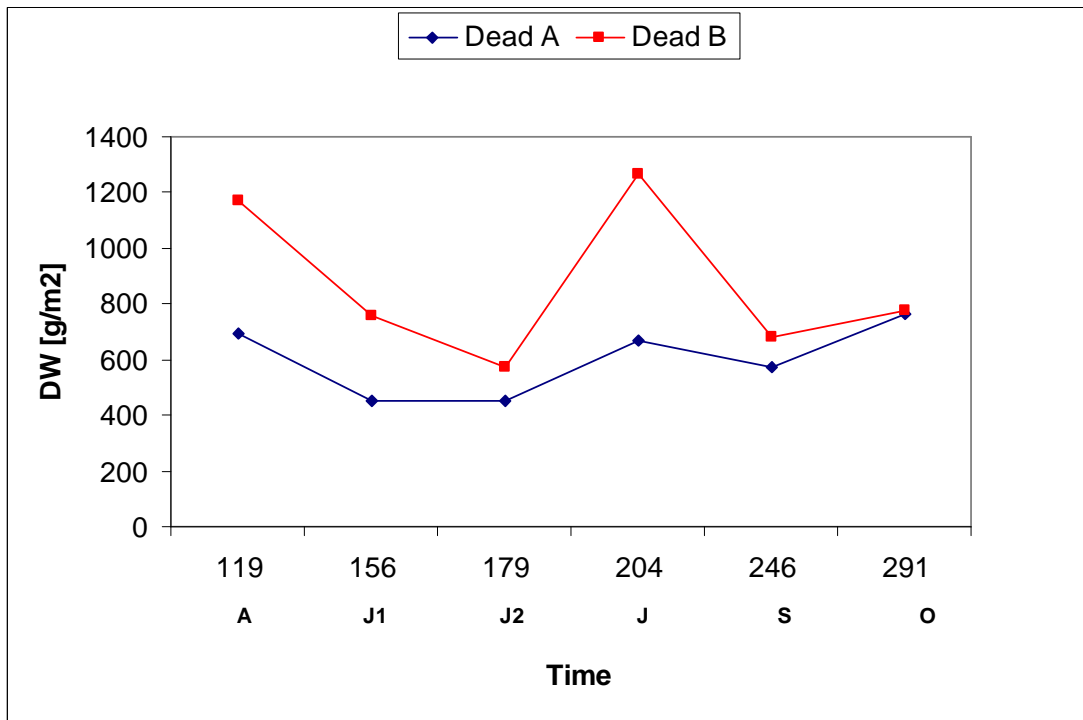


Fig. 15: Biomass of dead material (standing dead + litter) for the two study areas over the 2008 growing season.

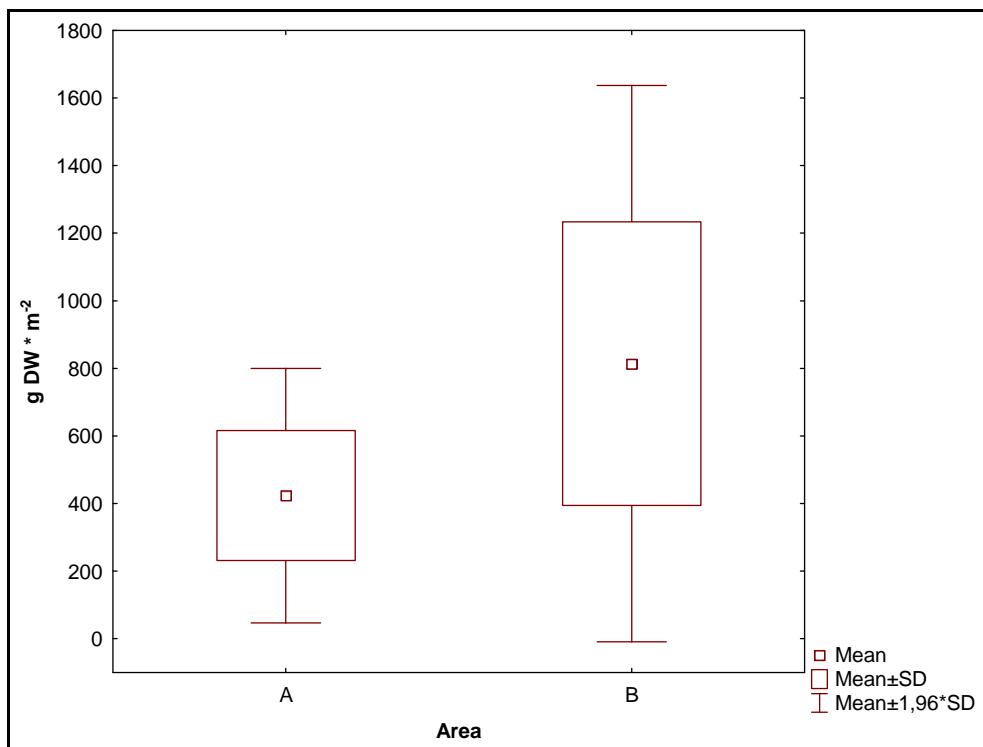


Fig. 16: Box and whiskers plot showing mean and standard deviations (SD) of aboveground biomass in sites A and B for the Mokré Louky study area in 2008.

5.3 Plant nutrient contents - 2007

Percentage of total phosphorus (TP) per gram of aboveground material of *P. arundinacea* was greater in plants growing in site B than for those in site A in the early part of the growing season (May 2007; Figure 17). However, neither nitrogen (N) nor carbon (C) levels differed between the two sites at this time (Figures 18 and 19).

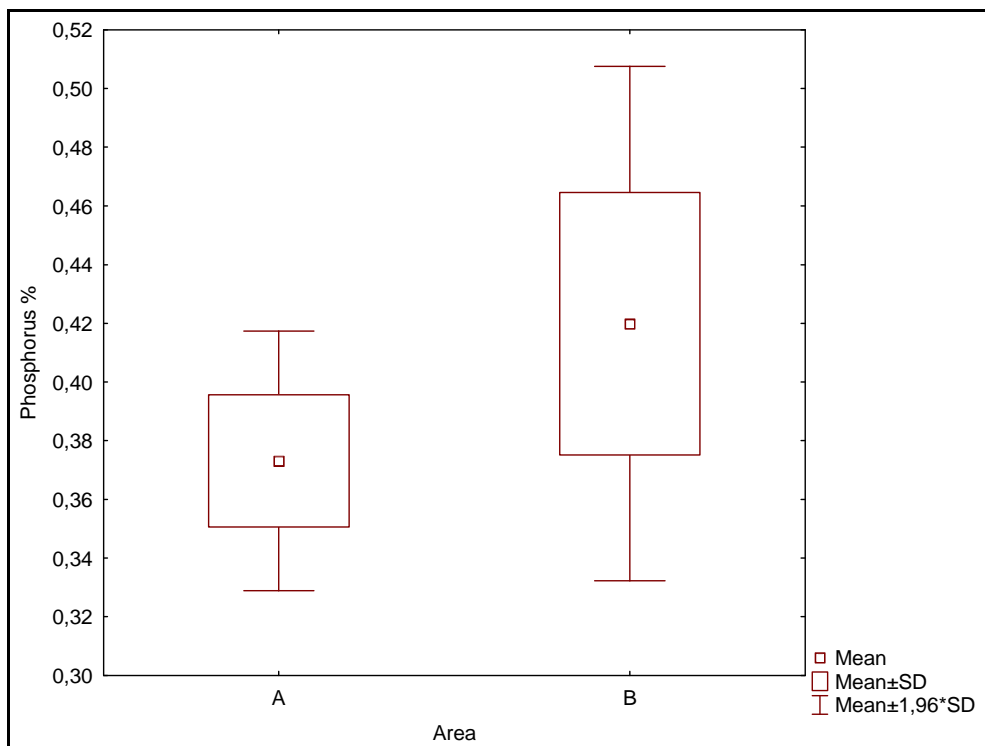


Fig. 17: Box and whiskers plot showing percentage of total phosphorus (TP) in sites A and B in May 2007.

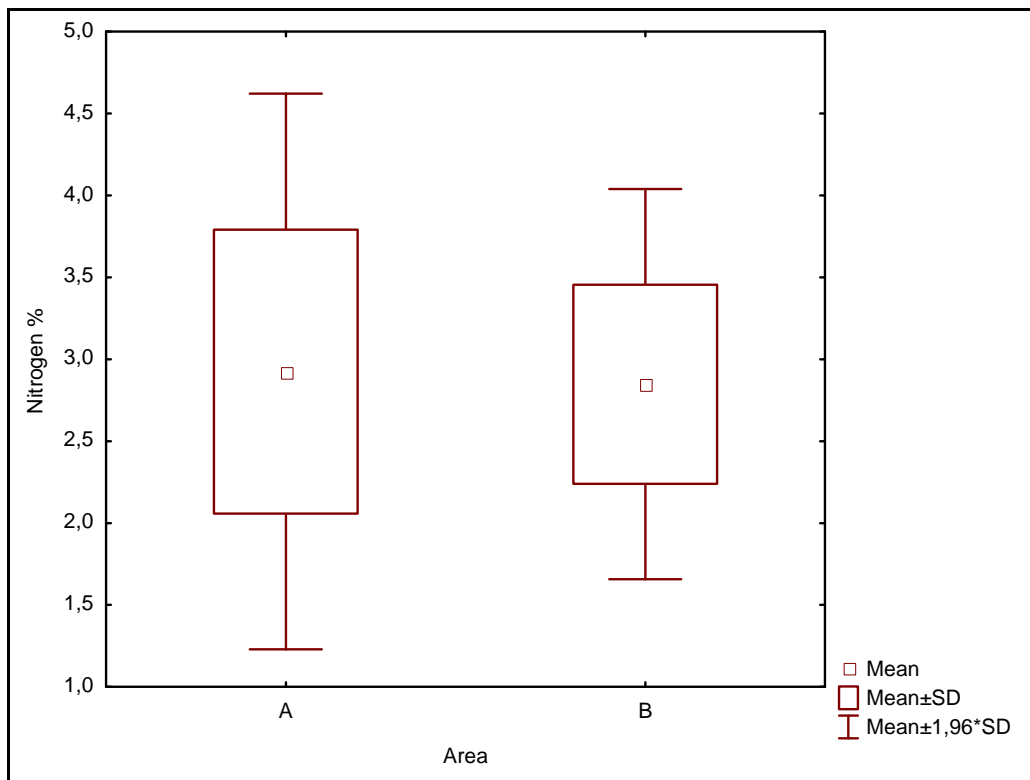


Fig. 18: Box and whiskers plot showing percentage of total nitrogen (TN) in sites A and B in May 2007.

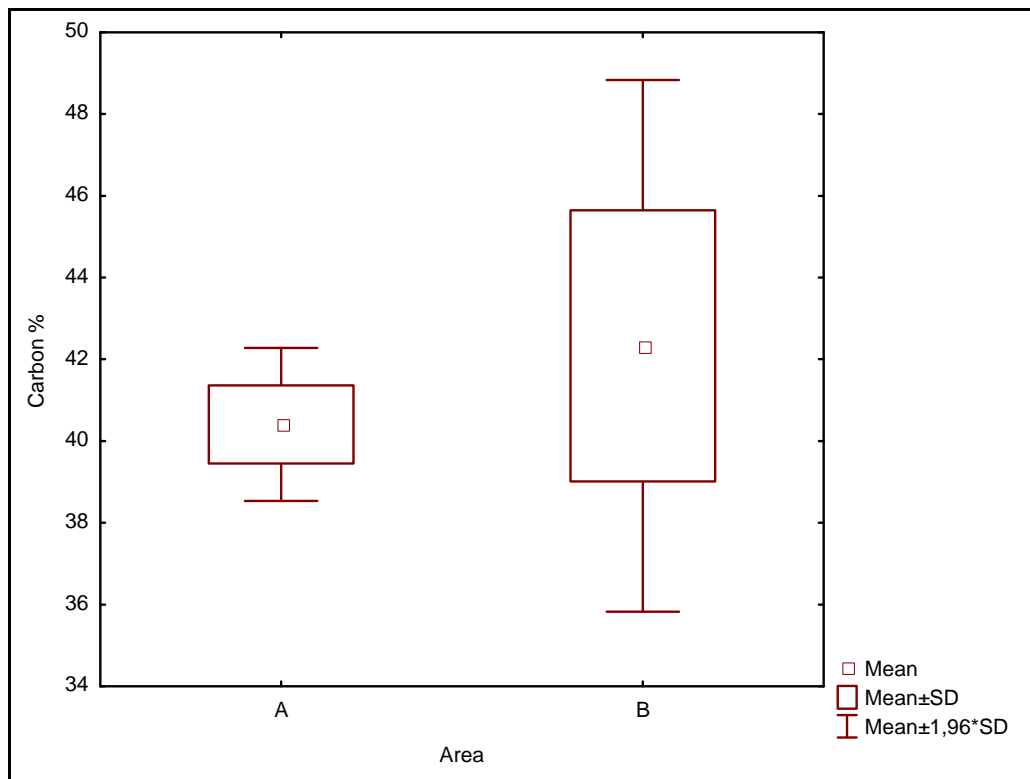


Fig. 19: Box and whiskers plot showing percentage of total carbon (TC) in sites A and B in May 2007.

Nutrient concentrations were also measured at the time of maximum biomass (August 2007). At this time, the percentage of TP was very similar in both parts, being slightly higher in B (Fig. 20). However, both TN and TC percentages were significantly ($p < 0,01$) higher in the *P. arundinacea* plants growing in site B (Figures 21 and 22).

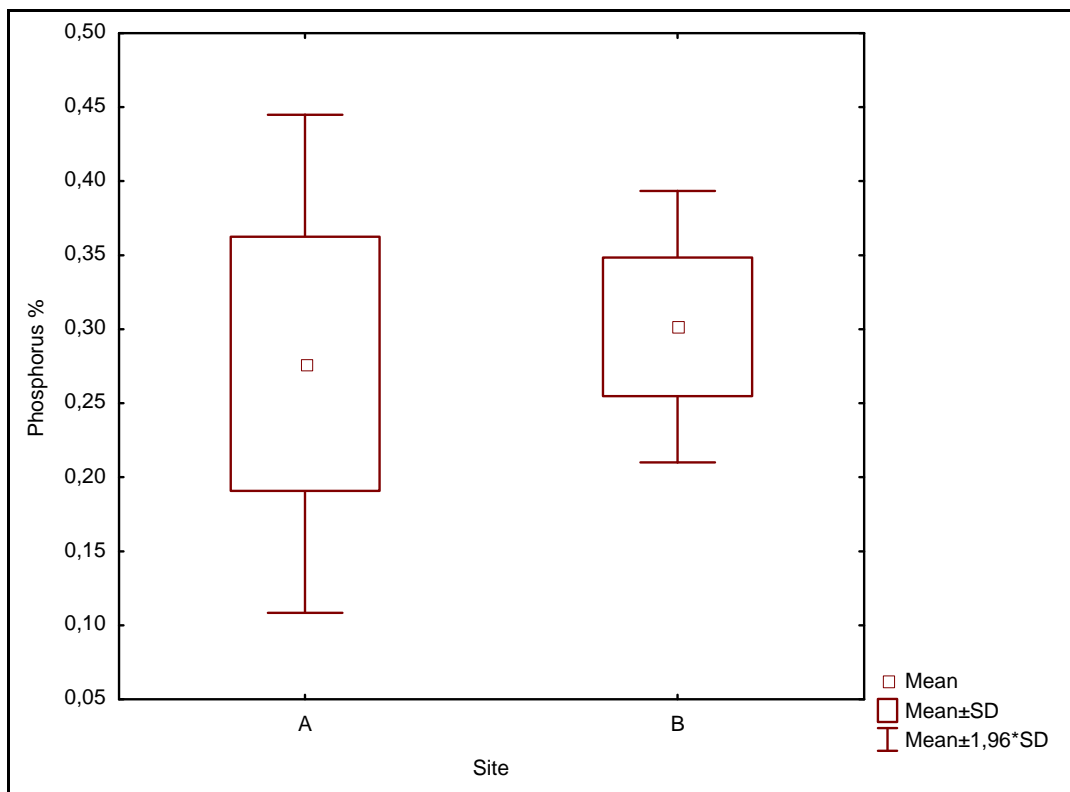


Fig. 20: Box and whiskers plot showing the percentage of total phosphorus (TP) in sites A and B in August 2007.

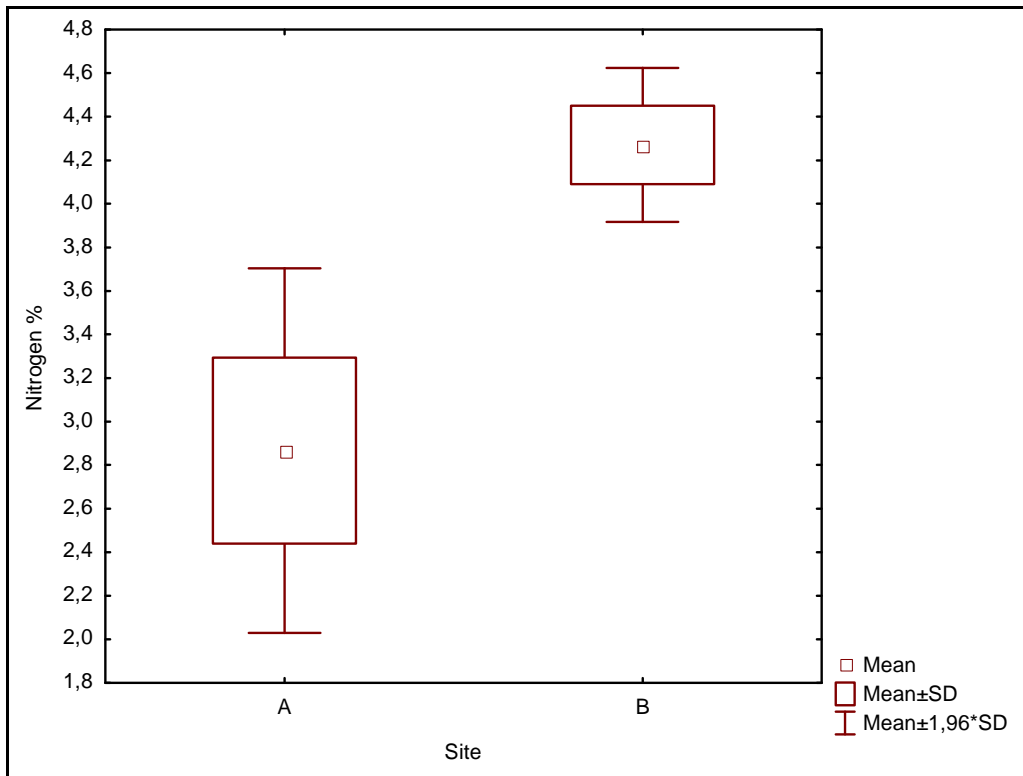


Fig. 21: Box and whiskers plot showing the percentage of total nitrogen (TN) in sites A and B in August 2007.

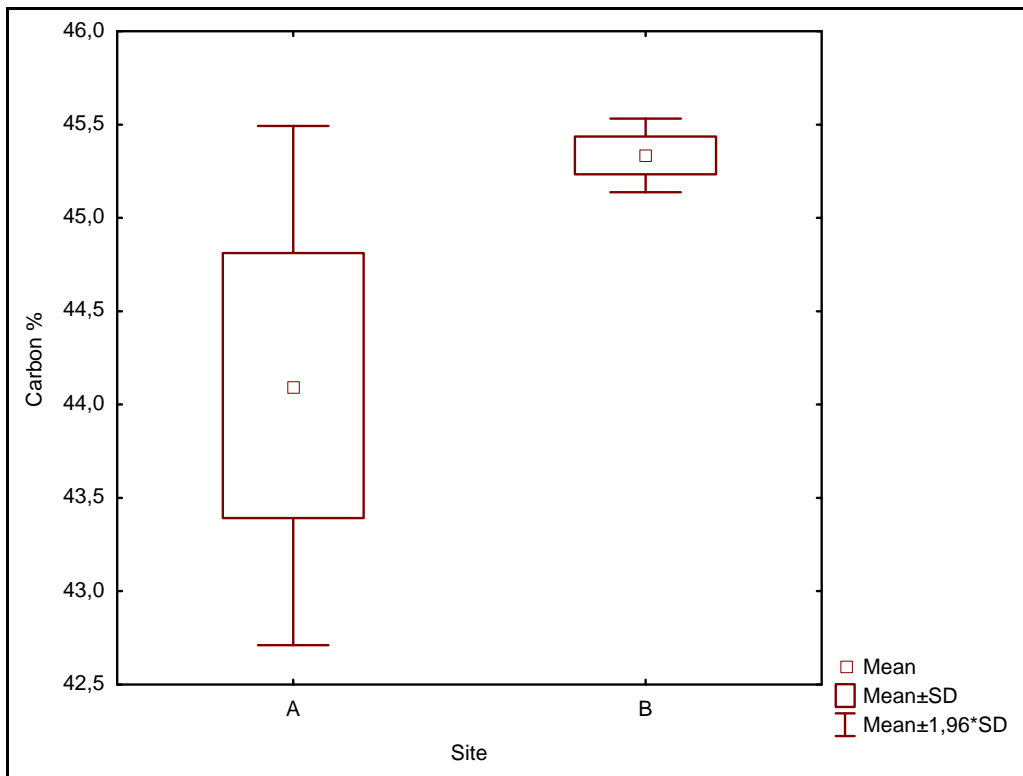


Fig. 22: Box and whiskers plot showing the percentage of total carbon (TC) in sites A and B in August 2007.

Nitrogen, carbon, and phosphorus contents (mg C, N, or P per m²) were calculated in both May and August 2007. In May 2007, nitrogen content was slightly but not significantly higher in site B (Figures 23) while carbon and phosphorus contents were significantly higher in site B (p= 0,008 for carbon; Fig. 24; p= 0,009 for phosphorus; Fig. 25). However, all three nutrient contents were significantly higher in site B in August 2007 (p< 0,01; Fig. 26, 27, and 28).

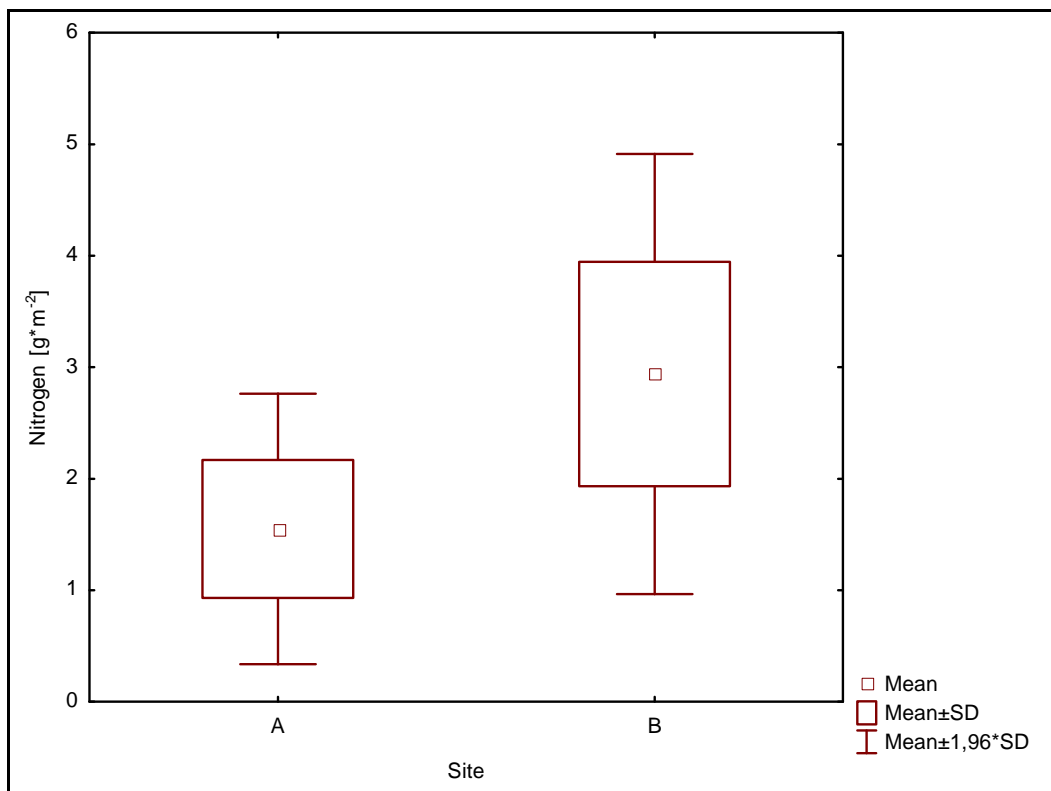


Fig. 23: Mean (± 1 SD) nitrogen content (g N * m⁻²) in sites A and B for May 2007.

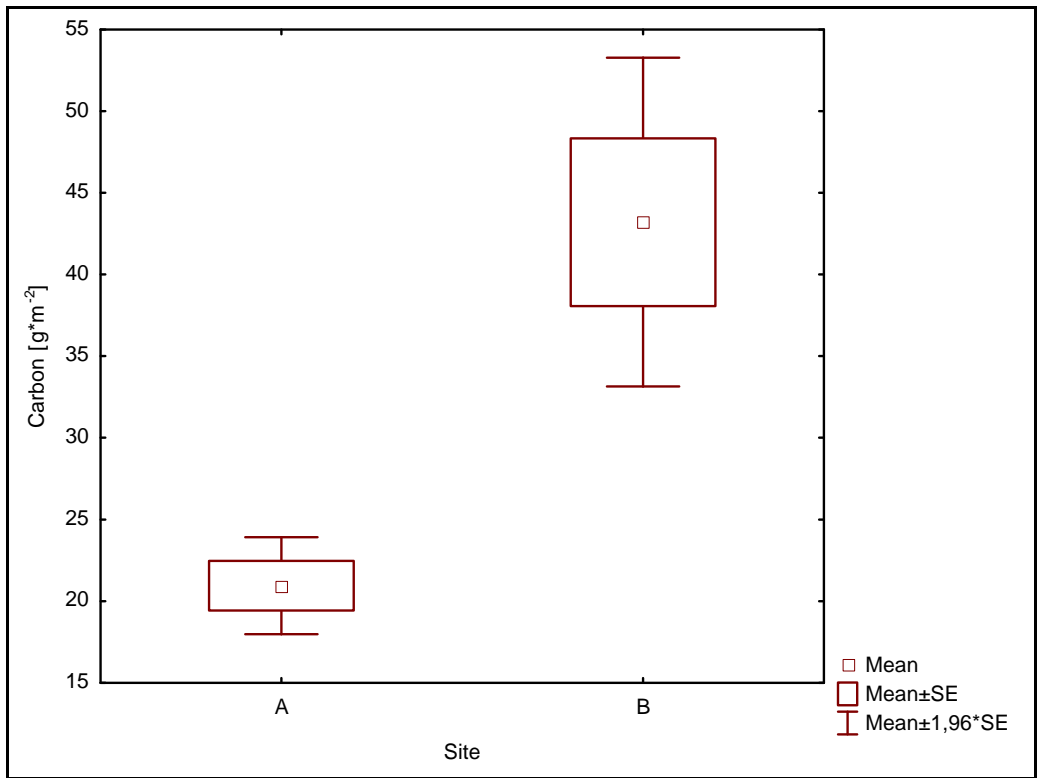


Fig. 24: Mean (± 1 SE) carbon content ($\text{g C} \cdot \text{m}^{-2}$) in sites A and B for May 2007.

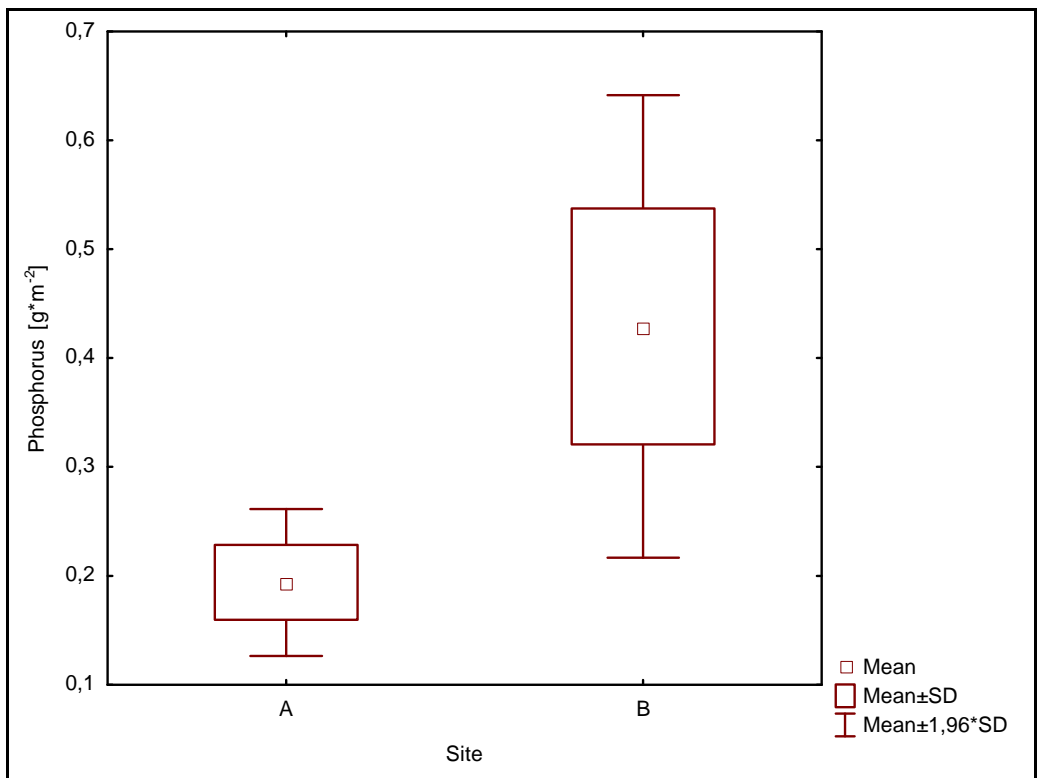


Fig. 25: Mean (± 1 SD) phosphorus content ($\text{g P} \cdot \text{m}^{-2}$) in sites A and B for May 2007.

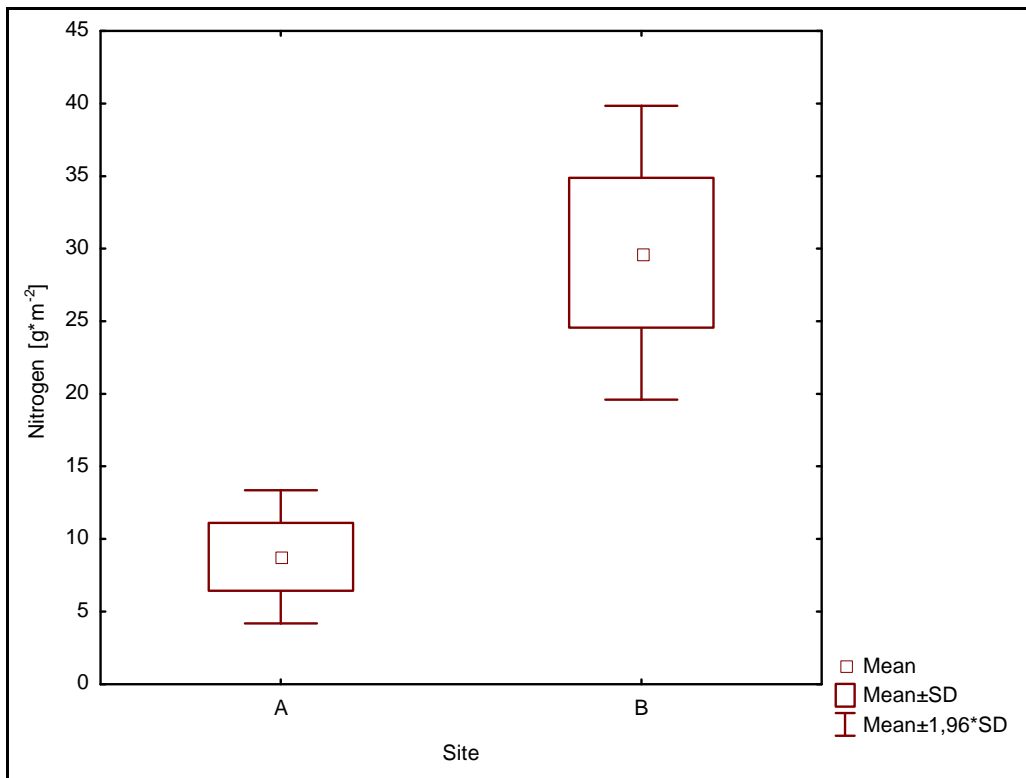


Fig. 26: Mean (± 1 SD) nitrogen content ($\text{g N} * \text{m}^{-2}$) in sites A and B for August 2007.

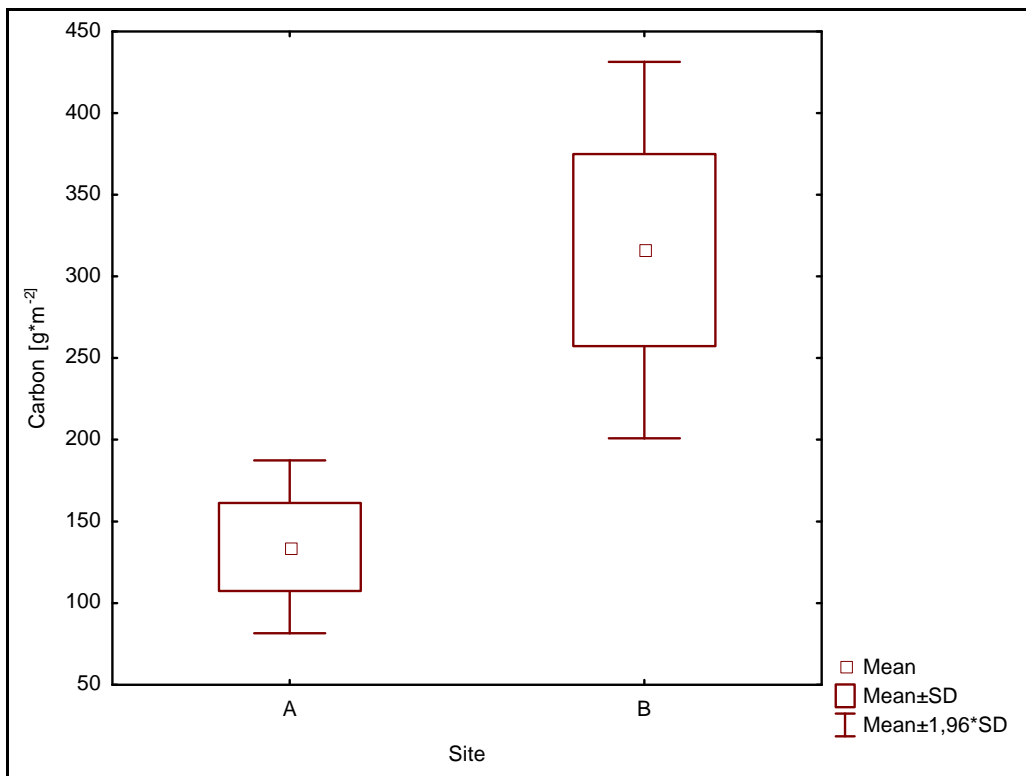


Fig. 27: Mean (± 1 SD) carbon content ($\text{g C} * \text{m}^{-2}$) in sites A and B for August 2007.

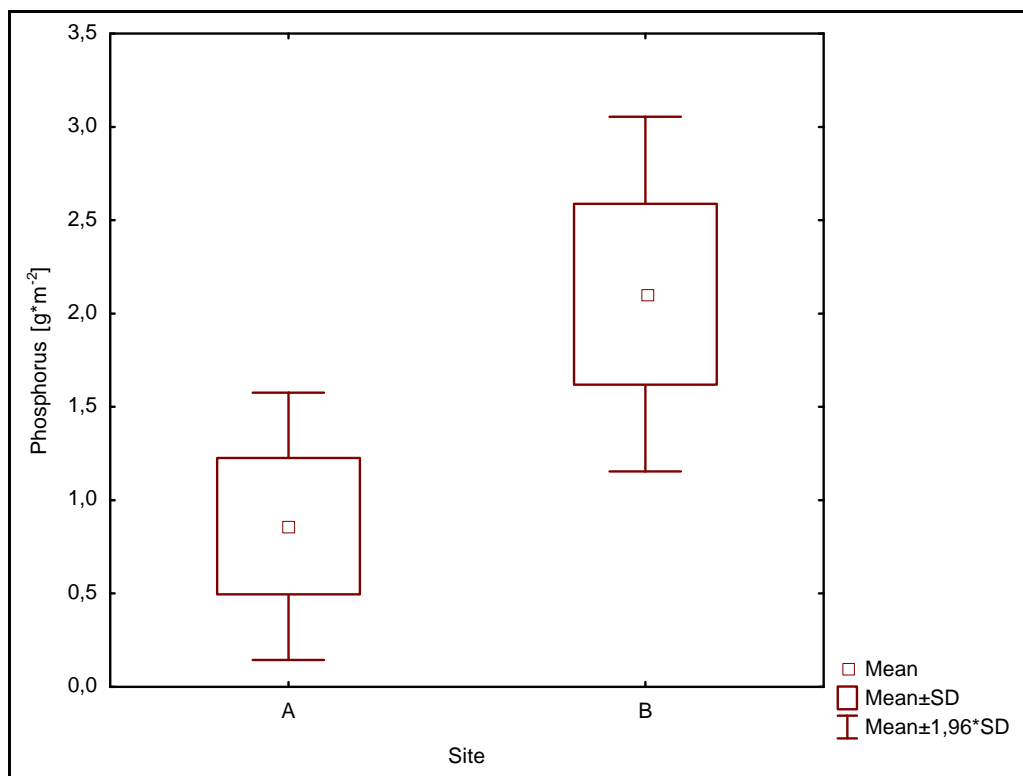


Fig. 28: Mean (± 1 SD) phosphorus content ($\text{g P} \cdot \text{m}^{-2}$) in sites A and B for August 2007.

Stoichiometric ratios were counted for both study sites in both sampling times (Table 4). CN ratio in the aboveground structure of *P. arundinacea* was similar in site A for both sampling times. However, it decreased from May to August in site B, reflecting greater uptake of N by the *P. arundinacea* plants in this site over the growing season. Meanwhile, both CP and NP ratios increased in plants growing in both sites from May to August.

Table 4: Stoichiometric ratios for *Phalaris arundinacea* aboveground plant parts in both study sites from May and August 2007.

Site	Time of sampling	C/N	C/P	N/P
A	May 2007	14,85	108,54	7,82
A	August 2007	15,63	169,52	11,22
B	May 2007	15,28	101,27	6,73
B	August 2007	10,63	152,76	14,33

5.4 Line intercepts

Site A has two co-dominant species, *Phalaris arundinacea* and *Carex spp.*, while site B is clearly dominated still by *P. arundinacea* (visual inspection). The percent cover of the two co-dominant species in site A was 39,78 % and about 60% for *P. arundinacea* and *Carex spp.* respectively in 2007 (see Tables 5 and 6). Percent cover of *P. arundinacea* in site A increased slightly when measured in August 2008, being about 45,28 %, while the cover of *Carex spp.* decreased to about 49, 22 % (Tables 7 and 8).

Table 5: Percent cover of *Phalaris arundinacea* along three transects in site A. Measurements were taken in late August 2007

Table 6: Percent cover of *Carex spp.* along three transects in site A. Measurements were taken in late August 2007

Line	Phalaris [m]	%
A1	11,70	39,00
A2	10,65	35,50
A3	13,45	44,83
Mean ± 1 SD	11,93 ± 1,41	39,78 ± 4,72

Line	Carex [m]	%
A1	18,10	60,33
A2	19,35	64,50
A3	16,55	55,17
Mean ± 1 SD	18 ± 1,40	60 ± 4,68

Table 7: Percent cover of *Phalaris arundinacea* along three transects in site A. Measurements were taken in early September 2008.

Table 8: Percent cover of *Carex spp.* along three transects in site A. Measurements were taken in early Septembert 2008.

Line	Phalaris [m]	%
A1	14,08	46,93
A2	11,92	39,73
A3	14,75	49,17
Mean ± 1 SD	13,58 ± 1,48	45,28 ± 4,93

Line	Carex [m]	%
A1	15,03	50,10
A2	16,67	55,57
A3	12,60	42,00
Mean ± 1 SD	14,77 ± 2,05	49,22 ± 6,83

Site B was still mostly dominated by *P. arundinacea* in 2008, having a percent cover of about 71,81 %. This value includes the first transect, where there were large patches of *Urtica*

dioica. Therefore, the frequency of *P. arundinacea* was lower with high variation (Table 9). The frequency of *Urtica dioica* was about 33, 27% in line B1. If line B1 is removed, then the percent cover of *P. arundinacea* increases to 81, 92 % (Table 10).

Table 9: Percent cover of *Phalaris arundinacea* along three transects in site B. Measurements were taken in August 2008.

Table 10: Percent cover of *Phalaris arundinacea* along three transects in site B without line B1. Measurements were taken in August 2008.

Line	Phalaris [m]	%
B1	15,48	51,60
B2	23,45	78,17
B3	25,70	85,67
Mean ± 1 SD	21,54 ± 5,37	71,81 ± 17,9

Line	Phalaris [m]	%
B1	Na	Na
B2	23,45	78,17
B3	25,70	85,67
Mean ± 1 SD	24,58 ± 1,59	81,92 ± 5,3

6 Discussion

Net aboveground primary production was significantly higher in site B of the study site than in site A in both growing seasons. This is more likely due to different nutrient availability between the sites, probably as a result of the closer proximity of site B to the still-fertilized field, in comparison to site A. This conclusion is further supported by the significant differences found between sites A and B in terms of above - to- belowground (A:B) ratios, differences in nutrient contents and stoichiometric ratios.

A: B ratios reflect the above- and belowground partitioning of carbon. It is expected that, when there is nutrient limitation, plants will allocate proportionally more resources belowground for the acquisition of nutrients (Saggar *et al.*, 1997; Bloom *et al.*, 1985). Our A: B production ratio, which is much higher in site B, indicates an increase in photoassimilate allocation to shoots due to increased nutrient availability in site B.

Furthermore, nutrient contents in the plant reflect differences between site fertility and the amount of available nutrients. The higher the level of resources, the greater is their consumption by plants (Prach *et al.*, 1993). Carbon and phosphorus contents (mg per m²) were significantly higher in site B at the beginning of the growing season in May 2007, while nitrogen was not significantly greater but still higher in B. However, all three nutrients were significantly higher in site B at the time of maximum biomass in August 2007. Percentages of total carbon, phosphorus, and nitrogen per gram of aboveground material of *P. arundinacea* were not significantly different between the sites in May 2007, even though percent phosphorus was greater in B. However, percent carbon and nitrogen were significantly higher in the *P. arundinacea* plants growing in site B in August 2007, whereas phosphorus content was very similar in both areas. These values indicate that nutrient levels and nutrient availability were probably greater in site B. Again, it is likely that continued fertilization of the adjacent field results in nutrients leaching into our study site.

Stoichiometric ratios serve as an indicator of ecosystem behavior and functioning. The ratio of carbon to nitrogen (C: N ratio), for example, has frequently been used as an index of litter quality, because litter with a low C: N ratio (high nitrogen concentration) generally decomposes faster (Chapin *et al.*, 2002). The smaller C: N ratio in site B may mean faster plant decomposition and more rapid nutrient turnover compared to site A. Moreover, the C: N ratio decreased in site B during the 2007 growing season, while it remained almost the same

in site A. This could be evidence of more nitrogen uptake by plants due to greater nitrogen availability, which would consequently lead to faster decomposition of the plants in site B. Nitrogen: phosphorus (N: P) ratios in plant tissues and soils have been used to identify thresholds of nutrient limitation in wetlands (Shaver, 1998). As with the CN ratio, the N: P ratios in site A indicate that this area may have been nitrogen limited in both sampling times (May and August 2007). In site B, nitrogen was probably limiting in May 2007, but both nitrogen and phosphorus were co-limiting factors in August 2007. Nevertheless, the N: P ratios increased in both sites during the growing season. Carbon to phosphorus (C: P) ratios increased in both sites, which could mean that phosphorus was also a limiting nutrient in August.

The second objective of this study was to compare the biomass and production values from this study to those of past studies conducted in this area of Mokré Louky. Such a comparison would be helpful in demonstrating any possible effects of different management practices and/or changing species composition on these ecosystems. Net aboveground primary production values in both seasons are in the range given by Květ (1983) for an unmown stand in Mokré Louky (625 g.m⁻² - 1800 g.m⁻²). Estimated aboveground production by Lukavská (1988) in an unmown stand in 1985 and 1986 (1577, 4 g.m⁻² and 1498 g.m⁻² respectively) was similar to those found in site B. Both Květ and Lukavská had quite high production numbers, but with different species composition. The unmown stand studied by Lukavská was dominated mostly by *Calamagrostis canescens*, while other parts of Mokré Louky were dominated mostly by *Carex gracilis* and *Glyceria maxima*, which was mixed in some places with stands of *Phalaris arundinacea* (Hroudová, 1988). On the contrary, Kuncová (2007) estimated the production of a site dominated by *Carex vesicaria* at only 352 g.m⁻². Apparently, production by *Carex spp.* may be lower than for other robust species. Increased cover of *Carex* in site A, resulting in a more diverse stand, is likely a main reason why primary production is lower in this site than in site B, which contains a strong dominant (Slavíková, 1982).

Site B was dominated mostly by *P. arundinacea*, with cover values of more than three quarters (Table 10). The estimated aboveground primary production for this site was similar to production values found recently by Rychterová (2007) and Filipová (2006) in other stands dominated by *Phalaris arundinacea* in Mokré Louky (1407,6 g.m⁻² by Rychterová and 1459,3 g.m⁻² by Filipová). Also, the amount of *Urtica dioica* increased in site B during the time after the flood in 2002. This can be due to the cessation of mowing in this site, starting in 2005.

It seems that site A has been undergoing succession due to the absence of fertilization since 2005. The rate of succession in terms of species turnover is generally expected to be positively related to site fertility (Prach *et al.*, 1993). Site A seems to be changing back to its former species composition, dominated mostly by *Carex spp.* and other wet meadows species. This fact is supported by results of the line intercepts, which provide a visual inspection in order to estimate percent species representation in a stand. Currently, site A has two co-dominant species, *Phalaris arundinacea* and *Carex spp.* (mostly *Carex gracilis*). *Phalaris arundinacea* was clearly the dominant species in this site in 2005, with > 80% cover. Since then, there has been an increase in *Carex spp.* cover, while the percent cover of *P. arundinacea* has decreased to half of the 2005 cover value. The differences in percent cover values for these two species in 2007 and 2008 probably represent random placement of the intercept lines. Site B is more monospecific, mostly dominated by *P. arundinacea* due to eutrophication and still continuing input of nutrients via runoff from the neighbouring still fertilized field. Thus, continued nutrient inputs, resulting in the perseverance of eutrophic conditions, are probably retarding the rate of species change in this site.

The Mokré Louky area has been notably changing since 1956 when the first phytosociological description was made by Holubičková (Holubičková, 1959). The manner in which site formation has occurred reflects considerable changes in management and alteration of site conditions by humans, especially due to intensive agricultural practices (Prach, 2008). These changes include limitation or cessation of mowing, cessation of collecting litter for bedding near Rožmberk Pond, and neglect of the drainage system in the 1960`s; degradation in soil quality caused by application of slurry, rebuilding of the previous fine channel system into a coarse system with deep transverse ditches at the end of the 1970`s; and finally abandonment of some part of the meadows as well as the current heterogeneous use of Mokré Louky. Such changes have led to considerable vegetation change. The formerly diversified mosaic of seminatural vegetation types mostly changed into monospecific stands with increasing numbers of ruderal or segetal species (Prach and Soukupová, 2002).

The presence of a monospecific stand of *P. arundinacea* indicates eutrophicated soil containing a large portion of mineral particles. Its ability to concentrate large amounts of nutrients in aboveground biomass and quickly overgrow an area under high nutrient and wet conditions allows it to outcompete other wet grassland species. Mature plants of *P. arundinacea* occur mainly in unmown grasslands but mowing has less of an effect on growth when nutrients and water are not limiting (Šrůtek *et al.*, 1988). However, systematic mowing 6-7 times per year can eliminate *P. arundinacea* from the vegetation (Klapp, 1956). Three

harvests per year is the suggested optimal management action to maintain this plant as the dominant species in meadows, at least when nutrient conditions are optimal (Lawrence and Ashford, 1969; Horrock and Washko, 1971).

In order to have a more diverse meadow, it is necessary to abate soil eutrophication and nutrient input. High nutrient levels help *P. arundinacea* dominate an area and also places other meadow species at a competitive disadvantage. For example, root porosity was reduced in *Carex* species when subjected to organic matter inputs combined with high nitrogen levels, resulting in decreased competitive ability (Klimešová and Čížková, 1996). In addition to reducing nutrient inputs, regular cutting of managed meadows result in *Alopecurus pratensis* replacing *P. arundinacea*, because of the inability of *P. arundinacea* to flower after mowing (Klimešová and Čížková, 1996). This is because mowing may result in nutrient limitations when nutrient inputs do not cover demands for *Phalaris* re-growth (Klimešová and Čížková, 1996).

Possible recovery of more diverse but still productive wet meadows is conditioned by substantially reducing manuring and establishing a cutting regime of three cuts a year. Changing the management regime is generally crucial for recovery of wet meadows unless abiotic site conditions are drastically altered. Management must be regular because any interruptions for even a few years will cause a rapid degradation (Prach, 2007). The longer such degradation continues, the more difficult will be any potential restoration of such meadows.

7 Conclusion

Net annual aboveground production and biomass levels were significantly higher in the high nutrient area (site B) compared to the low nutrient area (site A) in both growing seasons. As a result of eutrophication and greater nutrient availability, site B is almost a monospecific stand of *P. arundinacea*, composed of larger plants with higher production than in site A. Higher above- to belowground ratio, nutrient contents and different stoichiometric ratios also lend support for this conclusion.

The almost monospecific stand of *P. arundinacea* in site B reflects changes in species diversity since the 1960s as a result of increased fertilization and intensive agricultural practices. On the contrary, the recovery of other wet meadows species, especially *Carex spp.*,

in site A may mean that this site is reverting to a previous stable state due to lower amounts of available nutrients in the soil. This enables these species to recover to their previous extent and predominate over the expansive robust species adapted to eutrophic conditions.

8 References

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