



University of South Bohemia
Faculty of Science

THE ROLE OF CLONAL PLANTS
IN WETLANDS

PhD. thesis

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PhD. thesis

(shortened electronic version)

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Annotation

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This thesis is focused on clonal growth traits and their response to changing environment in wetlands. Specifically, plant responses to both abiotic (e.g. waterlogging, salinity) and biotic (surrounding vegetation) stressors were evaluated in field and mesocosm experiments. Trait responses to additions of contrasting concentrations of nutrients and their implications for wetland heterogeneity were studied.

Declaration – Prohlášení

I hereby declare that this PhD. thesis has been fully worked out by myself and the named co-authors, and with the use of the cited references.

I declare that in accordance with the Czech legal code § 47b law No. 111/1998 in its valid version, I consent to the publication of my PhD. thesis (in an edition made by removing marked parts archived by the Faculty of Science) in an electronic way in the public access to the STAG database run by the University of South Bohemia in České Budějovice on its web pages.

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České Budějovice, 30th November 2008

Petr Macek

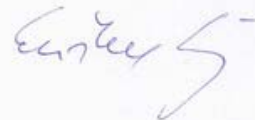
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I hereby certify that Petr Macek participated the project „Linking ecosystem processes and community structure along salinity and nutrient gradients in tropical marshes” carried out under University of California, Davis, USA. He has been involved in planning, conducting and evaluating the experiment. Further, I agree that Petr includes the paper “Wetland ecosystem changes after three years of phosphorus addition” published in *Wetlands* (2008, in press) as a part his PhD thesis.

In Třeboň, September 11, 2008

Eliška Rejmánková



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To my biological parents – Věra, Eliška, Pavel and Jan

Contents

General introduction	1
The effect of long term submergence on functional properties of <i>Eleocharis cellulosa</i> Torr.	8
Macek P., Rejmánková E., Houdková K. (2006) <i>Aquatic Botany</i> 84: 251-258	
Environmental correlates of growth traits of stoloniferous plant <i>Potentilla palustris</i>	14
Macek P., Lepš J. (2008) <i>Evolutionary Ecology</i> 22: 419-435	
Response of emergent macrophytes to experimental nutrient and salinity additions in oligotrophic tropical wetlands.	20
Macek P., Rejmánková E. (2007) <i>Functional Ecology</i> 21: 478-488	
Wetland ecosystem changes after three years of phosphorus addition.	26
Rejmánková E., Macek P., Epps K. (2008): <i>Wetlands</i> (in press)	
Dynamics of <i>Typha domingensis</i> spread in oligotrophic tropical wetlands following nutrient enrichment	32
Macek P., Rejmánková E., Lepš J. (submitted)	
Biological activities as patchiness driving forces in wetlands of northern Belize.	38
Macek P., Rejmánková E., Fuchs R. (submitted)	
General discussion	44
Curriculum vitae	54





General introduction

WETLAND CHARACTERIZATION AND VALUE

Swamp, marsh, floodplain, wet meadow, peat bog, fen, tidal marsh, alluvium, lakeshore, flooded forest, prairie pothole etc. Each of these terms represents a special type of environment differing from others in, e.g., physical or chemical properties, vegetation structure or species composition. However, they all could be encapsulated into a single term: wetlands. They share several major features distinguishing them from both aquatic and terrestrial systems (Denny 1995; van der Valk 2006). Contrary to terrestrial systems, water table is elevated, at least temporarily, resulting in anaerobic soils in wetlands. A second feature, distinguishing them from aquatic systems, is a presence of macrophytes, large plants usually emerging from water surface. Wetlands often represent an ecotone or transitional zone between aquatic and terrestrial environment sharing fauna and flora of both systems.

Suitable conditions for plant growth rank some wetland types between the world most productive ecosystems (Armstrong et al. 1994; Roggeri 1999). Besides, large amounts of people, and animals, depend on wetlands as a source of food, and wetlands usually provide further socio-economic benefits to local communities (Silvius et al. 2000; Dixon and Wood 2003). Wetlands are considerable reservoirs of (drinking) water and in the view of ongoing climate change and increasing precipitation variability and irregularity, they can play a crucial role in water management, e.g., sedimentation processes or flood control (Dugan 2005). Wetland biodiversity is another extremely important value and various wetlands are considered as biodiversity hotspots (Rejmánková et al. 2004; van der Valk 2006). Wetland ecosystems play a crucial role in the nutrient cycling. In addition, they typically have a high retention capacity of nutrients, which, under certain circumstances, opens possibility to use some of them for water quality improvement (Hammer and Bastian 1989; Dugan 2005). On the other hand, increased land use and agricultural pressure result in eutrophication and salinization of many natural wetlands (Downing et al. 1999; Jolly et al. 2008).

CLONAL PLANTS IN WETLAND ECOSYSTEMS

In majority of above mentioned processes macrophytes play a significant, if not crucial, role. Since macrophytes are major living constituents of wetlands, it is important to study, among others, their responses to different factors affecting their growth in various wetland systems. Wetland plant growth is frequently constrained by several stressful factors such as prolonged anoxia, elevated salinity or lower nutrient availability frequent under natural conditions (Crawford and Brändle 1996; Noe et al. 2001). To deal with wetland stressors, plants employ various physiological, metabolic or structural adaptations (Brändle 1991; Jackson and Colmer 2005). Vegetative reproduction, i.e. clonal growth, is one of the structural traits helping plants in wetlands (Suzuki and Hutchings 1997; Vartapetian and Jackson 1997), especially if coupled with physiological adaptations (e.g. Lenssen et al. 2000). Some authors regard an increase in clonal modules as a general adaptive response to the stress of waterlogging (Soukupová 1994). Although the presented studies cover only few wetland types, the mechanisms underlying plant growth are most probably similar in other ones. It further fills a gap in our knowledge of species poor systems of clonal plants in highly productive habitats (Herben and Hara 1997).

All studies presented partially focus on different factors affecting plant growth in wetlands. This could be achieved in two dimensions: vertical via changes in plant height and horizontal via clonal spreading, plant vegetative reproduction. The ability to clonally spread is among the most important, crucial, for plant growth in wetlands. Because of large portion of wetland plant tissue consists of aerenchyma (porous tissue full of air space), the gas space continuum between shoots and roots is maintained (Armstrong et al. 1994). Such continuum can be functional in between ramets as well. For example, when flooded, emergent shoots can supply air to submerged shoots, or mother ramet can support (by air and/or nutrients) its vegetative offspring in growth (Allen 1997). The air supply can be functional even between dead broken and living shoots, e.g. venturi-induced pressure flow in *Phragmites australis* (Armstrong et al. 1992).

However, besides the above mentioned advantages of clonal growth for individual plants, the main outcomes of plant clonality in wetlands still require further studies. Herben and Hara (1997) point out the insufficient

attention paid to processes of spatial extension of plants, although they anticipate these processes to be of major importance for community structure. In addition, a spatial pattern of clonal plant communities is specifically affected by growth architecture and the way in which ramets interact and replace each other (Herben and Hara 1997). Studies of plasticity of clonal growth traits, physiological integration between ramets, foraging behaviour and vertical ramet competition form a backbone of this thesis because they represent the critical factors affecting spatial structure of plants.

Asking a general question, such as what is the role of clonal plants in wetlands, leads to more complex or large scale ecosystem studies. However, such questions usually cannot be directly solved without a more detailed knowledge of separate parts of the system. Therefore, I believe, a combination of studies of different levels resulting eventually in a multidimensional approach is extremely valuable for understanding processes at the ecosystem level. Hence, in this thesis, I focus on different mechanisms underlying plant functioning at an individual level, in interactions between plants and also in interactions between plants and animals.

AIMS AND OUTLINES OF THIS THESIS

I focused on different aspects of macrophyte ecology in two contrasting wetland systems: neotropical freshwater marshes of Belize and temperate wetlands (from wet meadows to fens) of Czech Republic. In this series of studies the first aim was to characterize plant ability to deal with stressful environment of seasonally flooded marshes and especially cover the extreme water fluctuations (Chapter 2). Later on, I examined the combined effects of salinity and nutrient (nitrogen and/or phosphorus) enrichment on growth of emergent macrophytes. This was studied in a mesocosm experiment with three different dominant species of Belizean wetlands, *Cladium jamaicense*, *Typha domingensis* and *Eleocharis cellulosa* s.l. (Chapter 3). In the two former studies, only the influence of abiotic factors was investigated. However, to estimate the relative importance of both biotic and abiotic factors, I differentiate them in a large field study of *Potentilla palustris* growth characteristics survey (Chapter 4). When changing the perspective from a small scale to a larger scale and estimating more

realistically marsh responses to various factors, large field experiments are needed. Results from such experiment are discussed in the next chapter allowing comparisons with earlier similar experiments under more controlled conditions (Chapter 5). Previous experiments imply that some plant growth traits are influenced by a combination of different factors. In following chapter I asked, whether a change in conditions and consequently in growth traits can also be reflected in species coexistence. Furthermore, I compared growth dynamics of populations with and without changes in clonal growth traits (Chapter 6). In the last chapter, I looked for the natural causes of vegetation pattern emergence. A combination of field experiments with animal behavioral studies resulted in multidimensional study overlapping from plant – plant interaction to larger ecological study including various trophic levels (Chapter 7). Such consecutive change of perspective enabled me to fully appreciate a phenomenon of plant clonality in wetland ecosystems (see also Herben and Hara 1997). Additional aim of this thesis was to demonstrate a wide range of methods and approaches which can be used for studying plant clonality in wetland ecosystems.

More specifically, in the studies presented I asked following questions:

1. How does *Eleocharis cellulosa* investment into vegetative growth change under conditions of prolonged submergence?
2. What are the effects of increased salinity and nutrients on clonal growth traits of three emergent macrophytes dominating Belizean wetlands?
3. Are there any differences in abiotic and biotic factors in terms of their effect on clonal growth traits? Which of them are better predictors?
4. What is the effect of elevated nutrients on marsh community structure formed mainly by clonal plants? Is it reasonable to expect only negative effect? In other words: could nutrient enrichment increase local heterogeneity and diversity?

REFERENCES

- Allen, L.H. (1997) Mechanisms and rates of O₂ transfer to and through submerged rhizomes and roots via aerenchyma. *Soil and crop science society of Florida proceedings* **56**, 41-54.

- Armstrong, J., Armstrong, W. & Beckett, P.M. (1992) *Phragmites australis* – venturi-induced and humidity-induced pressure flows enhance rhizome aeration and rhizosphere oxydation. *New Phytologist* **120**, 197-207.
- Armstrong, W., Brandle, R. & Jackson, M.B. (1994) Mechanisms of flood tolerance in plants. *Acta Botanica Neerlandica* **43**, 307-358.
- Bobbink, R., Beltman, B., Verhoeven, J.T.A. & Whigham, D.F. (2006) *Wetlands: Functioning, biodiversity conservation and restoration*. Springer-Verlag, Berlin.
- Brändle, R.A. (1991) Flooding resistance of rhizomatous amphibious plants. *Plant life under oxygen deprivation* (eds M.B.Jackson, D.D.Davies, & H.Lambers), pp 35-46. Academic Publishing, The Hague.
- Crawford, R.M.M. & Brändle, R.A. (1996) Oxygen deprivation stress in a changing environment. *Journal of Experimental Botany* **47**, 145-159.
- Denny, P. (1995) *Tropical wetlands and their management*. IHE Delft, The Netherlands.
- Dixon, A.B. & Wood, A.P. (2003) Wetland cultivation and hydrological management in eastern Africa: Matching community and hydrological needs through sustainable wetland use. *Natural Resources Forum* **27**, 117-129.
- Downing, J.A., McClain, M., Twilley, R., Melack, J.M., Elser, J.J. & Rabalais, N.N. (1999) The impact of accelerating land-use on the N-cycle of tropical aquatic ecosystems: current conditions and projected changes. *Biogeochemistry* **46**, 109-148.
- Dugan, P. (2005) *Guide to wetlands*. Firefly Books Ltd., New York.
- Hammer, D.A. & Bastian, R.K. (1989) Wetland ecosystems: natural water purifier. *Constructed wetlands for wastewater treatment – municipal, industrial and agricultural* (ed. D.A.Hammer), Lewis Publishers, Michigan, pp 6-20.
- Herben, T. & Hara, T. (1997) Competition and spatial dynamics of clonal plants. *The ecology and evolution of clonal plants* (eds H.de Kroon & J.van Groenendael), Backhuys Publishers, Leiden, The Netherlands, pp 331-357.
- Jackson, M.B. & Colmer, T.D. (2005) Response and adaptation by plants to flooding stress - Preface. *Annals of Botany* **96**, 501-505.
- Jolly, I.D., Mcewan, K.L. & Holland, K.L. (2008) A review of groundwater-surface water interactions in arid/semi-arid wetlands and the consequences of salinity for wetland ecology. *Ecohydrology* **1**, 43-58.

- Rejmánková,E., Komárek,J. & Komárková,J. (2004) Determinants of cyanobacterial diversity in alkaline marshes of northern Belize (Central America). *Diversity and Distributions* **10**, 189-199.
- Lenssen,J.P.M., Menting,F.B.J., van der Putten,W.H. & Blom,C.W.P.M. (2000) Vegetative reproduction by species with different adaptations to shallow-flooded habitats. *New Phytologist* **145**, 61-70.
- Noe,G.B., Childers,D.L. & Jones,R.D. (2001) Phosphorus biogeochemistry and the impact of phosphorus enrichment: Why is the Everglades so unique? *Ecosystems* **4**, 603-624.
- Roggeri,H. (1995) *Tropical freshwater wetlands: A guide to current knowledge and sustainable management*. Kluwer Academic Publishers, Dordrecht.
- Silvius,M.J., Oneka,M. & Verhagen,A. (2000) Wetlands: Lifeline for people at the edge. *Physics and Chemistry of the Earth Part B-Hydrology Oceans and Atmosphere* **25**, 645-652.
- Soukupová,L. (1994) Allocation plasticity and modular structure in clonal graminoids in response to waterlogging. *Folia Geobotanica & Phytotaxonomica* **29**, 227-236.
- Suzuki,J.-I. & Hutchings,M.J. (1997) Interactions between shoots in clonal plants and the effect of stored resources on the structure of shoot populations. *The ecology and evolution of clonal plants* (eds H.de Kroon & J.van Groenendael), Backhuys Publishers, Leiden, The Netherlands, pp 311-329.
- van der Valk,A.G. (2006) *The biology of freshwater wetlands*. Oxford University Press, New York.
- Vartapetian,B.B. & Jackson,M.B. (1997) Plant adaptations to anaerobic stress. *Annals of Botany* **79**, 3-20.



New growth of *Eleocharis cellulosa* almost seven months after a tropical storm Chantal (20th August 2001). This storm raised the water level in a large marsh system called Doubloon from 21 cm to more than 190 cm within four days. However, the opposite process of water level recession to the same level lasted until 11th March 2002, when this picture was taken.

The effect of long-term submergence on functional properties of *Eleocharis cellulosa* Torr.

Macek P., Rejmánková E. and Houdková K.
Aquatic Botany 84, 251–258, 2006

ABSTRACT

Eleocharis cellulosa Torr., a macrophyte dominating marshes of northern Belize, often experiences great water level fluctuations varying from dry conditions to prolonged submergence. We investigated morphological and ecophysiological responses (shoot length, biomass, CO₂ exchange, chlorophyll content and regeneration) to partial and complete submergence followed by emergence in two field experiments.

Submergence greatly enhanced shoot elongation, but it also resulted in a low number of viable shoots, lower biomass and consequently in lower plant fitness. The decline in live shoot length started after 3 months of submergence. The shoots produced by submerged plants were thin and would break easily if the water level decreased fast. Photosynthetic activity, as well as respiration rate, was highly reduced in shoots just emerged from complete submergence. The ability of *E. cellulosa* to retain some level of photosynthesis after emergence is undoubtedly a useful trait in coping with seasonal floods.

Submerged plants produced chlorophyll, especially Chl *a*, for at least a period of three months. Shoot regeneration was significantly slower in the case of plants submerged for a longer time, probably due to depleted

energy reserves, but there were no significant differences in the total shoot length among treatments after two months following the emergence.

Eleocharis cellulosa demonstrated high tolerance to long term (more than 4 months) complete submergence and resulting anoxic conditions and showed rather fast recovery after emergence. This can be viewed as an advantageous trait in habitats of rapid and prolonged increases of water level and also after water recedes, when vegetation starts to colonize newly opened space.



Vliv dlouhodobého zanoření na funkční vlastnosti druhu *Eleocharis cellulosa* Torr.

Macek P., Rejmánková E. and Houdková K.
Aquatic Botany 84, 251–258, 2006

SHRNUTÍ

Eleocharis cellulosa Torr., dominantní rostlinný druh mokřadů severní Belize, roste v prostředí s velkými fluktuacemi vodní hladiny od úplného sucha do dlouhodobého zanoření. Ve dvou následných experimentech jsme zkoumali dlouhodobý vliv částečného a plného zaplavení na výšku rostlin, biomasu, výměnu CO₂, obsah chlorofylu a regeneraci.

Zaplavení prokazatelně povzbudilo růst rostlin do výšky, na druhou stranu způsobilo snížení počtu lodyh, biomasy a v důsledku i fitness. Odumírání živých lodyh začalo třetí měsíc úplného zanoření. Lodyhy vytvořené pod vodou byly tenké a snadno by se lámaly při poklesu hladiny vody. Fotosyntetická aktivita i respirace byly velmi nízké u čerstvě vynořených rostlin. Přesto, i takto nízká fotosyntéza je zřejmě důležitá pro rostliny zažívající pravidelný stres zaplavením.

U zanořených rostlin byla regenerace podstatně pomalejší, pravděpodobně kvůli vyčerpání energetických zásob. Tento deficit se smazal po dvou měsících od vynoření, kdy se délka regenerovaných lodyh nelišila mezi částečně a plně zanořenými rostlinami.

Eleocharis cellulosa prokázala velmi vysokou toleranci k dlouhodobému zaplavení a anoxickým podmínkám (více než 4 měsíce) a dokázala celkem rychle regenerovat. Tyto schopnosti jsou velmi výhodné pro

rostliny rostoucí v podmínkách s častými náhlými změnami vodní hladiny a při kolonizaci prostoru po opadnutí vody.





A part of a large clone of *Potentilla palustris* excavated at location Řásnice in July 2003. The clone is not complete, of course, due to unfortunate lost of its previous parts during digging. However, the stolons were all in rather good shape with no obvious mark of decay. The orientation of rhizomes does not correspond to the original position in the field.

Environmental correlates of growth traits of the stoloniferous plant *Potentilla palustris*

Macek P. and Lepš J.

Evolutionary Ecology, 22, 419-435, 2008

ABSTRACT

Growth form is one of the important life history traits ultimately influencing plant fitness. *Potentilla palustris* is a stoloniferous plant growing in a range of habitats from densely vegetated wet meadows to acidic transitional fens, and its growth form varies according to habitat. In a four year multi-site comparative study, we investigated which biotic and abiotic characteristics influence most its growth traits. Vegetation composition and physiognomy, as well as numerous abiotic environmental variables, were recorded at 32 study sites located on an altitudinal gradient.

Growth traits of *P. palustris* were best explained by the surrounding vegetation physiognomy and not by abiotic conditions, although the latter obviously represents the factors indirectly influencing its growth. Stolon length traits and branching were positively correlated with vegetation density and height, and negatively with altitude. Plants flowered more in taller vegetation, and leaf area was greater in wetter sites with lower vegetation cover.

Potentilla palustris appeared to be well adapted to transitional fens, but its vegetative growth was fastest in wet meadows and alluvial habitats on highly organic humid soils. It produced more branches and larger leaves in alluvial habitats with open water, while it had enhanced generative

reproduction in wet meadows. Species composition was less important than vegetation physiognomy. In less favorable habitat types, *P. palustris* prefers an escape strategy of linear growth. Internode length exhibited pronounced plasticity, increasing particularly in tall dense vegetation of lower altitude, whereas internode number remained fairly constant over various habitats.

It is evident that both plastic low cost growth traits (internode elongation), and constant high cost traits (internode number) contribute to the *P. palustris* escape strategy under tall dense vegetation. Phenotypic plasticity enhances the potential of *P. palustris* to grow in a wide range of habitats and so increases plant fitness on regional scale.



Korelace podmínek prostředí s růstovými vlastnostmi klonálně se šířícího druhu *Potentilla palustris*

Macek P. and Lepš J.
Evolutionary Ecology, 22, 419-435, 2008

SHRNUTÍ

Růstová forma je jednou z důležitých vlastností rostlin ovlivňující jejich fitness. Klonální druh *Potentilla palustris* je schopen růstu v relativně velkém rozpětí přírodních podmínek od podmáčených luk k přechodovým rašeliništím. Ve čtyřleté studii jsme zkoumali vliv abiotických a biotických podmínek na jeho růstové vlastnosti. Složení vegetace, její fyziognomie a řada abiotických podmínek prostředí byly zaznamenány na 32 lokalitách rozmístěných na gradientu nadmořské výšky.

Růstové charakteristiky druhu *P. palustris* lépe korelovaly s biotickými vlastnostmi prostředí (výška vegetace) než s abiotickými vlastnostmi či složením vegetace, ačkoliv abiotické vlastnosti je dozajista ovlivňují také. Délka výběžků a jejich větvení korelovaly pozitivně s hustotou a výškou okolní vegetace a negativně s nadmořskou výškou. Rostliny kvetly více v hustší vegetaci, větší listová plocha byla zaznamenána na vlhčích místech s nižší vegetací.

Potentilla palustris je dobře adaptována na podmínky přechodových rašelinišť, ale nejlépe se jí daří na vlhkých loukách (nejvyšší generativní reprodukce) a v aluviích, na půdách s vysokým obsahem organického materiálu (větší listy a vyšší větvení).

Na méně příhodných místech, např. ve vysoké vegetaci, si *P. paslustris* jako slabší kompetitor poradí zvýšením vegetativního šíření pomocí plastické délky internodia (vlastnost s nízkými investičními náklady) a naopak konstantního počtu internodií (vlastnost s vysokými investičními náklady). Tyto vlastnosti jí umožňují efektivně osidlovat různé typy prostředí.





The beginning of the mesocosm experiment at our platform on the outskirts of Orange Walk town, Belize. Plants were located in the vicinity of water in order to provide the most similar microclimate to the natural marshes.

Response of emergent macrophytes to experimental nutrient and salinity additions

Macek P. and Rejmánková E.
Functional Ecology 21, 478–488, 2007

SUMMARY

Nutrient additions often result in species dominance/compositional changes in wetland ecosystems, but the impact of nutrients may be constrained by different salinity levels. Wetlands of northern Belize, distributed along a salinity gradient, are strongly phosphorus limited and dominated largely by three species of emergent macrophytes: *Eleocharis cellulosa*, *Cladium jamaicense*, and *Typha domingensis*.

We conducted a mesocosm experiment to assess changes in growth characteristics (biomass allocation, plant height, RGR, rhizome length) and nutrient uptake of these three species in response to simultaneous changes in nutrient levels (N, P) and salinity.

The growth characteristics of *Typha* and *Eleocharis* responded positively to N and especially P addition, whereas the growth response of *Cladium* was largely insignificant. RGR of *Typha* increased under P additions, while RGR of *Eleocharis* increased with N and decreased with salinity additions. Nutrient addition increased rhizome number of both *Typha* and *Eleocharis*. However, plasticity in rhizome length was observed only in *Typha*, which increased rhizome length at medium and high P.

Salinity decreased plant height, shoot and root biomass of *Cladium* and *Eleocharis*, while in *Typha* it only reduced the height. Rhizome number and rhizome length were decreased only in *Eleocharis*.

Both medium and high P additions increased tissue P content in all three species, but *Eleocharis* accumulated significantly more P than *Cladium* and *Typha*. N additions increased tissue N content in *Cladium* and *Eleocharis*, but not in *Typha*,

Cladium exhibited strong morphological constraint and behaved as a stress tolerator that was well adapted to low nutrients. *Typha*, characterized by its plastic opportunistic guerrilla growth strategy, fast and efficient space occupancy and rather wasteful nutrient management, behaved as a typical competitor. *Eleocharis* rapidly responded to nutrients, but displayed limited rhizome plasticity and its growth was impacted at higher salinity.

According to recorded traits, we hypothesize that P input into wetlands will result in expansion of *Typha* leading to competitive exclusion of both co-occurring species. The only conditions allowing coexistence of all three species are those limiting vertical and horizontal growth of *Typha*, i.e., low P and higher salinity. To ensure stability of Belizean wetlands, the maintenance of oligotrophic status is therefore crucial.



Reakce mokřadních makrofyt na experimentální přídavek živin a solí

Macek P. and Rejmánková E.
Functional Ecology 21, 478–488, 2007

SHRNUTÍ

Přídavek živin do mokřadních ekosystémů vede často k výměně druhů či změnám v druhové dominanci. Vliv živin však může ovlivňovat i vysoká salinita. Oligotrofní, fosforem limitované mokřady severní Belize s hlavními dominantami *Eleocharis cellulosa* (*Ec*), *Cladium jamaicense* (*Cj*), a *Typha domingensis* (*Td*) se vyskytují na širokém gradientu salinity a umožňují tak zkoumání vlivu živin a salinity dohromady.

Založili jsme květináčový pokus s různými variantami obsahu živin (N,P) a salinity a zjišťovali změny růstových charakteristik (alokace biomasy, výška rostlin, délka rhizomů, relativní růstová rychlost – RGR) a příjem živin u těchto tří dominantních druhů.

Zatímco druhy *Td* a *Ec* svými růstovými charakteristikami pozitivně reagovaly na přídavek N a obzvláště P, odpověď *Cj* nebyla průkazná. RGR u *Td* byla vyšší po přidání P, RGR u *Ec* se naopak zvýšila po přidání N, a snížila ve vyšší salinitě. Po přidání živin se zvýšil počet rhizomů jak u *Td*, tak u *Ec*, nicméně pouze *Td* byla schopna plastické změny délky rhizomů.

Zvýšením salinity se snížila výška všech druhů, navíc se snížila celková nadzemní biomasa i biomasa kořenů u *Ec*, i *Cj*. Počet a délka rhizomů se snížila pouze u *Ec*.

Jak střední, tak vyšší přídavek P měl za následek zvýšení koncentrace P v listech všech tří druhů. Navíc druh *Td* kumuloval prokazatelně více P než ostatní druhy, avšak jako jediný nereagoval pozitivně na přídavek N zvýšením jeho koncentrace v listech.

Velmi omezené změny byly pozorovány u druhu *Cj*, který je považován za druh tolerující stres a dobře adaptovaný na nízké obsahy živin. Naopak druh *Td* vynikal svou plasticitou a je charakterizován jako typický kompetitor a oportunistický druh využívající strategii „guerilla“, rychlé a efektivní zabránění prostoru a neúspěšné hospodařením se živinami. Střední cestu v reakci na změny zaujímá druh *Ec*, který sice rychle odpovídá na změnu živin, ale je omezen salinitou a větší rigiditou v délce rhizomů.

Na základě měřených vlastností dominantních rostlin předpokládáme, že přídavek P do mokřadů způsobí expanzi druhu *Td* vedoucí nakonec ke kompetitivnímu vyloučení ostatních druhů. Jedinou možností koexistence všech tří druhů je tedy prostředí limitující jak vertikální, tak horizontální růst *Td*: nízké koncentrace P a vyšší salinita. K zajištění stability belizských mokřadů je proto nutné udržet jejich oligotrofní charakter.





Second year of the fertilization of 10 x 10 m plots in a large field experiment. During fertilization and within next 48 hours, the plastic walls were installed to prevent nutrient leak from the plots. The picture was taken from NP plot and shows the N, P and Control plots behinds respectively. Location New, August 2002.

Wetland ecosystem changes after three years of phosphorus addition

Rejmánková E., Macek P. and Epps K.
Wetlands 2008 (in press)

ABSTRACT

We used oligotrophic, P-limited herbaceous wetlands of northern Belize to assess how changes in nutrient availability impact species composition and ecosystem processes. The P, N, and NP enrichment plots were established in replicated marshes of three salinity levels to document potential salinity constraints.

Addition of P or combination of N and P resulted in rapid switch from a microphyte (cyanobacterial mats, CBM) to macrophyte (*Eleocharis* spp., *Typha domingensis*) domination, while N addition did not have any impact. The switch was caused by significant changes in *Eleocharis* stem density and height, and consequently, the aboveground biomass, which increased from an average 120 g m⁻² in control and N plots to > 500 g m⁻² in P and NP plots. Decreased light under the dense canopy of *Eleocharis* in P and NP plots caused significant reduction in CBM growth.

Biomass of *Eleocharis* in P and NP plots decreased with increasing salinity, but salinity did not affect biomass production in control and N plots. Tissue P of *Eleocharis* from P and NP plots increased 4- to 5-fold compared to P content in plants from control and N plots. Tissue P remained high due to internal nutrient recycling even after P addition ceased. *Typha* transplanted into plots grew exponentially in P and NP plots, while in control and N plots it grew slowly or did not survive.

There were significant differences in $\text{NH}_4\text{-N}$ both in soil extracts and in the interstitial water with soil and water $\text{NH}_4\text{-N}$ being significantly lower in P-addition plots. The elimination of N_2 -fixing CBM is a potential reason for a decrease in available sediment N as documented by a negative correlation between CBM cover and interstitial $\text{NH}_4\text{-N}$.



Změna mokřadního společenstva po tříletém přidávání fosforu

Rejmánková E., Macek P. and Epps K.
Wetlands 2008 (in press)

SHRNUTÍ

Studovali jsme vliv změn dostupnosti živin na druhové složení a ekosystémové procesy oligotrofních, fosforem limitovaných mokřadů severní Belize. Faktoriální kombinace ploch s přidavkem P a N byla opakována v mokřadech na gradientu salinity, aby se zjistil její potenciální vliv.

Přídavek P či kombinace N a P vyústily v rychlý nárůst makrofyt (*Eleocharis* spp., *Typha domingensis*) a kompetitivní vyloučení mikrofyt (sinicové nárosty – CBM), zatímco přídavek samotného N neměl na dominanci druhů žádný vliv. Vyloučení CBM bylo způsobeno zvýšením hustoty a výšky druhu *Eleocharis*, potažmo zvýšením biomasy, která vzrostla ze 120 g m⁻² (kontroly a N) na > 500 g m⁻² (P a NP). Omezené množství světla v podrostu znemožnilo růst CBM. Naopak vysazené ramety druhu *Typha domingensis* se velmi rychle rozrůstaly v P a NP plochách; v kontrolách a N plochách živořily.

Množství biomasy *Eleocharis* v P a NP plochách bylo nižší v mokřadech s vyšší salinitou, která však v kontrolách a N plochách neměla na biomasu žádný vliv. Obsah P v listech *Eleocharis* z P a NP ploch se zvýšil 4–5 krát v porovnání s listovým obsahem P v kontrolách a N plochách. Obsah P v listech zůstal poměrně vysoký i po konci hnojení především díky účinné recyklaci živin.

Ve všech variantách byly nalezeny průkazné rozdíly v obsahu amonného dusíku jak v půdním extraktu, tak v půdní vodě, nižší hodnoty byly zjištěny v plochách s přidavkem P. Eliminace N₂-fixujících CBM je pravděpodobnou příčinou poklesu dostupného N, což je dobře

dokumentováno negativní korelací mezi pokryvností CBM a $\text{NH}_4\text{-N}$ v půdní vodě.





The growth of *Typha domingensis* clone three years after establishment of a single individual into nitrogen and phosphorus enriched plot. Extension of *Typha* clone is 23 m from left to right. Location Calabash, 12th May 2006.

Dynamics of *Typha domingensis* spread in oligotrophic tropical wetlands following nutrient enrichment

Macek P., Rejmánková E. and Lepš J.
(Submitted)

ABSTRACT

Accelerated land use in tropical countries has increased nutrient input into wetland ecosystems. Higher nutrients often lead to changes of vegetation structure and, eventually, shifts in species dominance.

We studied a dynamics of species shift in a manipulative nutrient enrichment experiment (N, P, NP) in oligotrophic wetlands of northern Belize distributed along a salinity gradient. We monitored a spread and biomass accumulation of an introduced single individual of *Typha domingensis* within a four years period. We focused on speed of the spreading and the relative importance of neighbouring ramets in this process.

Large differences were found between control (C) and N addition plots versus P and NP addition plots. The ramets planted in C and N plots died or barely survived, while ramets in P and N&P plots grew vigorously and almost completely outcompeted original vegetation represented by *Eleocharis* spp. Average numbers of ramets at the end of the experiment were 2 and 576 per 100 m² for C and N versus P and NP plots. The filling dynamics of P-enriched plots of differing salinity changed in time. The spreading was delayed in low salinity plots compared to high and medium salinity plots, although it finally reached comparable rates and values. We

attribute this delay to originally denser vegetation and less suitable soil conditions in low salinity plots than to a direct salinity effect. Eventually, the number of ramets stabilized and often even decreased due to self-thinning and insect damage.

Spatiotemporal model extrapolating observed vegetative spread suggested that in P-enriched conditions, a clone originating from a single individual is able to cover 1-ha plot completely within 9 years. We conclude that P-enrichment highly increase the possibility of fast take over of Belizean wetlands by *Typha domingensis*.



Dynamika vegetativního rozrůstání druhu *Typha domingensis* v oligotrofních tropických mokřadech po přídání živin

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(Podáno k publikování)

SHRNUTÍ

Intenzifikace zemědělství v tropech měla za následek zvýšené splavování živin do mokřadních ekosystémů. Vyšší obsah živin následně vede ke změnám vegetační struktury a druhové dominance.

Studovali jsme dynamiku změny druhů v pokusu s manipulativním zvýšením živin (N, P, NP) v oligotrofních mokřadech severní Belize rozložených na gradientu salinity. Monitorovali jsme vegetativní rozrůstání a akumulaci biomasy vysazeného jedince druhu *Typha domingensis* v průběhu čtyř let. Zaměřili jsme se na sledování rychlosti šíření a relativní důležitosti okolních rašelin v tomto procesu.

Velké rozdíly byly pozorovány mezi kontrolami (C) a N versus P a NP plochami. Rašelin vysazené do C a N ploch sotva přežily, naopak jedinci v P a NP plochách bujně rostli a téměř kompetičně vyloučili původní dominantu – *Eleocharis* spp. Průměrné počty rašelin na konci experimentu byly 2 (C a N) a 576 (P a NP) na 100 m². U ploch s přidavkem P se dynamika rozrůstání lišila mezi jednotlivými salinitami. V nízké salinitě bylo rozrůstání zpomalené, ačkoliv na konci pokusu dosahovalo podobných rychlostí, jako u P hnojených ploch ve vyšších salinitách. Toto zpomalení přisuzujeme

mnohem vyšší původní biomase (*Eleocharis* spp.) a méně vhodným půdním podmínkám v mokřadech s nízkou salinitou spíše než přímému vlivu salinity. Koncem pokusu se počet ražet stabilizoval a v některých plochách dokonce klesal kvůli vlivu samoředění a napadení herbivorním hmyzem.

Z časoprostorového modelu extrapolujícího pozorované rozrůstání vyplývá, že v P hnojených mokřadech se může jeden jedinec druhu *Typha domingensis* rozrůst na 1-ha porost během pouhých 9-ti let. Obohacení belizských mokřadů P tedy významně zvyšuje pravděpodobnost jejich celkového zarůstání druhem *Typha domingensis*.





A young individual of limpkin, *Aramus guarauna*, caught in the close vicinity of patches of denser and taller *Eleocharis*. These patches and limpkins were at the birth of following chapter, since their occurrence was very obvious within this marsh; Location Quiet, April 2006.

Biological activities as patchiness driving forces in wetlands of northern Belize

Macek P., Rejmánková E. and Fuchs R.
(Submitted)

ABSTRACT

Patchiness in wetlands is a common and well documented phenomenon. Oligotrophic wetlands of northern Belize display noticeable vegetation heterogeneity at both large and small scales. In this paper, we document the small scale patches in herbaceous wetlands, describe differences between patches and surrounding wetland habitats and explain patch formation and sustenance.

We conducted a survey of patches and confirmed their occurrence by spatial analysis. Patches were distinguished from a surrounding wetland by denser and taller vegetation, higher amount of empty snail shells and elevated soil phosphorus (P). Plants in patches had higher tissue nitrogen (N) and P content and there was also higher total N and P per m² incorporated in plant biomass. In terms of stable isotopes, plants in patches were enriched in ¹⁵N; patch soils were depleted in ¹³C.

Observations of focal individuals of *Aramus guarauna*, limpkin, a wading bird feeding almost exclusively on snails, revealed the origin of the snail shell piles frequently found in patches. An adult limpkin captured on average 18 snails daily, of these 80% were handled in patches and birds often repeatedly used the same patch.

Experimental patch creation by adding chicken manure or P to 1 m² plots resulted in higher and denser vegetation with values increasing in order: control, P, manure plots. The effect was significant at both experimental locations 6 months after the treatment and at one location even 40 months after the treatment.

We present a simple mechanistic explanation for nutrient redistribution in wetlands and their eventual accumulation in patches. Both nutrient and isotopic differences result from animal input into patches, e.g. bird droppings or prey remnants. Foraging activity of *Aramus guarauna* is most likely responsible for patch formation. A positive feedback (repeated use of a suitable patch) is apparently the mechanism sustaining patches in these marsh environments.



Biologická aktivita jako hnací síla heterogenity mokřadů severní Belize

Macek P., Rejmánková E. and Fuchs R.
(Podáno k opublikování)

SHRNUTÍ

Ostrůvkovitost mokřadní vegetace je známý a dokumentovaný jev. Také oligotrofní mokřady severní Belize vykazují značnou heterogenitu – jak malo-, tak velkoplošnou. V tomto článku jsme popsali maloplošnou heterogenitu mokřadů, charakterizovali rozdíly mezi ostrůvky tvořenými vegetací a okolní mokřadní vegetací a nakonec se pokusili vysvětlit vznik a udržení ostrůvků.

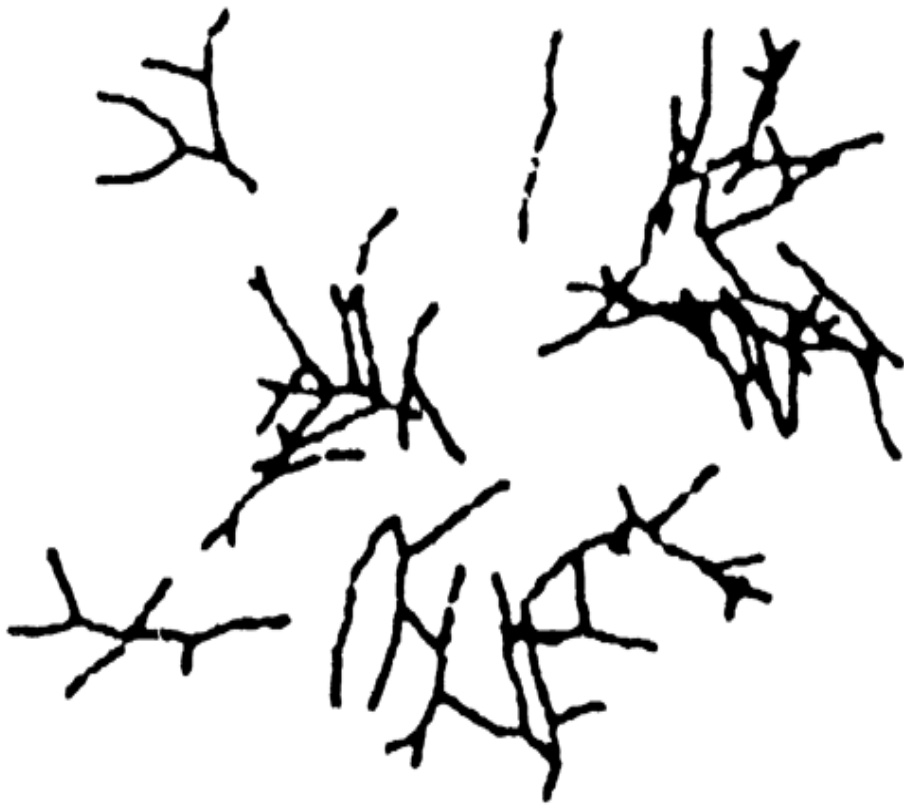
Výskyt ostrůvků byl doložen prostorovou analýzou; od okolní vegetace se lišily především hustší a vyšší vegetací, větším počtem prázdných šnečích ulit a zvýšeným půdním P. Rostliny ostrůvků měly vyšší obsah P a N, ostrůvky měly tedy i vyšší P a N v biomase na m². Dále zde bylo dokumentováno obohacení o ¹³C izotop v půdním uhlíku a obohacení o ¹⁵N izotop v rostlinném dusíku.

Pozorování fokálních jedinců druhu *Aramus guarauna*, kurlana, brodivého ptáka živícího se téměř výhradně šneky, odhalilo původ hromádek šnečích ulit uvnitř ostrůvků. Dospělý jedinec ulovil v průměru 18 šneků denně a 80% jich konzumoval na ostrůvcích. Byla zaznamenána konzervativnost chování kurlanů vracejících se opakovaně na stejné ostrůvky.

Hnojením části mokřadní vegetace (plošky 1 m²) slepičím trusem byly vytvořeny ostrůvky hustší a vyšší vegetace. Ostrůvky byly dobře odlišitelné po 6-ti měsících a na jedné lokalitě i po 40-ti měsících od pohnojení.

V závěru prezentujeme mechanismus redistribuce živin v mokřadech a jejich postupnou akumulaci v biomase ostrůvků. Jak živinové, tak isotopové rozdíly mezi ostrůvky a okolním mokřadem jsou pravděpodobně důsledkem aktivit živočichů: obohacení ptačím trusem či zbytky šneků. Chování kurlanů při lovu a zpracování kořisti jsou pravděpodobnou příčinou vzniku ostrůvků. Pozitivní zpětná vazba, opakované návštěvy stejného ostrůvku, je zřejmým mechanismem udržujícím ostrůvkovitost mokřadní vegetace.





General Discussion

INDIVIDUAL BENEFITS OF CLONALITY AND FACTORS RULING CLONAL GROWTH TRAITS

Across main vegetation types, the wetlands include the largest portion of plants capable of clonal growth (Klimeš et al. 1997). This can have several causes, but the type of substrate is undoubtedly among plausible explanations: wetland soils are often rather soft and thus not constraining rhizome growth as much as other soils. Further, another selection pressure frequently exerted in harsh wetland environment is represented by frequent changes of water level. This phenomenon mainly limits plant success in generative reproduction. Flooded seedlings of emergent plants usually do not survive under prolonged anoxic conditions, which decrease their relevance. Hence, clonality is of major importance for plant survival in wetlands, although it is not overwhelming: for a long term survival there, generative reproduction is often needed (van der Valk 2006).

Examples of clonality enhancing plant survival under stressful conditions as described in the first chapter have been reported quite frequently, I will not report them here (but see e.g. Suzuki and Hutchings 1997). Our results agree with part of these findings: plants with at least some of the shoots emerging above water level can support greater amount of ramets than completely submerged plants (Chapter 2). Under natural conditions, this leads to partial survival within whole population subjected to extreme long-term flooding events. Plants keeping the contact with the atmosphere support the neighbouring connected ramets and enhance their survival. Furthermore, after the water recedes and plants start to reoccupy the newly opened space, surviving young individuals have an advantage, even though the original supporting shoot usually dies due to its tendency to break down without the water support after emergence (see also Suzuki and Hutchings 1997). Similar partial survival has been previously observed in the field with *Eleocharis cellulosa* after an extreme flood caused by tropical storm Chantal in 2001 (Macek and Rejmánková, pers. obs.).

Not only abiotic factors (e.g. water level or nutrient poor patches) can represent stressful conditions affecting clonal growth traits. Biotic factors represented by vegetation physiognomy (e.g. vegetation height or biomass) exert an influence on clonal traits as well. Often, biotic factors have even better predictive value than abiotic factors ultimately causing them (Chapter 4). However, the mechanism by which clonal plants respond to unsuitable habitat is similar regardless whether habitat unsuitability is represented by biotic or abiotic factor: an escape strategy (Macek and Lepš 2003). Apart from generative reproduction, an escape in clonal plants is effectuated by an increase of distance between two ramets. Importantly, a change in two clonal growth traits with contrasting costs can result in similarly increased distance: these traits are internode length and internode number. If an escape strategy is about to be useful, it should be rather inexpensive for plant. Since the increase of internode number results in additional costs of leaf and/or root production, the only meaningful strategy would be to increase the length of internodes. Similarly I conclude, the efficient escape strategy in competitively poorer species *Potentilla palustris* is keeping stable high cost traits and plastic low cost traits of clonal growth (Chapter 4).

Apart of other factors, both systems studied differ in nutrient limitation: in limestone based Belizean marshes plants are strongly P-limited while in more acidic temperate fens and bogs plants are rather N limited. However, plant response to enrichment by limiting nutrient, i.e., the increased branching, is common to species from both systems: (Chapters 3 and 4). This is consistent with foraging theory in clonal plants which expects concentration of resource acquiring structures in more favorable places (de Kroon and Hutchings 1995; Salemaa and Sievanen 2002). Although increase of branching in taller vegetation might seem to be in contradiction with an escape strategy from less suitable places (plants also increased internode length as response to lower light availability there), it is not mutually exclusive, since taller vegetation often also represents elevated nutrients. A positive effect of nutrients may further be reflected in better space capture. However, this result is valid only for species with high phenotypic plasticity of clonal growth traits. Three macrophyte species of Belizean marshes can serve as a good example of variability in phenotypic plasticity among clonal plants. The most rigid species, *Cladium jamaicense*, shows no change in rhizome length and branching in response to nutrient and salinity changes. An

intermediately plastic *Eleocharis cellulosa* alters branching accordingly to conditions, but it does not change its rhizome length. The last species, *Typha domingensis*, shows the most plastic response in both rhizome length and branching (Chapter 3). Such differences in architectural constraint and plasticity ultimately drive emergency of different patterns in wetlands based on portion occupied by different species: a mixture of tussocks and monodominant stands (Herben and Hara 1997; see below).

INTERACTIONS BETWEEN CLONAL PLANTS

An equally interesting consequence of plant clonality can be noticed in processes of competition between species. In nutrient limited environments, a possibility of competitive exclusion of inferior species is reduced. On the other hand, when nutrient enrichment occurs, fast changes in species abundance can result in dominance of competitively superior species and outcompeting of other species in plant community (de Kroon and Bobbink 1997). Altered conditions may lead to a change in invasiveness of native species: they can take an advantage of changes in environmental conditions and may spread out of their normal range through the means of various dispersal mechanisms. Under this scenario, clonal growth is an efficient and important dispersal mechanism in wetland systems. The rhizomatous expansion can speed up the process of space filling resulting ultimately in a dense and uniform cover, as was reported for the case of both *Eleocharis* spp. and *Typha domingensis* in Belizean marshes (Chapters 4, 5 and 6). While invasive behaviour is less likely in *Eleocharis* spp. due to its limited horizontal spreading, the behaviour of the second species, *Typha domingensis*, under altered nutrient regime should be considered as invasive. The results of simulations in Chapter 6 clearly demonstrate invasive nature of *Typha domingensis* spreading. This is in concordance with "fluctuating resource availability" hypothesis stating that a community is more susceptible to invasion when nutrient surplus occur (Davis et al. 2000).

Compared to other habitats, wetlands host relatively large amount of clonally spreading invaders (Pyšek 1997). A bottleneck in their success at this habitat lies in establishment, which is often difficult. After all, once established, clonal plants seem to be more persistent and competitive, which leads to an effective occupation of the available space. Limitation due to

low survival after initial establishment was also observed in our implant experiment: where the original vegetation was too dense, ramets of *Typha* sometimes died (Chapter 6).

Such a contrasting output from plant performance in various nutrient enriched plots is an excellent example of two different strategies in horizontal growth competition: dominance and founder control (Herben and Hara 1997). When original density of *Eleocharis* shoots was lower, *Typha* growth was not limited and consecutively by overtopping of shorter *Eleocharis*, *Typha* succeeded to capture space in both vertical and horizontal dimensions. Hence, this community looked to be dominance controlled. Alternatively, when original stands of *Eleocharis*, due to its extreme density, prevented further establishment of competitively stronger invader - *Typha*, the community was founder controlled (mainly in low salinity locations; Chapter 4 and 6). Nevertheless, in part of founder controlled plots, *Typha* was able to survive and eventually succeed in spite of dense original vegetation, although this success was delayed by several years. What were the reasons of this switch between founder and dominance control? Possible starters were natural disturbances frequent to these wetlands: fire and/or elevated water level. In both cases, aboveground biomass was removed, at least partially. The newly open space enabled a full expression of *Typha* competitive superiority over *Eleocharis* spp. Last but not least, a third operating mechanism leading to ultimate expression of dominance control was a clonal growth trait: a functional connection between ramets enabling a support of small daughter *Typha* ramets competing directly with *Eleocharis* (specifically nutrient transport; Macek and Rejmánková, data not shown). In fact, there was an indispensable necessity of clonal growth in all these processes of species switch (Chapter 6).

CLONALITY AND ECOSYSTEM PROCESSES

Altered nutrient conditions resulting in macrophyte species switch can furthermore lead to changes of the whole system (e.g. Grieco et al. 2007). Spread of invasive species can also modify chemical and physical properties of habitat and also decrease biodiversity (de Kroon and Bobbink 1997; Chiang et al. 2000; Svengsouk and Mitsch 2001; Boers et al. 2007). Furthermore, rather homogeneous soil fertility increase in Belizean marshes

(due to nutrient runoff from agricultural fields) would lead to a decrease of spatial heterogeneity, which is originally present there thanks to coexistence of several morphologically different species. Keeping wetland oligotrophic status should be therefore among primary objectives (Chapters 5 and 6). It is a well known fact, that wetland restoration is much more costly than their protection.

On the other hand, not all nutrient enrichment does necessarily result in loss of species diversity or environmental heterogeneity. Actually, the nutrient enrichment originating from animal activities investigated in the Chapter 7 has a completely opposite effect. Here, the processes involved in the response of plants are the same, i.e. increased branching in nutrient rich patches. However, animal caused nutrient input is very local and also much lower than in our previous experiments. This is far the most important difference, because animal caused nutrient enrichment result in vegetation differentiation, i.e. pattern emergence, due to variation of vegetation density and height. Over time, this pattern reflects in soil elevation. It has been reported several times, that any local increase in topography can increase wetland biodiversity (Vivian-Smith 1997; Sklar and van der Valk 2002; Wetzel 2002). An increase in heterogeneity due to differential growth of emergent macrophytes in response to small scale nutrient enrichment will eventually have an important effect on wetland biodiversity. Although a direct link between small and large scale heterogeneity is not supported by any strong evidence yet, it is likely that a small scale patchiness caused by animal activity is antecedent of large scale tree islands. Plasticity in clonal growth traits is therefore at the very beginning of heterogeneity in wetlands.

While nutrient enrichment is the ultimate cause of above mentioned changes, its effect is mediated through the plasticity of clonal growth traits. In agreement with the intermediate disturbance hypothesis (Huston 1979), I conclude that nutrients can increase heterogeneity at lower doses, while both extremes, i.e. no nutrients or high nutrients often result in lower heterogeneity. Nevertheless, both processes of environmental heterogeneity change similarly result from the changes of plastic clonal growth traits: branching and spacer length.

So far, I focused on the effect of more plastic species on vegetation pattern. However, I believe the species with constant clonal growth traits are of similar importance. In case of *Cladium jamaicense*, a production of

relatively short rhizomes with rather constant length frequently results in large tussocks formation. Such tussocks represent a suitable habitat for numerous bird species as a good place for nesting. Larger animals seek for tussocks of *Cladium* as well, e.g. *Crocodylus moreletii* use them for prey handling and as platforms for resting above water. Hence, also plants with constant traits may result in vegetation pattern emergence.

SUMMARY AND CONCLUSIONS

Species with plastic clonal growth traits are able to better accommodate to changing wetland conditions in terms of both resource acquiring strategy and/or escape strategy. Clonally growing plants are more efficient in new space occupation after biomass removing events, such as fires, grazing or high water levels. Variable phenotype enables them to occupy a wider range of habitats and eventually to succeed in competition with co-occurring species when growth conditions are changed. In some cases, a plasticity of clonal growth traits mediate loss of heterogeneity, while in others it can be the important property responsible for greater heterogeneity in wetlands: it largely depends on external factors driving these traits, e.g. nutrient availability. On the other hand, rigid clonal growth may also result in pattern eventually increasing wetland heterogeneity and habitat diversity. Clonal plants are extremely important in wetland functioning, although only coexistence of both plastic and rigid species (in terms of clonal growth traits), which is favored particularly under oligotrophic conditions, can be beneficial for wetland diversity.

REFERENCES

- Boers,A.M., Veltman,R.L.D. & Zedler,J.B. (2007) *Typha x glauca* dominance and extended hydroperiod constrain restoration of wetland diversity. *Ecological Engineering* **29**, 232-244.
- Chiang,C., Craft,C.B., Rogers,D.W. & Richardson,C.J. (2000) Effects of 4 years of nitrogen and phosphorus additions on Everglades plant communities. *Aquatic Botany* **68**, 61-78.

- Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**, 528-534.
- de Kroon, H. & Hutchings, M.J. (1995) Morphological plasticity in clonal plants - the foraging concept reconsidered. *Journal of Ecology* **83**, 143-152.
- de Kroon, H. & Bobbink, R. (1997) Clonal plant dominance under elevated nitrogen deposition, with special reference to *Brachypodium pinnatum* in chalk grassland. *The ecology and evolution of clonal plants* (eds H. de Kroon & J. van Groenendael) Backhuys Publishers, Leiden, The Netherlands, pp 359-379.
- Grieco, J.P., Rejmánková, E., Achee, N.L., Klein, C.N., Andre, R. & Roberts, D. (2007) Habitat suitability for three species of *Anopheles* mosquitoes: Larval growth and survival in reciprocal placement experiments. *Journal of Vector Ecology* **32**, 187.
- Herben, T. & Hara, T. (1997) Competition and spatial dynamics of clonal plants. *The ecology and evolution of clonal plants* (eds H. de Kroon & J. van Groenendael), pp 331-357.
- Huston, M. (1979) General hypothesis of species-diversity. *American Naturalist* **113**, 81-101.
- Klimeš, L., Klimešová, J., Hendriks, R. & van Groenendael, J. (1997) Clonal plant architecture: a comparative analysis of form and function. *The ecology and evolution of clonal plants* (eds H. de Kroon & J. van Groenendael), Backhuys Publishers, Leiden, The Netherlands, pp 1-29.
- Macek, P. & Lepš, J. (2003) The effect of environmental heterogeneity on clonal behaviour of *Prunella vulgaris* L. *Plant Ecology* **168**, 31-43.
- Pyšek, P. (1997) Clonality and plant invasions: can a trait make a difference? *The ecology and evolution of clonal plants* (eds H. de Kroon & J. van Groenendael), Backhuys Publishers, Leiden, The Netherlands, pp 405-427.
- Salemaa, M. & Sievanen, R. (2002) The effect of apical dominance on the branching architecture of *Arctostaphylos uva-ursi* in four contrasting environments. *Flora* **197**, 429-442.
- Sklar, F.H. & van der Valk, A.G. (2002) Tree islands of the Everglades: An overview. *Tree islands of the Everglades* (eds F.H. Sklar & A.G. van der Valk), Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 1-18.
- Suzuki, J.-I. & Hutchings, M.J. (1997) Interactions between shoots in clonal plants and the effect of stored resources on the structure of shoot

- populations. *The ecology and evolution of clonal plants* (eds. H.de Kroon & J.van Groenendael), Backhuys Publishers, Leiden, The Netherlands, pp 311-329.
- Svengsouk,L.J. & Mitsch,W.J. (2001) Dynamics of mixtures of *Typha latifolia* and *Schoenoplectus tabernaemontani* in nutrient-enrichment wetland experiments. *American Midland Naturalist* **145**, 309-324.
- van der Valk,A.G. (2006) *The biology of freshwater wetlands*. Oxford University Press, New York.
- Vivian-Smith,G. (1997) Microtopographical heterogeneity and floristic diversity in experimental wetland communities. *Journal of Ecology* **85**, 71-82.
- Wetzel,P.R. (2002) Tree islands ecosystems of the world. *Tree islands of the Everglades* (eds. F.H.Sklar & A.G.van der Valk), Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 19-69

Curriculum vitae

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Nationality: Czech

Citizenship: Czech Republic

EDUCATION AND DEGREES

2004 - present: PhD studies (Faculty of Sciences, University of South Bohemia)

2007: University Joseph Fourier, Grenoble, three week stay at lab of prof. S. Lavorel, LECA, Laboratory of Alpine Ecology

2001 - 2004: Department of Botany, Faculty of Biological Sciences, University of South Bohemia: Ms. studies, graduation in May 2004

2004 RNDr. degree in Botany, Department of Botany, Faculty of Biological Sciences, University of South Bohemia

1997 - 2001: Faculty of Biological Sciences, University of South Bohemia: bachelor studies, graduation in May 2001

1992 - 1997: Bilingual Czech-French lyceum finished by "Maturita bilingue"

EMPLOYMENT

2008: Institute of Botany, AS ČR, Section of Plant Ecology, Třeboň, research fellow

2004 - present: Faculty of Biological Sciences, Univ. of South Bohemia, České Budějovice, research fellow

2001 - 2003: University of California, Davis – postgraduate research position: Linking ecosystem processes and community structure along salinity and

nutrient gradients in tropical marshes; Belize, Central America. Project manager at research station based in Orange Walk, Belize

FIELDS OF PROFESSIONAL INTEREST

plant interactions; plant clonality and its role in stressful environments (including spatiotemporal models); wetland plant ecology and ecophysiology; ecophysiology of plants in highest range of their distribution; tree line in semiarid regions of the world; plant traits

ONGOING PROJECTS

Comparative ecology of tropical and temperate plants in the equatorial páramo (GAAV A601110702, Sklenář P., member of team)

Linking ecosystem processes and community structure in tropical marshes: the role of macrophytes and microbial communities (MSMT ME 912 Šantrůčková H., member of team)

Upward migration of sub-nival plants in E Ladakh: the role of plant traits and interactions under climate warming (GAAV IAA600050802, Klimeš/Doležal, member of team)

PUBLICATIONS

Rejmánková E., Macek P., Epps K. Wetland ecosystem changes after three years of phosphorus addition. (Wetlands, in press)

de Bello F., Thuiller W., Lepš J., Clément J-C., Macek P., Sebastià M.T. & Lavorel S. The spatial components of functional trait diversity. (Journal of Vegetation Science, in press)

Královec J., Pocová L., Jonášová M., Macek P., Prach K. Spontaneous recovery of an intensively used grassland after cessation of fertilizing (Applied Vegetation Science, in press)

Macek P., Lepš J. (2008) Environmental correlates of growth traits of stoloniferous plant *Potentilla palustris*. *Evolutionary Ecology* **22**: 419-435

Rejmánková E., Macek P. (2008): Response of root and sediment phosphatase activity to increased nutrients and salinity. *Biogeochemistry* (DOI 10.1007/s10533-008-9242-3)

Karbulková J., Schreiber L., Macek P., Šantrůček J. (2008): Differences between water permeability of astomatous and stomatous cuticular membranes: Effects of air humidity in two species of contrasting drought resistance strategy. *Journal of Experimental Botany* **59**: 3987-3995

Macek P., Rejmánková E. (2007): Response of emergent macrophytes to experimental nutrient and salinity additions in oligotrophic tropical wetlands. *Functional Ecology* **21**: 478-488

Macek P., Rejmánková E., Houdková K. (2006): The effect of long term submergence on functional properties of *Eleocharis cellulosa* Torr. *Aquatic Botany* **84** (3): 251-258

Macek P. and Lepš J. (2003): The effect of environmental heterogeneity on clonal behaviour of *Prunella vulgaris* L. *Plant Ecology* **168**: 31-43

PRESENTATIONS

2008: 8th INTECOL, Cuiaba, Brazil: "The dynamics of the spread of *Typha domingensis* in oligotrophic subtropical wetlands following nutrient enrichment."

2008: The Herbario Nacional de Bolivia: conference "Avances de investigacion en bosques de *Polylepis* y sus alrededores" [Latest studies in *Polylepis* forests and surrounding ecosystems]. Different morphological and ecophysiological traits of three congeneric tree species from contrasting environment and their distributional consequences.

2003: First Belizean Freshwater Summit, Belize City, Belize, CA: "The wetland ecology of northern Belize and its linkages to malaria transmitting mosquitoes."

POSTERS

Macek P., Rejmánková E. 2006: Biological activities as a patchiness driving forces in wetlands

Society of Wetland Scientists 27th Annual Conference, Cairns, Australia

Macek P., Rejmánková E. 2006: Response of emergent macrophytes to experimental nutrient and salinity gradients; 8th Clonal plant workshop, Parnu, Estonia

Macek P. 2004: The effect of long term submergence on functional properties of *Eleocharis cellulosa* Torr. INTECOL, Utrecht, The Neetherlands

Macek P. 2003: Growth characteristics of *Potentilla palustris* (L.) Scop. from different habitats in Šumava Mts. 7th clonal plant workshop, Kuusamo, Finland

Macek P. 1999: Effect of environmental heterogeneity on clonal behaviour of *Prunella vulgaris*. British Ecological Society, Winter and Annual General Meeting.

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