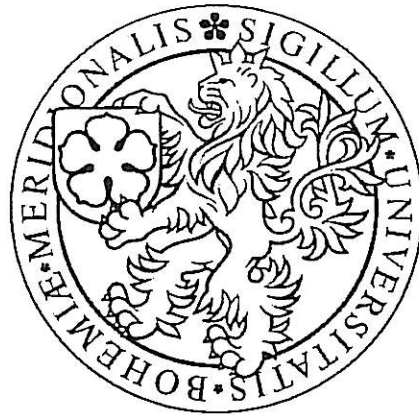# Faculty of Biological Sciences
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Growth dynamics and architecture of clonal species *Potentilla palustris* and *Prunella vulgaris* as a response to the heterogeneous environmental conditions.

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Magisterská práce

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Anotace:

Stolon growth dynamics of clonal species *Potentilla palustris* and *Prunella vulgaris* were investigated in two separate studies. Attention was paid especially to branching pattern and internode length variability under different growth conditions. Two-dimensional simulation of medium term *P. palustris* clone growth was presented. The *P. vulgaris* stolon orientation was analyzed using methods of circular statistics.

Prohlašuji, že jsem uvedenou práci vypracoval sám s použitím uvedené literatury.
V Českých Budějovicích 20.04.2004

Content

Preface

Various aspects of clonality and clonal plant growth are attractive issues in numerous studies. This is not surprising, considering that two thirds of European plant species are clonal, or at least, possess organs that may under certain conditions exhibit clonal behavior. Vegetative reproduction is not restricted to a small number of plant taxa, but is of polyphyletic origin occurring largely across the plant kingdom (de Kroon & van Groenendael 1990).

Clonal plants grow under different environmental conditions and in various vegetation types. But the ratio of clonal plants to non-clonal differs among habitats. Lower number of clonal plants is observed, for example, in synanthropic vegetation subjected to frequent disturbances. On the other hand, clonality is most common in alpine and wetland environments (Klimeš et al. 1997). High occurrence of clonal behavior is mostly found at the extreme ends of environmental gradients (e.g. low temperature, high altitudes, frequent flooding, low nutrient or low light levels). Clonal behavior can therefore be of adaptive nature under stressful conditions (Grace 1993).

The variability in growth forms of clonal plants has resulted in many attempts for classification schemes. One of the recent works concerning this topic is the classification of 21 growth forms of clonal plants according to the origin of the clonal organ, its position toward the soil surface and longevity of the connections (called internodes or spacers) within individual parts (ramets) of the whole clone (Klimeš et al. 1997).

This thesis consists of two independent studies of two constrasting clonal plants. The two plant species investigated in this work differ in spacer longevity. *Potentilla palustris* has persistent connections between ramets preventing clone splitting. Its clonal growth allows long term studies of plant growth and clone architecture. On the other hand, spacers of annual to short lived *Prunella vulgaris* disintegrate rapidly. Such behavior allows the study of immediate answer of the plant morphology to the altered environmental conditions.

GROWTH CHARACTERISTICS OF *POTENTILLA PALUSTRIS* (L.) Scop. FROM DIFERENT HABITATS IN ŠUMAVA MTS.

Abstract

1. *Potentilla palustris* has a patchy distribution in alluvial wet meadows and peatlands of the Šumava Mts. and adjacent foothills. It is a creeping macrophyte with monopodial growth and long lignifying stolons penetrating deep into the surrounding vegetation and in several sites it forms almost monospecific stands.

2. The spatial pattern of plant growth depends on plant architecture, comprising usually linear growth characteristics and branching characteristics. This study proposes to analyze growth of *P. palustris* in space and time across the environmental gradients.

3. Growth dynamics of *P. palustris* (included characteristics are mainly: stolon and internode lengths, branching, leaf area and flowering) was recorded at 32 locations in area of Šumava Mts. during complete two growing seasons. Numerous abiotic and biotic characteristics recorded at each location (such irradiance, pH, soil contents of water, organic matter and nutrients, height and biomass of vegetation, species composition) were correlated to the growth characteristics of *P. palustris* using multivariate ordination methods.

4. More detailed studies of growth dynamics were carried out in two extreme locations with especial attention paid to the seasonal internode production and internode length along stolons.

5. Growth of *P. palustris* was well correlated with physiognomy of the vegetation rather than with general abiotic conditions, which seem to exert their effects indirectly. Branching was mostly a result of apical growth termination caused by flowering and in a less extent due to herbivory. While annual internode production was more stable across the environmental gradients, the internode length exhibited high plasticity between locations. But both internode number and internode length were changed between years. Short internodes were formed after branching and at the end / beginning of each season.

6. Stolon age estimates can be attained via tracing the plant growth history with respect to the variability in internode lengths. Growth simulations based on the field observations can be useful to analyze the spatial extent of *P. palustris* clones. Simulations were shown to correspond well with plants growing under natural conditions.

Introduction

Under natural conditions, plants often compete for water, nutrients and light (Lepš 1999). Even under relatively high levels of these resources, plant growth in some environments may be impacted by stressful factors such as anoxia, low pH, heavy metals, etc. Peatlands can be an example of such harsh environments. Peatlands can be divided along the gradient of pH into acidic bogs, moderate (transitional) fens and rich (alkaline) fens (Bedford et al. 1999). Bogs are strictly ombrotrophic, in fens the water source is mostly minerotrophic. All these types accumulate peat, but the rate of accumulation increases with acidity. Vegetation in bogs is *Sphagnum* dominated, while in fens graminoids with abundance of *Carex* species prevail. One of the species typical for vegetation of all these peatland types is *Potentilla palustris*.

The rates of decomposition are usually extremely low mostly due to the negative effect of phenolic compounds (released from dead tissue of *Sphagnum* mosses) on microbial processes (Aerts et al. 1999). Accumulation of dead plant material results in peat formation. In organic soils majority of both phosphorus (P) and nitrogen (N) are incorporated in the dead plant biomass, thus unavailable for plants. Furthermore, in the case of P, the formation of insoluble compounds with either Fe or Al occurs, deepening the phosphorus deficiency. Peatlands are consequently in most cases P-limited, sometimes co-limited by N (Bedford et al. 1999). An easy method of assessing nature of nutrient limitation is N to P ratio in plant tissue with values under 14 indicating N limitation and values above 16 indicating P limitation (Koerselman and Meuleman 1996, Bedford et al. 1999).

Clonal plant growth is widespread in peatlands. Clone, a genetic individual, consists of potentially independent parts, ramets. Ramets differentiate from apical and axillary meristems. Ramets of the same clone are not readily identifiable in natural populations (Eriksson 1993), because they can be found quite far away from each other. Consequently, the clone can be extensively laterally spread and may cover areas of thousands of square meters (Oborny & Cain 1997). In fact, one single clone with simultaneously growing and dying ramets can persist for very long time periods, which is at the extreme cases bordering with immortality of the genet.

Taking this into account, an easy way to identify one genetic individual nearly does not exist. The issue of the identification of an individual has been very problematic for a long time (Eckert 1999). Recently, the methods of molecular biology might solve the problem, but these methods are financially and time demanding. Fortunately, the runners of some perennial clonal plants can lignify and clone integration can thus allow long term studies of plant growth (comp. Svensson & Callaghan 1988, Klimeš 1992, Cowie et al. 1995, Pornon &

Escaravage 1999, Salemaa & Risto 2002). *Potentilla palustris* has also lignifying stolons which designate it to be a suitable model plant.

There are not many studies about spatial patterns of plant growth (Kenkel 1995). For studying growth at spatial scale, one should understand the mechanisms and principles of growth during one season. A combination of many factors affects the growth pattern of a clonal plant. On of the most important factors, the apical dominance, is of a physiological nature. The growth of apical meristem at the stolon tip suppresses the differentiation of lateral meristems and branch formation from the undeveloped sleeping bud. The bud emergence is usually arrested early, not further than at a stage of few short internodes (Watson et al. 1997). The developmental signal is based mainly on phytohormone auxin produced in young leaves.

Strong apical dominance can be frequently observed at dense monoculture stands where plants try to avoid self-thinning among the ramets (Eriksson 1993, Kenkel 1995, Watson et al. 1997). The environmental stress such as reduced nutrient or light availability may also result in bud release prevention and the continuation of straight growth (Salemaa & Risto 2002). This investment in growth rather than branching seems to be an adaptation to crowded conditions or to resource poor habitats, the unfavorable environments from which the plants tend to escape (Eriksson 1986, Routledge 1990, Salemaa & Risto 2002).

Very often a bud remains inactive until some internal or external factor prevents the apical meristem from growth (Phillips 1975, Svensson & Callaghan 1988, Klimeš 1992). The *programmed death* (Carlsson & Callaghan 1990), referred to as the termination of the apical meristem growth due to the formation of an inflorescence (Svensson & Callaghan 1988, Salemaa & Risto 2002), is an example of such an internal factor. The *responsive death* is caused by an external factor of abiotic origin (e.g. low temperatures, seasonal flooding or pathogens) or by a biotic factor, mainly herbivore activity (Salemaa & Risto 2002, pers. obs.).

Suppression of apical dominance and subsequent compensatory growth facilitated by sleeping bud development into a new branch is thus a generalized response to different types of apical meristem damage (Salemaa et al. 1999). Undeveloped lateral meristems kept in form of a bud bank are very important for plant recovery after disturbance (Watson et al. 1997). But damage is not the only factor responsible for higher branching, favorable light or nutrient conditions might also enhance branch formation from available meristems (MacDonald & Lieffers 1993, de Kroon & Hutchings 1995, Huber et al. 1999, Salemaa & Risto 2002, Sammul et al. 2003).

Clone spreading by new ramet production via branching, clone persistence and sexual reproduction are factors influencing the expected contribution of an individual plant to the future generations – fitness (Watson et al. 1997, Winkler & Fisher 1999). Both vegetative and generative reproduction is, however, limited by levels of available resources (Winkler &

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Schmid 1995). As resources are rarely abundant, there is a strong trade-off between plant resource allocation to sexual or vegetative reproduction. In different plant species the proportion of resources allocated to sexual reproduction varies (Huber 1995) and investing in flower and seed formation may result in lowering of available resources and limitation of vegetative growth (Reekie & Bazzaz 1987).

Although considerable amount of resources may be invested in sexual reproduction, success is not ensured. The effectiveness of such investment strongly depends on seedling recruitment. Three types of recruitment can be distinguished. Firstly, seedling recruitment occurring only at the initial phases of species establishment at a site. Secondly, the recruitment repeated continuously in the course of population life and finally, recruitment when conditions are good, at a "window of opportunity" occurring randomly in time (Pornon & Escaravage 1999). Many clonal plant species seem to reproduce once at the beginning of the population establishment and later the seedling recruitment is not observed anymore (Carlsson & Callaghan 1990, Eriksson 1993, Cowie et al. 1995), although investment in sexual reproduction is not lower. This behavior allows the genes to leave disadvantageous conditions of local crowding and it ensures the possibility of new genet establishment at another site far away with conditions more suitable (Erikson 1992, Bouzillé et al. 1997, Nishitani et al. 1999).

The other two factors of fitness achievement, clone persistence and clone spreading, are largely dependent on the growth architecture. Different characteristics determine clone growth architecture, namely structural blue print, onthogenetic stage of the plant and phenotypic plasticity. While architectural blue print defines the structural framework and the limits within which a species can responds to its (biotic and abiotic) environment, the phenotypic plasticity provides possibility to adjust the plant form and function to the actual environment (Huber et al. 1999). Structural blue print, which is completely under genetic control, is therefore a kind of architectural constraint of plant growth. Phenotypic plasticity is hence a morphological variability of plant growth operating within the architectural limits set by structural blue print. This variability is believed to be determined mostly by environmental conditions. Numerous plant organs and plant growth characteristics may exhibit phenotypic plasticity (e.g. branching, flowering, internode or petiole length; D'Hertefeldt & Jónsdóttir 1994, Huber 1995).

One of the widely discussed topics is whether plasticity in internode length may enhance accumulation of plant resource acquiring structures in resource rich sites and therefore whether it can be considered as a foraging response. While some studies support the theory that spacer shortening potentially results in concentration of resource acquiring structures in rich patches (Oborny 1994), the other studies suggest this behavior to be rather exceptional among plants (Sutherland & Stillman 1988) and moreover also insignificant (Cain

1994, de Kroon & Hutchings 1995). Shortening of internodes is mostly believed not to be foraging response, but the opposite end of internode plasticity, their elongation, can be presented as a foraging response to locally disadvantageous conditions. Nevertheless, the successful ramet placing and its remaining in a suitable patch depends on the number and size of favorable patches and their spatial and temporal variability (Oborny & Cain 1997, Piqueras et al. 1999, Oborny et al. 2001, Kun & Oborny 2003).

There are three possible ways to describe the long term growth dynamics of clonal plants. 1. It can be attained either by long term observations of plant growth in natural conditions. 2. Plant growth dynamics can be followed by tracing the plant history through persistent organs, or 3. the description can be a result of plant growth simulation (Klimeš 1992). The first option is more appropriate but time consuming, the third one is less time demanding but not exact. The best option is comparison of growth simulation based on the field data with long term observations and history tracing, combining all approaches together. This combined approach has been used in the study of *P. palustris*.

Understanding apical dominance and data from field measurements are basic requirements for model construction (Svensson & Callaghan 1988). Usually a model comprises variables such as branching angle, branching probability, death probability, rhizome and internode length. More complicated models encompass also resource translocation between ramets, reproduction efficiency, density dependency and spatio-temporal heterogeneity of the habitat, according to the type of model used (comp. Klimeš 1992, Cowie et al. 1995, Cain et al. 1996, Herben & Suzuki 2002). The most simple architectural models are single clone simulations disregarding biotic neighborhood of a studied clone. This type of model is efficient in studying how plant architecture or internal developmental control affect ramet demography and lateral expansion of the clone (Oborny & Cain 1997).

The aim of this study was to analyze the growth and spatial patterns of *Potentilla palustris* across the gradients of environmental conditions. The following objectives were chosen to accomplish this aim: 1. To correlate the growth plasticity of stoloniferous *P. palustris* with the environmental characteristics. 2. To determine the architectural growth limits with special attention paid to internode length and seasonal internode production. 3. Using the data derived from plants growing in the field to analyze the seasonal variation in internode length, and 4. To create the prediction of *P. palustris* growth at different conditions by simulating long term clone growth in a computer simulation model and compare the result with plants from the field.

I expected the growth characteristics of *P. palustris* to be correlated with abiotic factors rather than the species composition. I further predicted that branching pattern will be defined by the fate of the stolon and available resources. The variability in the stolon length

increase was predicted to be caused equally by internode elongation and higher rate of internode formation. The lateral spread of plants from uneven conditions was expected to be highly different but predictable from seasonal growth measurements.

Material and methods

Study species

Potentilla palustris (L.) Scop. belongs to the family Rosaceae and its taxonomic classification has been problematic. Many botanists placed this species within the genus Potentilla, while others put it into a separate genus Comarum (for review of Potentilla taxonomy since 1753 see Eriksson et al. 1998). The issue is still discussed. According to analysis of ribosomal and chloroplast DNA, the monophyly of Potentilla is questionable, and Potentilla palustris should be separated from the genus Potentilla (Eriksson et al. 1998). I will use Potentilla palustris here to conform to the general nomenclature source for this study, Kubát et al. (2002).

Potentilla palustris is a creeping macrophyte with long lignifying stolons penetrating deep into the surrounding vegetation. Often the plant forms large monocultures with dense overlaying stolon system. The stolon's length increase can be as much as 10 mm/day at the height of the growing season, although it is generally much smaller (pers. obs.). Plant grows sympodially with terminal inflorescence. After flowering, the lateral branches take the role of main stolon and continue growing until terminated by succeeding flowering (Irmisch 1850, Irmisch 1861). If not flowering, the annual growth increases are separated by the short internodes and reduced leaves (Irmisch 1861). Sterile-stolon-growth is mostly horizontal, fertile stolons are ascendent to erect (Wydler 1860).

Alternate leaves are pinnate with toothed edges. At the end of each tooth there is a hydathode responsible for guttation (Curtis & Lersten 1986). On newly produced stolons, adventitious roots sprout early (most often on last year internodes, pers. obs.). Roots are generally short and branched up to third order. The absence of root hairs shows the hydrophilic character of P. palustris. (Metsävainio 1931). The oldest parts of the stolon are decaying, which results in clonal splitting and consequent total independence of ramets (Irmisch 1861).

Flowers are 5-merous with typically swollen receptacle. Potentilla palustris is protandrous with overlapping sexual phases, selfcompatible and spontaneous autogamy occurs, but outcrossing enhances seed set and seed weight (Olesen & Warnecke 1992). Produced nectar attracts insect pollinators mostly belonging to orders Diptera and

Hymenoptera (*Bombus* species). Seed set decreases in size during late season as a result of limited insect visits and also due to resource limitation. Germination is not related to seed weight (Olesen & Warnecke 1992). Seed dormancy does not seem to be broken by dry or wet chilling (pers. obs.), but it is broken by KNO_3 (Olesen & Warnecke 1992). Achenes are water dispersed and are a component of persistent soil seed bank in alluvial meadows (Jutila 2002). Seedling has first leaves simple and the 4th to 7th leaves are trimerous (Irmisch 1861).

Potentilla palustris has a boreal circumpoalar distribution (see Appendix 1). Stolons and achenes of *P. palustris* could be found as macrofossils in soil cores from peatlands and shallow lakes (Lavoie & Payette 1995, Jasinski et al. 1998, Saarinen 1996). The species plays important role in early stages of succession in open water wetlands where it can form floating vegetation (Pietsch 1991, Jasinski et al. 1998, pers.obs.). In Czech Republic it occurs in different vegetation types: peat bogs, fens, wet meadows, rivers alluvia, water bodies edges. *Potentilla palustris* is mainly associated with vegetation of Scheuchzerio - Caricetea fuscae and Phragmiti - Magnocaricetea (Slavík 1995).

Study sites

For this study, I choose the area in Šumava Mts. ranging from surroundings of Lipno water reservoir (about 725 m a.s.l.) in the south-east through the highest central part of the mountains (up to 1240 m a.s.l.) to western region around Křemelná river. I conducted a vegetation survey (5x5 m relevés) of locations with *P. palustris* based on unpublished location list from "Floristic database for the flora of Šumava" (Working group 1995 -1997) in the season of 2000. Two plants at each of 57 locations were labeled by a small plastic tag 5 cm from the stolon tip, to monitor their growth. For drawing of a typical plant selected for monitoring see Appendix 2. After evaluation of the preliminary survey, I selected 33 locations based on their geographic position, different abiotic and biotic conditions and their gradients. One location was later rejected because of its complete destruction by cattle. The list of locations with geographical coordinates and altitudes is in Appendix 3.

Habitat characteristics

At each location I recorded the following abiotic and biotic characteristics. The percentage irradiance was determined as a ratio of light intensity inside the vegetation (5 cm above the soil where also most leaves of *P. palustris* are located) to total light intensity above the vegetation. Water level in the soil (above soil) was measured at different times and soil water pH measured in June 2002. Two soil cores of surface soil layer (10 cm) where roots of *P. palustris* mostly grow were taken to the laboratory for determination of water and organic matter percentage (loss on ignition) in the soil by standard pedological methods.

Soil samples of upper 10 cm were analyzed for content of available phosphorus (ions PO_4^- soluble in H_2O) by water extraction (Olesen & Sommers 1982) and for available nitrogen by KCl extraction (2 M KCl, extractant:soil, 2:1, v/w, 1 hour and then filtered through 0,45 µm glass fiber filter and analyzed for NO_3^- and NH_4^+ by flow injection analyzer [Foss Tecator 5042]). Soil samples were analyzed for total N and C content on the Carlo-Erba series 5000 CHNS analyzer. Total phosphorus was measured spectrophotometrically after combustion and consequent acid digestion (McNamara & Hill 2000).

The height of vegetation was measured, biomass from three 30*30 cm squares was collected, sorted to *P. palustris* and other vascular plants, dried at 60°C and weighted in June 2002. At each location, in five 1m² plots, the total number of sterile and fertile ramets, and total number of flowers were recorded. Leaf area of *P. palustris* leaves (6 per location) was measured using portable leaf area meter (LI-COR 3000A). Leaves were then analyzed for C, N and P contents in the same way as soil samples.

Growth characteristics

Fourteen ramets of *P. palustris* were labeled at each location and their growth was monitored during two seasons. Whole sequences of internode lengths, branching and rooting were recorded on a main stolon and on all branches. Length of flowering stem and number of flowers was also recorded. The status of each ramet tip (alive, grazed or dead) and each leave (alive or grazed) was distinguished.

The vicinity of location # 21 "Řásnice" with a large monoculture of *P. palustris.* was selected as a suitable site for an extensive excavation of two different clones. Excavation was done by hand in June 2002.

For a detailed study, two extreme locations were selected based both on habitat and *P. palustris* characteristics. These were: Loc.# 9 – "Medvědí" and Loc.# 29 – "Kvilda". The location "Medvědí", situated in lower altitudes, is characterized by a tall and dense vegetation of wet meadows. Soil conditions there are more favorable, the soil contains higher level of total nutrients and soil pH reaches 5.3. On the contrary, location "Kvilda" situated in higher parts of the mountains is dominated by sparse and short vegetation of peatlands or mountain oligotrophic meadows. Soil nutrients are more scarce, especially phosphorus. Also soil acidity is higher. Mountain climatic conditions in this location indicate shorter growing season. For all variables including plant growth characteristics, see Appendix 3. The excavation of 72 ramets, about 1m long, was carried out at these two locations in summer 2003. Internode length, branching frequency, branching angle and ramet tip status (see above) were recorded on the main stolon of each excavated stolon.

A small nutrient addition experiment was conducted at vicinity of an intermediate location # 5 "Rothošť Men". In a homogeneous plot, nine plants were selected within an

area of 0,1m^2 and small amount of NPK fertilizer (50g) was added there in June 2003. Neighboring nine plants served as control. Internode length and leaf number was recorded before and after nutrient application, ramet tip status and leaf area was recorded 108 days after application. To restrict the total nutrient input, the design of pseudo-replicates and small number of measured plants was proposed. Consequently, these results are only preliminary.

Data analyses

To differentiate main vegetation types in which *P. palustris* grows, all available relevés with *P. palustris* from the Czech National Phytosociological Database (Chytrý & Rafajová 2003) were analyzed. The Detrended Correspondence Analysis (DCA) with the effect of rare species reduced by downweighting was used for ordination. Vegetation types were also distinguished by the Two Way Indicator Species Analysis (TWINSPAN – Hill 1979). Number of analyzed relevés was 1229.

Further analyses were done for data I have collected in the Šumava mts. Correlations between all growth variables from all *P. palustris* plants were first viewed using Principal Component Analysis (PCA). All variables and their mean values at each location are listed in Appendix 3. According to the results of PCA, I selected four growth characteristics: 1. Main stolon length (Main cm), 2. Leaf number on main stolon multiplied by leaf area (In ML*LA), 3. Percent of growing stolons (Branch) and 4. Percent of flowering stolons (Flower) as relatively independent and well biologically interpretable. Their means for each location were calculated, and subsequently related to biotic and abiotic characteristics of environment and vegetation composition (relevés) of the locations. In the case of relevés, the growth characteristics were used as explanatory variables rather than species composition, to reduce the number of explanatory variables. Because the growth response to environmental conditions was expected to be rather linear, linear ordination method of direct gradient analysis, Redundancy Analysis (RDA), with Monte Carlo permutation test was used. Ordination methods were carried out with the aid of the program Canoco and their visualization was done using CanoDraw (ter Braak and Šmilauer 2002). List of all species abbreviations and full names used in ordination analyses are in Appendix 4.

Relations among selected variables and other growth and environmental characteristics were further examined using multiple regression analysis, and forward selection was used when needed. Log transformation (natural log) was applied where needed to improve normality and homoscedascity. Analysis of variance was used to test the effect of main stolon damage status on branching. Multiple regression was also used to examine the effect of the probability of internode termination (i.e. herbivory, inflorescence or

death) on the percentage of growing stolons. The number of internodes and internode mean length on the main stolon were analyzed across all locations and variability among locations was tested using Analysis of variance.

Data from stolon excavations were used to compare the annual growth at both locations. To analyze the growth in the years 1999 to 2002, ANOVA, repeated measures was used in both locations. For statistical analysis, I selected this period only, because the older data were not obtained for each excavated stolon. Comparison between "Kvilda" and "Medvědí" locations and between stolon excavation data and data from periodical measurements were done for the growing season of the year 2002 using t-test for independent samples. Nutrient addition experiment was also analyzed using t-test for independent samples. Multiple regression, ANOVA and t-test were carried out using the Statistica package. For visualization of seasonal growth at "Kvilda" and "Medvědí" locations, the program Statgraphic was used.

The age and number of produced internodes of the excavated clone from location # 21 was estimated using the spatial extent and annual growth rate of stolons (comp. Pornon & Escaravage 1999).

Simulation model

The simulation model "Rhizome" was developed to study the spatio-temporal processes within plant communities. The model is individual-based and it allows to follow the growth dynamics and interactions (e.g., intraspecific and interspecific competition) of both clonal and nonclonal species. Model includes numerous useful parameters such as resource translocation, resource dynamics, density dependent and density independent mortality parameters etc. Nevertheless, for my purposes, the most important are basic growth processes of single established individual affecting the clone architecture, i.e. horizontal growth, branching and ramet mortality parameters.

The parametrization of simulation model

The model was parametrized separately for each of the intensively studied locations, i.e., "Medvědí" and "Kvilda". Combination of both plant growth characteristics from two year measurement and all types of excavation data was used to determine and estimate the parameters for the computer growth simulations. Simulations were carried out using .program "Rhizome" (Herben and Suzuki 2002) and graphical presentation was done in CartaLinx program.

Time necessary for producing one internode was taken as one time step (plastochron equals time step), one season corresponds in this case to ten time steps. The density

independent mortality was estimated as proportion of dead or grazed ramet tips. To this ramet mortality a number of complete plant deaths divided by the total number of internodes of monitored plants was added. This procedure reduced the error of including only living plants in the model and disregarding dead plants which were, in fact, not measured. Branching angle and its standard deviation was implemented to the model. This standard deviation was also used as a variation in stolon growth orientation. Branching angles ranged from 10' to 90'. Branching probability was determined by dividing the sum of all branches by the sum of all internodes. The possibility of branch formation was set at each step because all internodes possess suitable meristems. However, meristem activation probability was set extremely low because as model plant increases, the model reuses the same probability for each produced internode. Consequently as these probabilities sum up, the higher number will soon result in unrealistic exponential branching increase. Model plants were prohibited to split up or disintegrate.

Model was simulated for 150 time steps, it corresponds to 15 year growth simulation. Simulations were repeated 3000 times and mean values were determining the selection of suitable model plants. List of some important model parameters is in Appendix 5.

Results

Habitat type differentiation

The DCA (Fig. 1) and TWINSPAN (Fig. 2) analyses of the National database relevés delineated four main vegetation types (labeled A, B, C and D here) in which *P. palustris* occurs. They were characterized by the following species composition (the environmental characteristics can be deduced from the known biology of constituent species): A. Wet meadows with moderate to strong N limitation, without the formation of peat. Typical species are *Carex panicea*, *Cirsium palustre*, *Ranunculus acris* and *Valeriana dioica*. B. Species poor communities, with stronger peat or organic mud accumulation, higher water level and favorable light conditions. Anoxic conditions can be limiting for the growth. Typical species are *Carex rostrata* and *Menyanthes trifoliata*. C. Margins of water bodies and alluvia mostly with denser vegetation and generally poor light conditions. Light conditions in this vegetation type are favorable only at the edges between vegetation and water body. Characteristic species are *Calamagrostis canescens*, *Lysimachia vulgaris*, *Lythrum salicaria* and *Naumburgia thyrsiflora*. D. Transitional fens with great accumulation of organic matter and lower pH. Typical species are *Sphagnum* species, *Eriophorum angustifolium* and

E. vaginatum, *Carex limosa* and *Oxycoccus palustris*. This type is rather heterogeneous, and includes also some habitats with higher representation of *Phragmites australis*.

In all my locations at Šumava Mts., the values of N/P in plant tissue, ranging from 4.5 to 11.9 (see Appendix 3), show the plant growth may be limited by nitrogen. However, the total content of both N and P is well above the critical values and thus nutrient limitation is probably not the case (Rejmánková, pers. comm.).
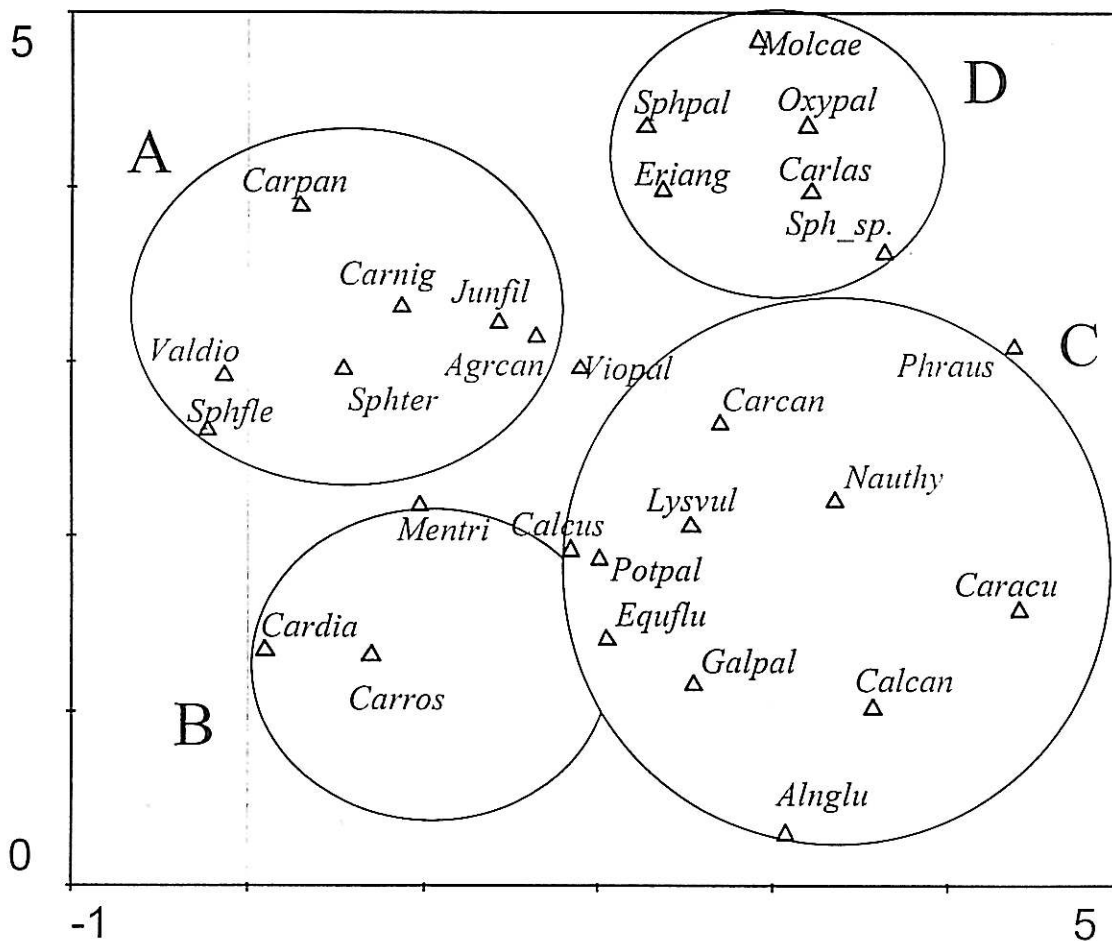

Fig. 1. The DCA results of all relevés from the national database containing *P. palustris* in Czech Republic. The circles and adjacent letters represent four main vegetation types (for explanation see the text). The species names are listed in the Appendix 4.

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           Carnig |————————————— 0,438 —————————————| Caracu
           Galuli |                                 | Phraus
                  |                                 | Calcan
                  |                                 | Nauthy
  Valdio |——————— 0,249 ———————|         Galpal |——————— 0,332 ———————| Phraus 3
  Potere |                     |         Lysvul |                     | Sph_sp.
  Carpan |                     |         Lytsal |                     | Carlas
  Galuli |                     |                |                     | Oxypal
  Viopal |                     |                |                     |
  Ranacr |                     |                |                     |
  Antodo |                     |                |                     |

       A                    B                 C                    D
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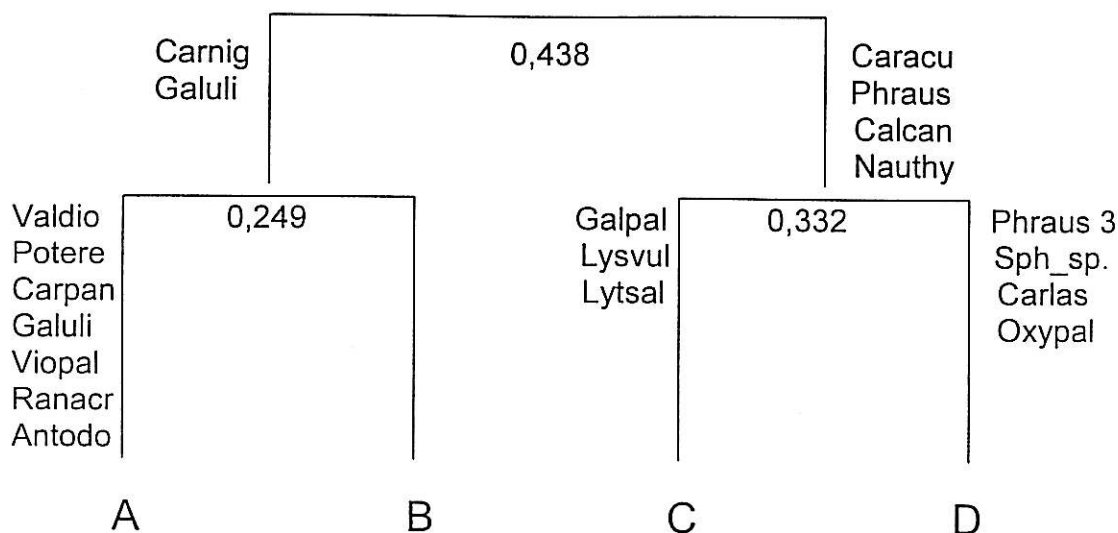
Fig. 2. Twinspan results of all relevés from the national database. The eigenvalue for each division is showed at each furcation. For each vegetation type (A, B, C and D – for explanation see the text), the indicator species are listed at each branch. Phraus 3 signify the third pseudospecies cutlevel (see Lepš & Šmilauer 2003). The species names are listed in the Appendix 4.

Correlations of growth plasticity to the environmental characteristics

PCA revealed the correlation structure of individual growth characteristics of *P. palustris* (Fig. 3). As expected, stolon length characteristics show strong correlation with both internode length and amount of produced internodes and flower production is logically positively correlated with length of flowering stem. Leaf production and area seem to correspond with plant carbon and nitrogen content. Consequently, selection of four meaningful growth characteristics, which are not strongly correlated with each other, was appropriate.

These responses of *P. palustris* were then explored in the context of habitat and vegetation characteristics. The 32 locations used in this study show similar habitat differentiation as all locations of *P. palustris* from the national database. Meadow (A), alluvial (C) and transitional fen (D) types are well represented by clusters of species (Fig. 4). Vegetation response is well correlated with the measured environmental characteristics (p < 0.05). Species rich meadow type is characterized by low organic matter content in soil contrary to rather species poor fen habitat, found at higher altitudes, with higher amount of undecomposed plant material in the soil. Alluvial habitat tends to be in lower altitudes simply because mountain river character does not allow appropriate soil sedimentation. In this figure, the four selected growth response variables of *P. palustris* are displayed as

supplementary variables (with no effect on the analysis) to show their relative position to the habitat type.
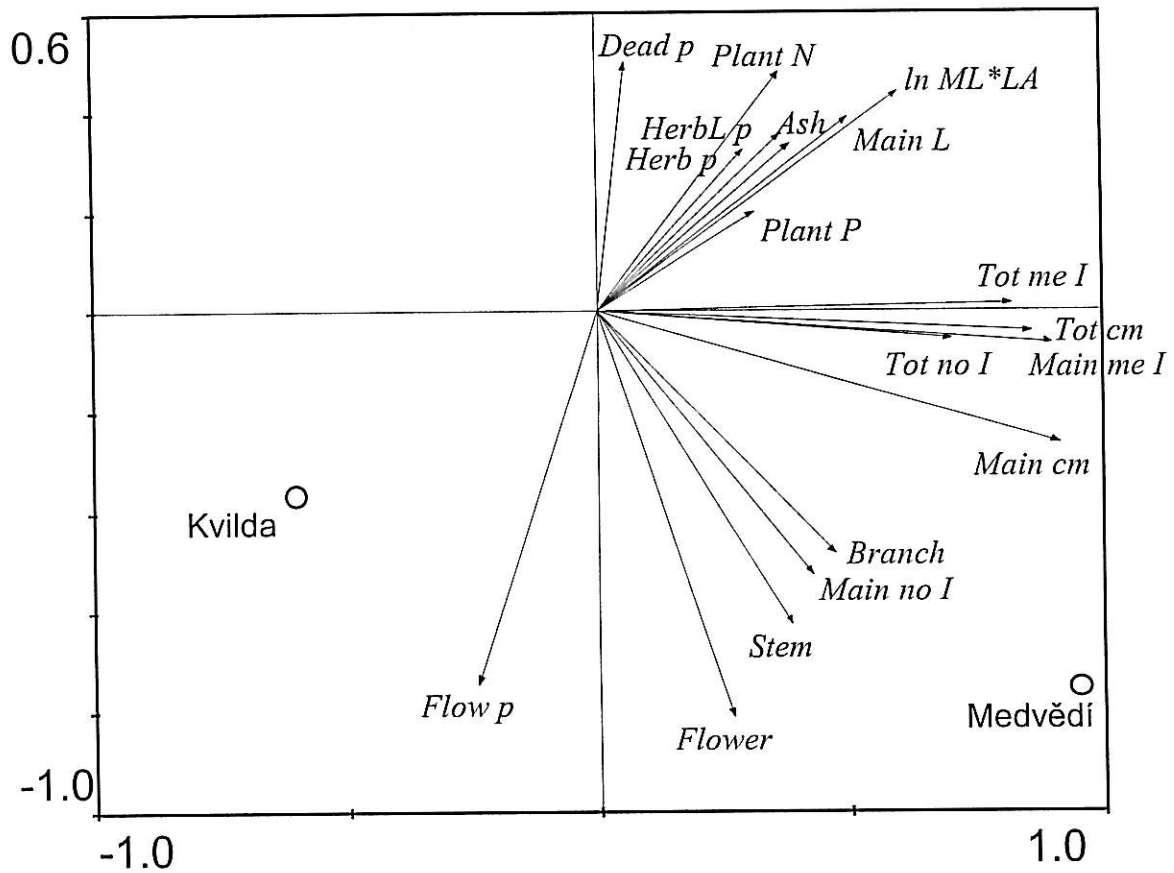

Fig. 3. The PCA results representing the correlations between recorded characteristics of *P. palustris*. Explanation of variable abbreviations are in Appendix 3. The position of two extreme locations at which more detailed studies were carried out is displayed by small circles.
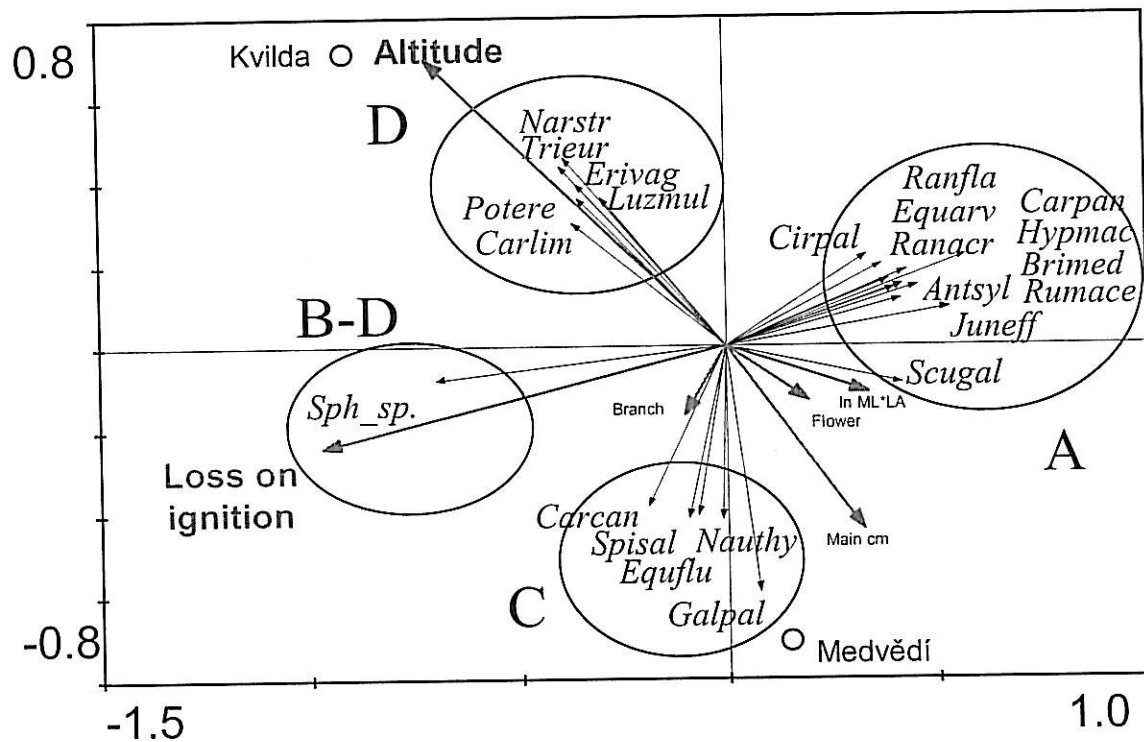
Fig. 4. The results of RDA showing the correlations between species composition and abiotic characteristic at each location. The explanatory variables were chosen using forward selection, Monte Carlo permutation test (p < 0.05). The circles and adjacent letters represent four main vegetation types. Growth characteristics of *P. palustris* were displayed in the figure as supplementary variables. Explanatory variables are in bolt, species names are in italics and supplementary variables are in small letters. The species names are listed in the Appendix 4. "Main cm" represents main stolon length; "In ML*LA" is leaf number on main stolon multiplied by leaf area; "Branch" means proportion of growing stolons and "Flower" represents proportion of flowering stolons. The position of two extreme locations is represented by small circles.

The correlation of *P. palustris* growth characteristics with species composition was studied by reverse analysis, i.e., using the growth characteristics as explanatory variables. (Fig. 5). In this figure, only three vegetation types are well distinguished. Plant species of the meadow type correspond with leaf production of the main stolon and species of the alluvial type are characterized by higher total stolon length. Both variables negatively correlate with species of the third vegetation type, the transitional fen.
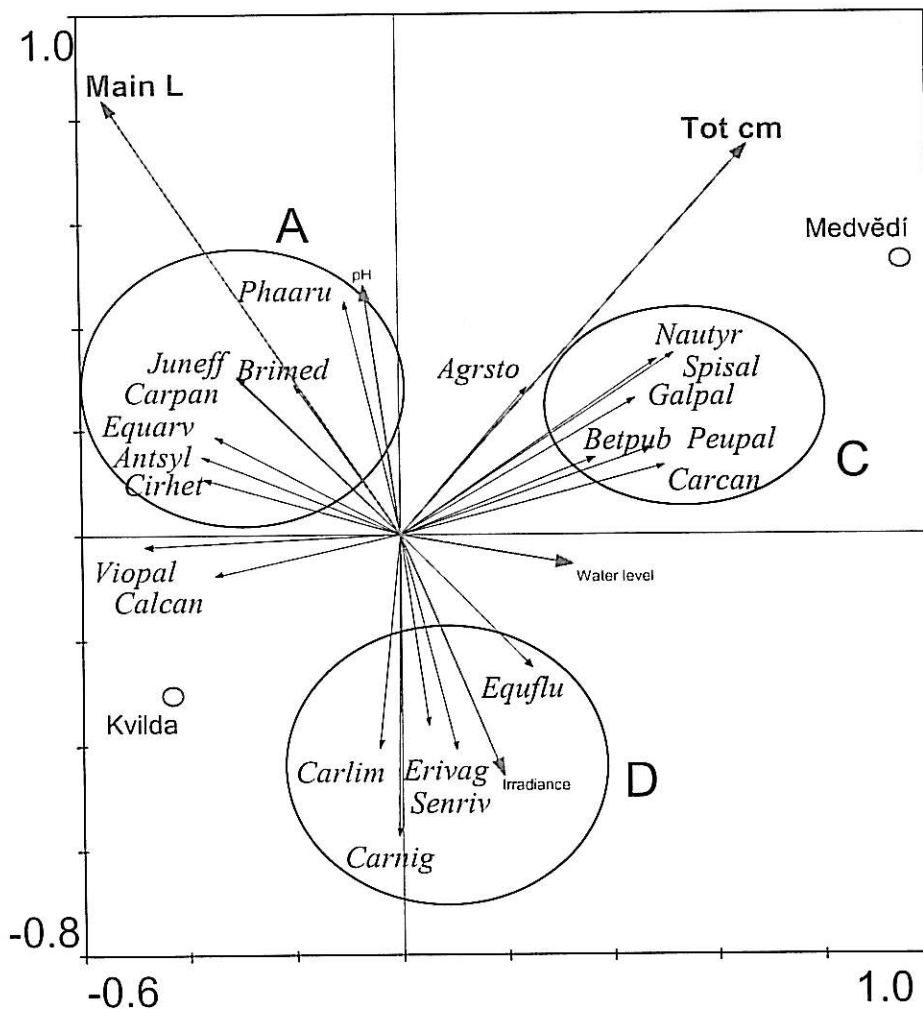
Fig. 5. The result of RDA where growth characteristics of *P. palustris* are used as explanatory variables for the species composition at each location. Growth characteristics were selected by forward selection, Monte Carlo permutation test (p < 0.05). The circles and adjacent letters represent four main vegetation types. The selected abiotic characteristics were displayed in the figure as supplementary variables. Explanatory variables are in bolt, species names are in italics and supplementary variables are in small letters. The species names are listed in the Appendix 4. "Main L" means number of leaves on the main stolon and "Tot cm" means total plant length including the length of branches. The position of two extreme locations is represented by small circles.

Habitat characteristics were divided into abiotic and biotic. From abiotic variables (Soil P, p = 0.05; pH, p = 0.08), phosphorus is correlated with flower production and pH correlates with main stolon length, but the relationship are weak (Fig. 6).
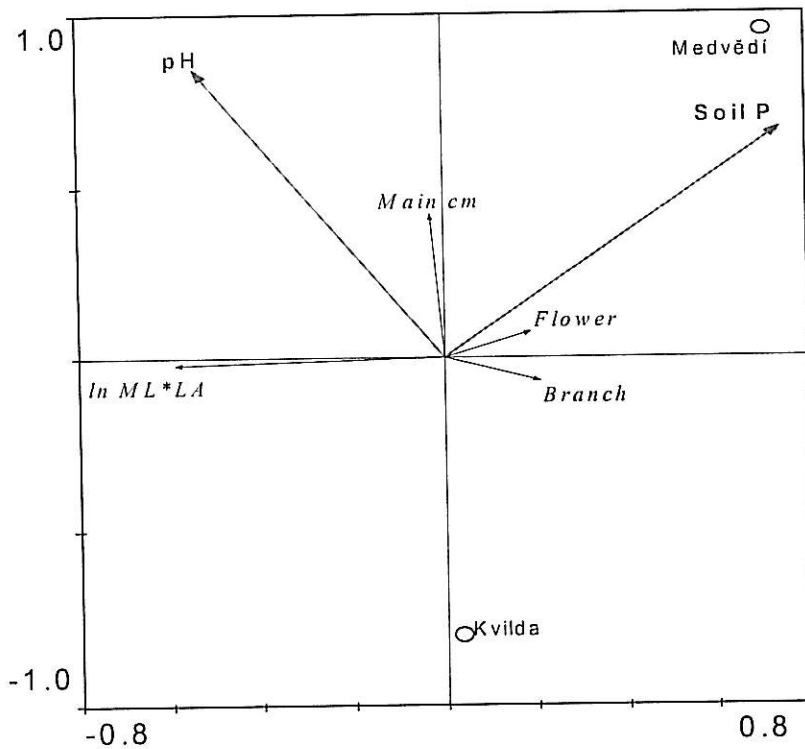
Fig. 6. The relation between abiotic conditions and growth characteristics of *P. palustris*. Growth characteristics were selected by forward selection, Monte Carlo permutation test (for pH, p = 0.082; for Soil P, p = 0.054). "Main cm" represents main stolon length; "ln ML*LA" is leaf number on main stolon multiplied by leaf area; "Branch" means proportion of growing stolons and "Flower" represents proportion of flowering stolons. The position of two extreme locations is represented by small circles.

On the other hand, the biotic characteristics of habitat seem to explain the variability in growth of *P. palustris* better (Fig. 7). Three different measures of vegetation density and height were used together with *Sphagnum* species cover (Height, p = 0.008; E1 cover, p = 0.038; Sphagnum, p = 0.05 and Biomass, p = 0.10). In a dense but low vegetation, the measured plants tend to flower more. On the contrary, in the tall but not very dense vegetation, *P. palustris* sems to invest more into vegetative growth and branching. Furthermore, tall dense vegetation promotes length increase rather than branching or flowering. Dominance of mosses negatively correlates with produced leaf area.
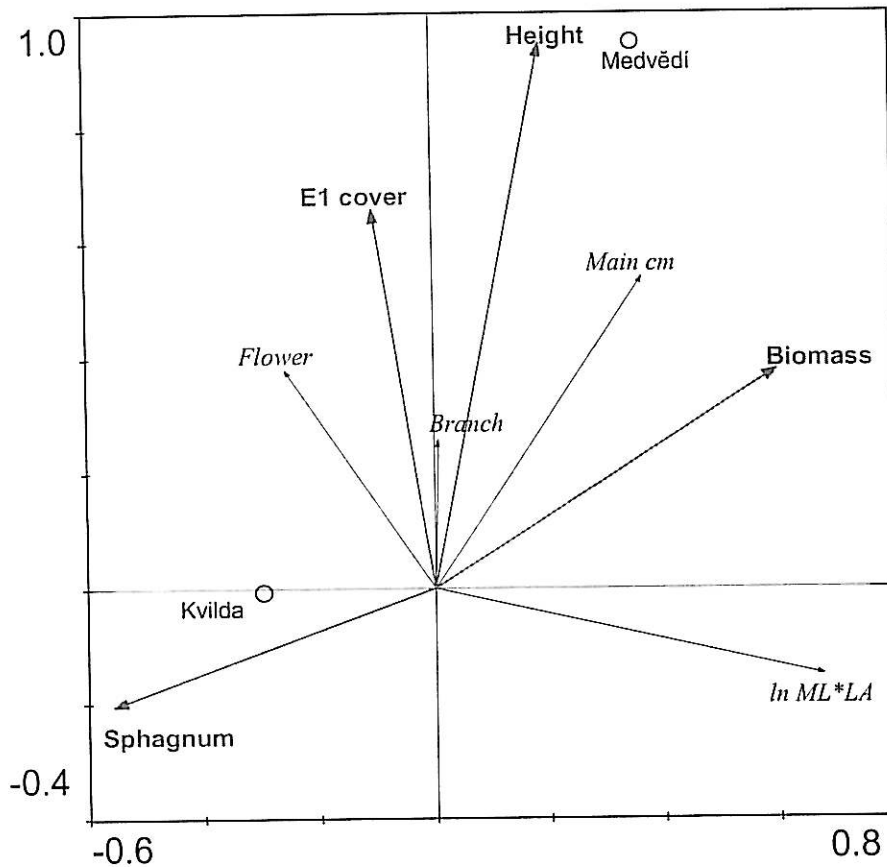
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Fig. 7. The relation between growth characteristics of *P. palustris* and biotic conditions described by RDA. Growth characteristics were selected by forward selection, Monte Carlo permutation test (p 0.05 except for Biomass, p = 0.10). "Sphagnum" means the percentage cover of moss layer; "E1 cover" represents percentage cover of herbaceous layer; "Height" is surrounding vegetation height and "Biomass" means biomass of surrounding vegetation excluded *P. palustris*. For the explanation of response variables see Fig. 6. The position of two extreme locations is represented by small circles.

Architecture of clone growth

Plants with damaged main stolons (terminated by death, grazing or flowering stem) had significantly greater branching than plants with unaffected main stolons (Fig. 8). Ratio of growing stolons to all stolons is determined by three probability measures: probability of death of internode (D), probability the internode is grazed (G) and probability the internode forms flowering stem (F), (Fig. 9). Probabilities were estimated as proportions of proportions of events within a plant. Stolon production (S) is given by regression equation (R^2 = 0.2; $p < 1*10^{-5}$).

$$S = 0.44 + 0.116*F - 0.37*D - 0.2*G \tag{1}$$

In this equation, the values for all plants were used.
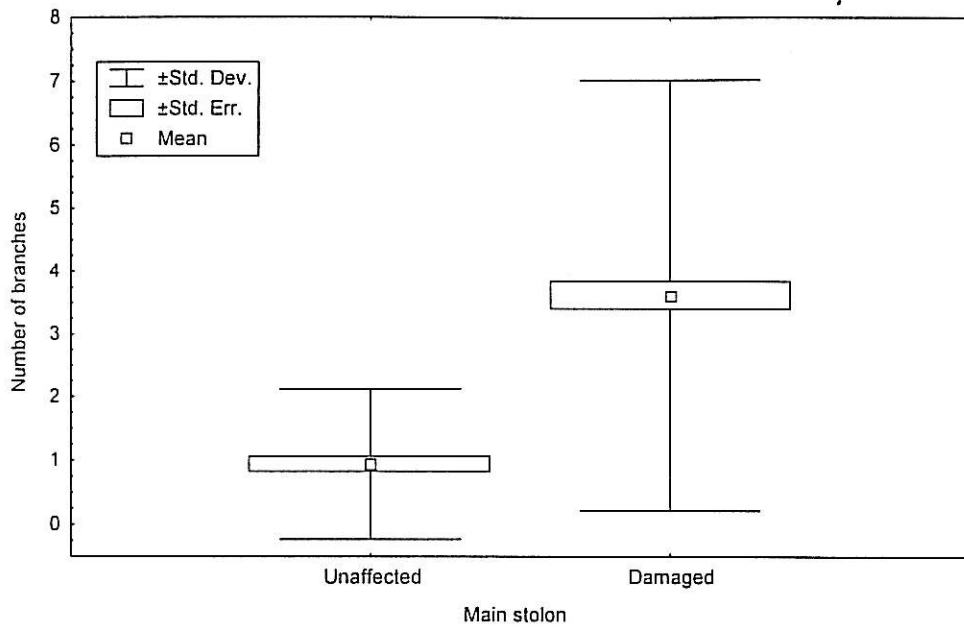
Fig. 8. The effect of main stolon status (damaged means either dead, grazed by herbivores or terminated by flowering) to branching in all plants from all locations. The difference is highly significant (df = 344; F = 63.2; p < $1*10^{-6}$).

Fig. 9. The proportion of growing stolons per one plant are visualized as multiple regression result of stolons damage status (see Equation 1). The three probabilities (each ranging from 0 to 1) of stolon to be grazed, become a flower or die, reach the maximal values at the three respective angles of the triangle. The null value of each probability is found at the triangle

basis opposite to the labeled angle. The proportion of growing stolons corresponds to the values shown at the scale aside from the triangle. The points represent the combination of recorded values.

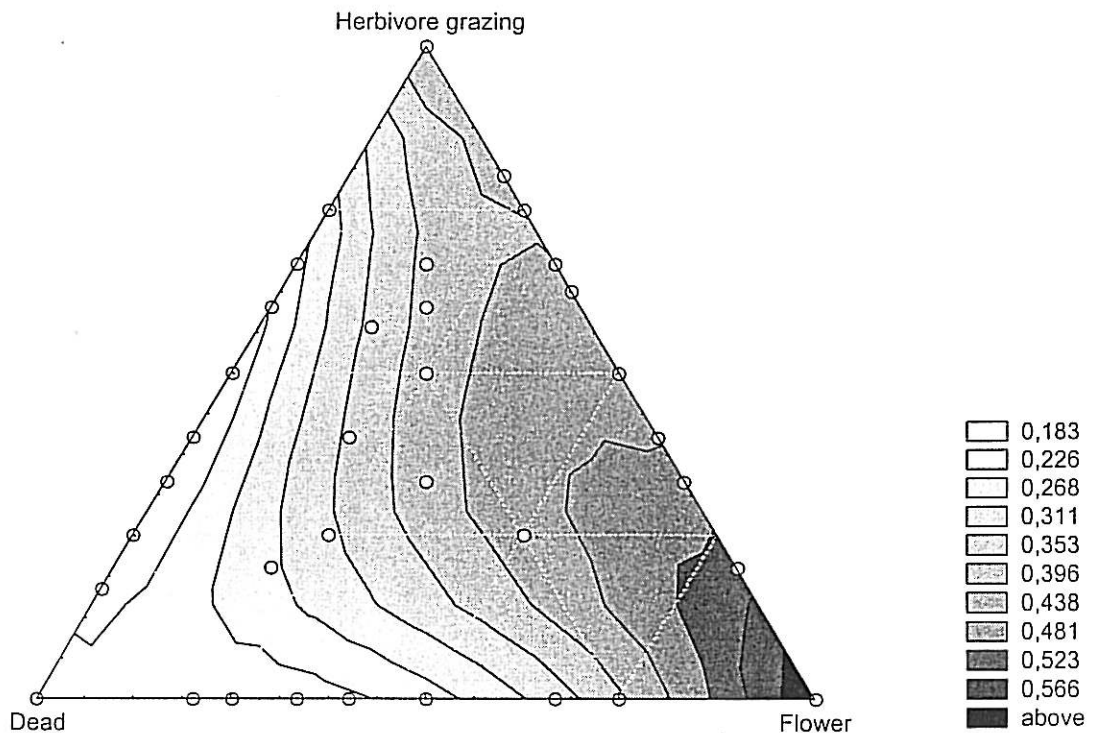Mean length (at each location) of the main stolon (L_m) is positively correlated with vegetation height (h) and water level (wd) at location ($R^2 = 0.42$; $p = 1*10^{-3}$) as follows

$$L_m = 122.6 + 0.54*h + 0.27*wd \qquad (2)$$

and also this length (L_m) is logically described by the number of internodes on the main stolon (N_i) and their mean length (M_i) in a regression equation ($R^2 = 0.94$; $p < 1*10^{-6}$) as

$$L_m = -323.2 + 0.586*N_i + 0.67*M_i \qquad (3)$$

The length of the main stolon is determined by both internode number and mean internode length. The correlation between internode number and internode length is very weak and the relation explains only 3% of the variability (data not shown). Mean annual production of internodes varies among locations between 8 and 11 internodes (ANOVA, F = 2.48, P < $1*10^{-4}$) among locations (Fig. 10).
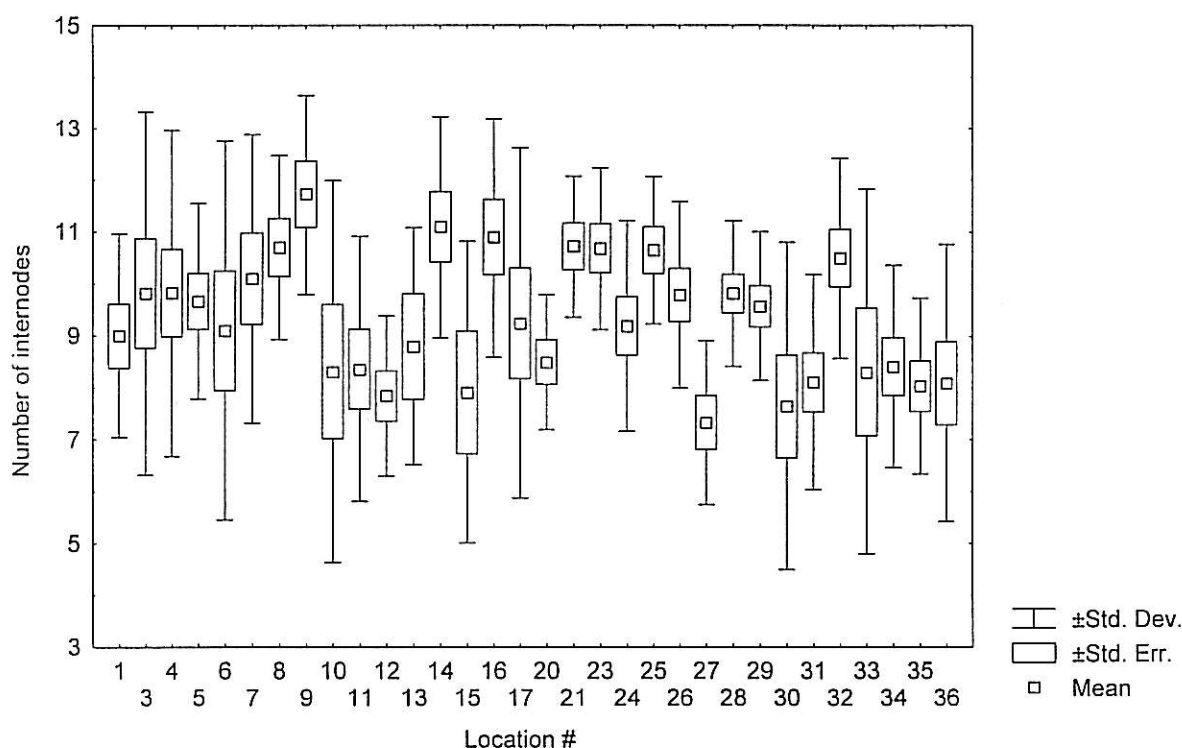
Fig. 10. The number of produced internodes on the main stolon per year at each location. Location characteristics are listed in Appendix 3.

Variability of mean internode length among locations is much higher (ANOVA, F = 7.48, p < $1*10^{-6}$) and ranges from 10 mm to 26 mm (Fig. 11). The photos of a typical

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representative stolons from two extreme locations "Medvědí" and "Kvilda" are shown in Appendix 6.
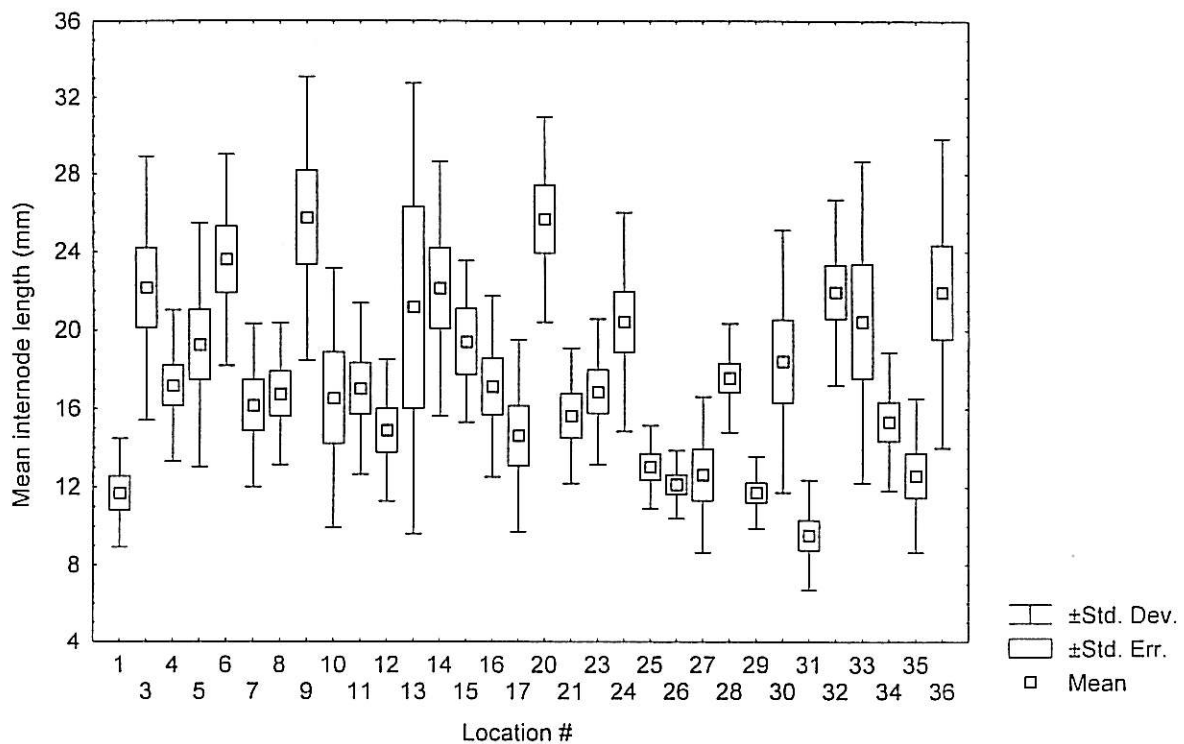
Fig. 11. The annual mean internode length of the main stolon at different locations. Location characteristics are listed in Appendix 3.

Seasonal variation

The same trend can be seen at both locations "Medvědí" and "Kvilda" where excavations were done (Fig. 12 and 13). Seasonal fluctuations in both variables are noticeable. However, mean internode length at location "Medvědí" is nearly twice as high as at location "Kvilda" which results in higher seasonal stolon length increase (Fig. 14). Investment into flower production is more constant in time at both locations. For significance of inter-seasonal differences at both locations see Table 1. Differences between both locations and also differences between excavation data and seasonal measurement of labeled plants during year 2002 are summarized in Table 2.

Fig. 12. The number of internodes from excavated plants at two extreme locations, "Kvilda" (Kvi ex) and "Medvedí" (Med ex), in the period of 7 and 5 years respectively. At the year 2002, the values from periodical measurements of plants at these two locations (Kvi 2002, Med 2002) were added for comparison. Symbol: Mean; Box: Mean-SE, Mean+SE; Whisker: Mean-SD, Mean+SD.
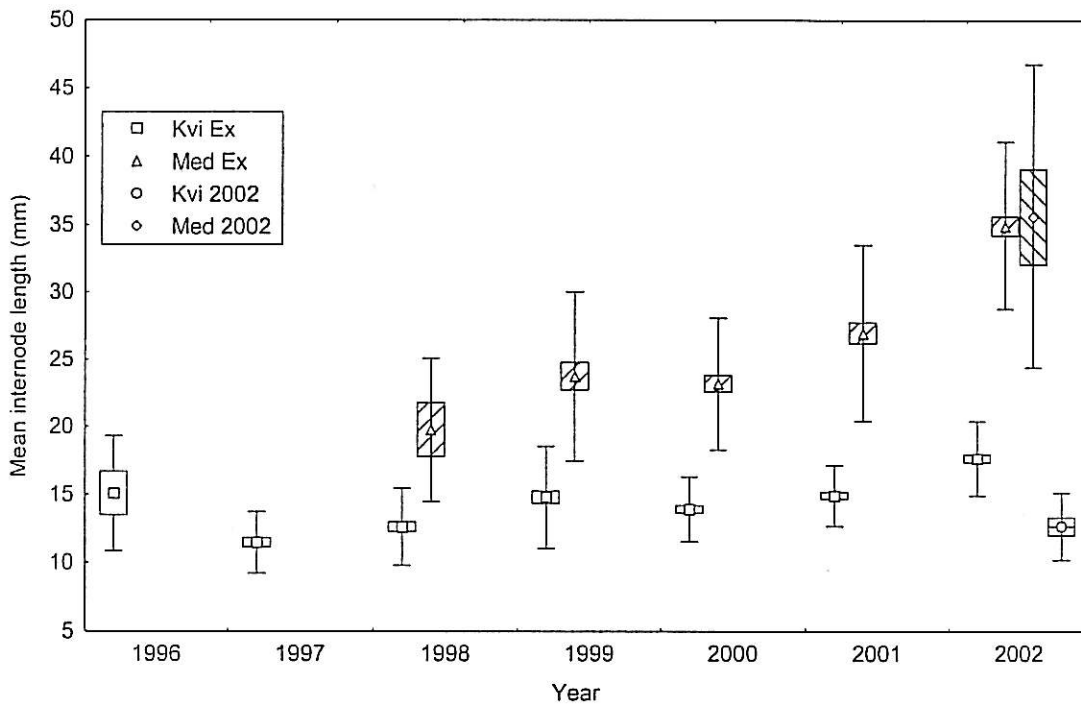
Fig. 13. The mean internode length from excavated plants at two extreme locations, "Kvilda"

(Kvi ex) and "Medvedi" (Med ex), in the period of 7 and 5 years respectively. At the year 2002, the values from periodical measurements of plants at these two locations (Kvi 2002, Med 2002) were added for comparison. Symbol: Mean; Box: Mean-SE, Mean+SE; Whisker: Mean-SD, Mean+SD.
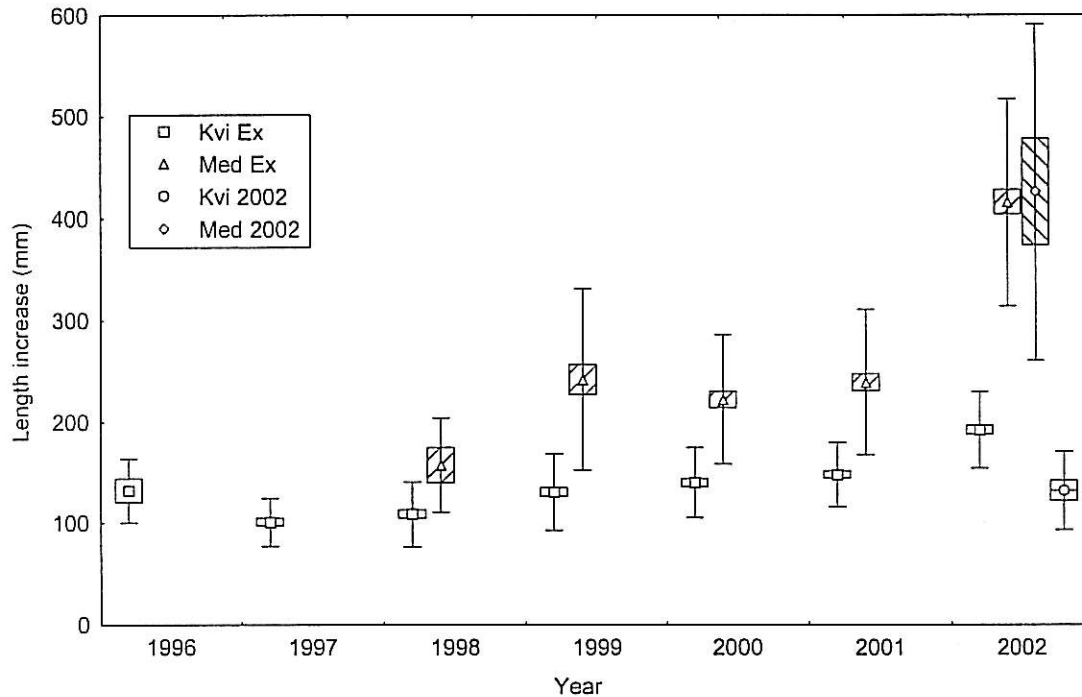
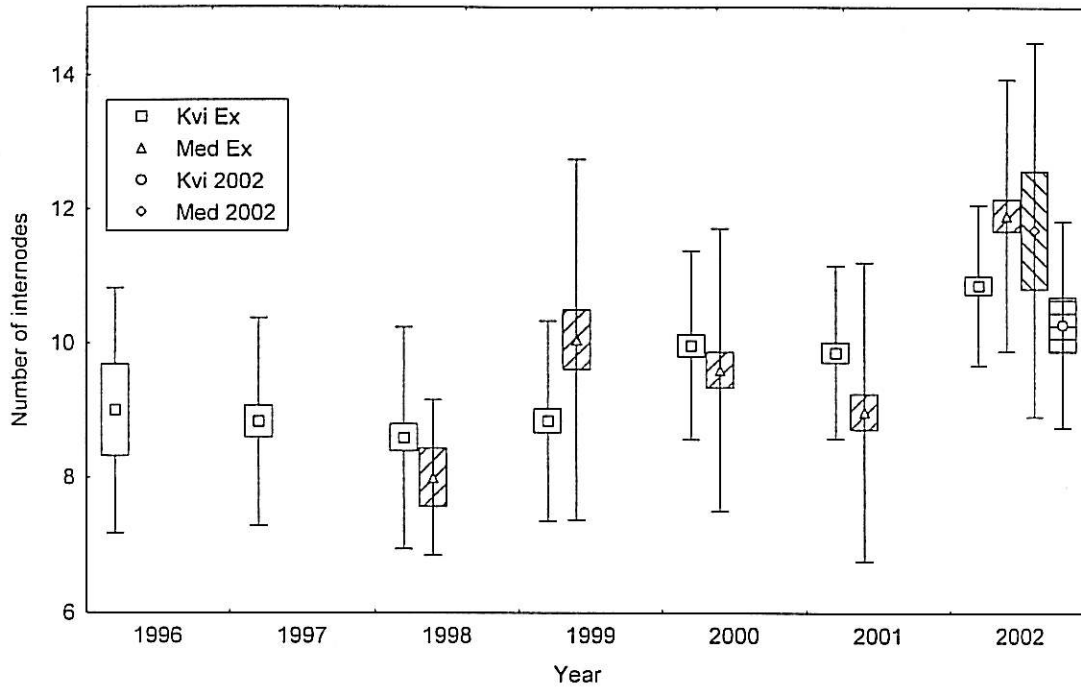Fig. 14. The total annual length increase of excavated plant stolons at two extreme locations, "Kvilda" (Kvi ex) and "Medvedi" (Med ex), in the period of 7 and 5 years respectively. At the year 2002, the values from periodical measurements of plants at these two locations (Kvi 2002, Med 2002) were added for comparison. Symbol: Mean; Box: Mean-SE, Mean+SE; Whisker: Mean-SD, Mean+SD.

Table 1.

The summarization of the differences in growth characteristics of *P. palustris* excavated stolons between locations "Medvědí" and "Kvilda" in the years 1999 - 2002. "p" are significance levels in the repeated measurement ANOVA.

No of flowering stolons	df Effect	MS Effect	df Error	MS Error	F	p
Location	1	0,00	105	0,12	0,0	0,871
Time	3	0,63	315	0,13	4,7	**0,003**
Location * Time	3	0,37	315	0,13	2,8	**0,042**
Length increase	df Effect	MS Effect	df Error	MS Error	F	p
Location	1	1255381,63	105	4593,58	273,3	**0,000**
Time	3	266319,09	315	2479,94	107,4	**0,000**
Location * Time	3	75121,55	315	2479,94	30,3	**0,000**
Mean internode length	df Effect	MS Effect	df Error	MS Error	F	p
Location	1	12288,12	105	26,33	466,7	**0,000**
Time	3	1011,99	315	15,39	65,8	**0,000**
Location * Time	3	280,62	315	15,39	18,2	**0,000**
No of internodes	df Effect	MS Effect	df Error	MS Error	F	p
Location	1	0,03	105	4,21	0,0	0,929
Time	3	75,51	315	2,44	30,9	**0,000**
Location * Time	3	31,28	315	2,44	12,8	**0,000**

Table 2.

Significance of differences in the growth characteristics of excavated stolons between locations "Medvědí" and "Kvilda" for each year. The table also summarizes differences in the growth characteristics between excavation data and seasonal measurement of labeled plants during the year 2002 (rows labeled location 2002). Significance levels for each performed t-test are showed.

Measured characteristic	Compared locations / Year	2003	2002	2001	2000	1999	1998
Mean internode length	"Medvědí" vs. "Kvilda"		$< 1*10^{-6}$	$< 1*10^{-6}$	$< 1*10^{-6}$		$< 1*10^{-6}$
	"Medvědí" 2002		0,709				
	"Kvilda" 2002		$< 1*10^{-3}$				
Number of internodes	"Medvědí" vs. "Kvilda"		$< 1*10^{-3}$	0,004	0,235	0,003	0,358
	"Medvědí" 2002		0,678				
	"Kvilda" 2002		0,364				
Main stolon length	"Medvědí" vs. "Kvilda"		$< 1*10^{-6}$	$< 1*10^{-6}$	$< 1*10^{-6}$	$< 1*10^{-6}$	0,001
	"Medvědí" 2002		0,714				
	"Kvilda" 2002		0,001				
Flowering stems	"Medvědí" vs. "Kvilda"	0,208	0,483	0,010	1,000	0,324	
	"Medvědí" 2002		0,371				
	"Kvilda" 2002		0,046				

Both locations show sinusoidal periodicity with similar number of internodes (9.2) in one period. The shortest internodes at both localities are 4 mm long, the longest reach 35 mm at "Kvilda" location as compared to 79 mm at location "Medvědí". Seasonal measurements of labeled plant stolon increments confirmed that the smallest increments usually occur at the beginning and at the end of a growing season. Furthermore the flowering of the main stolon causes very short internodia even within a growing season. A stolon from "Medvědí" location represents only four complete seasons and measures 1264 mm (Fig. 15) comparing to stolon from "Kvilda" location that represents five complete seasons but measures 843 mm only (Fig. 16).
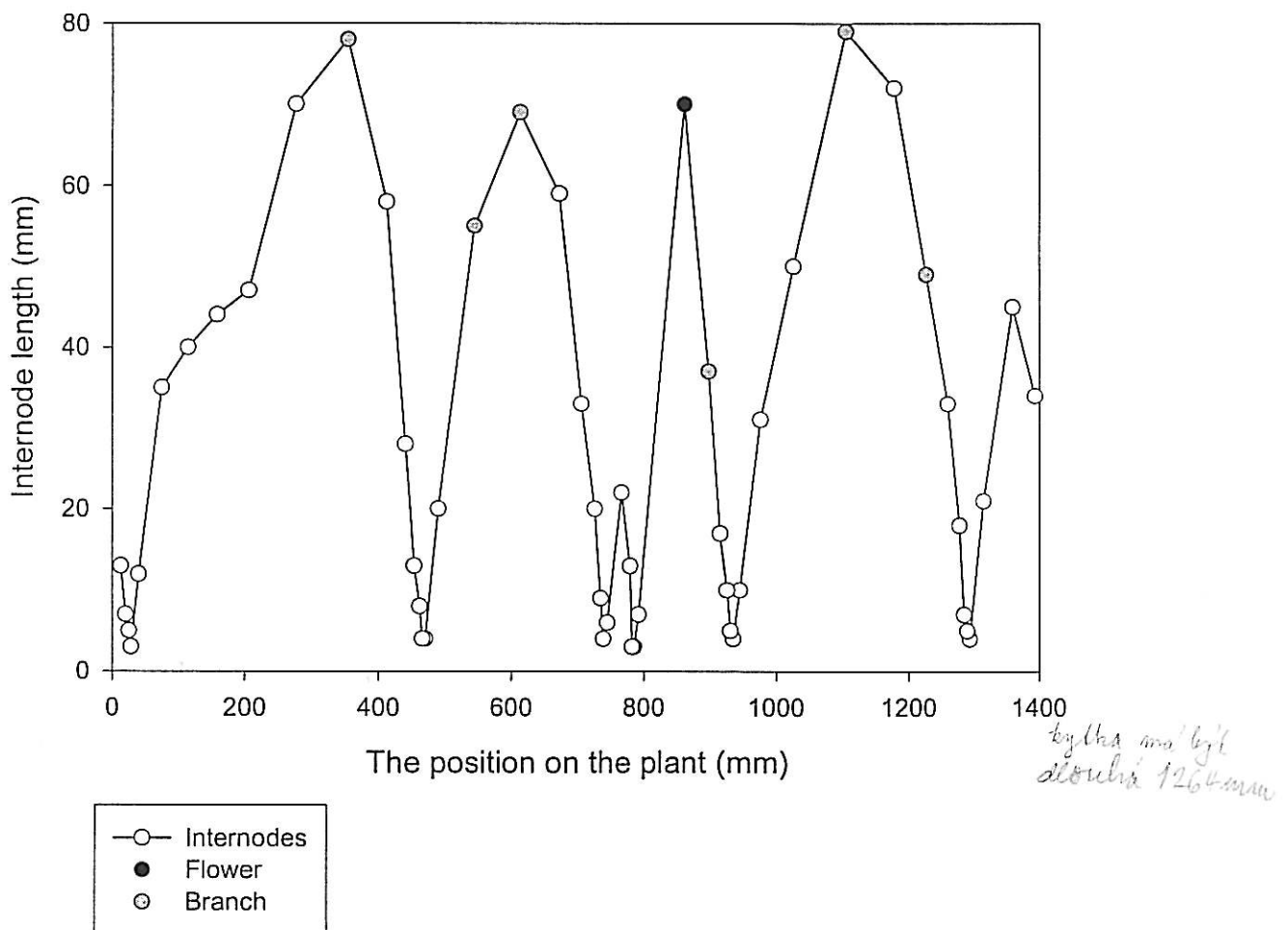
Fig. 15. The seasonal variation in internode length on location "Medvědí". The position on the plant is a distance of internode from the stolon tip. Note the different scales at both X and Y axes at Fig. 15 and Fig. 16.
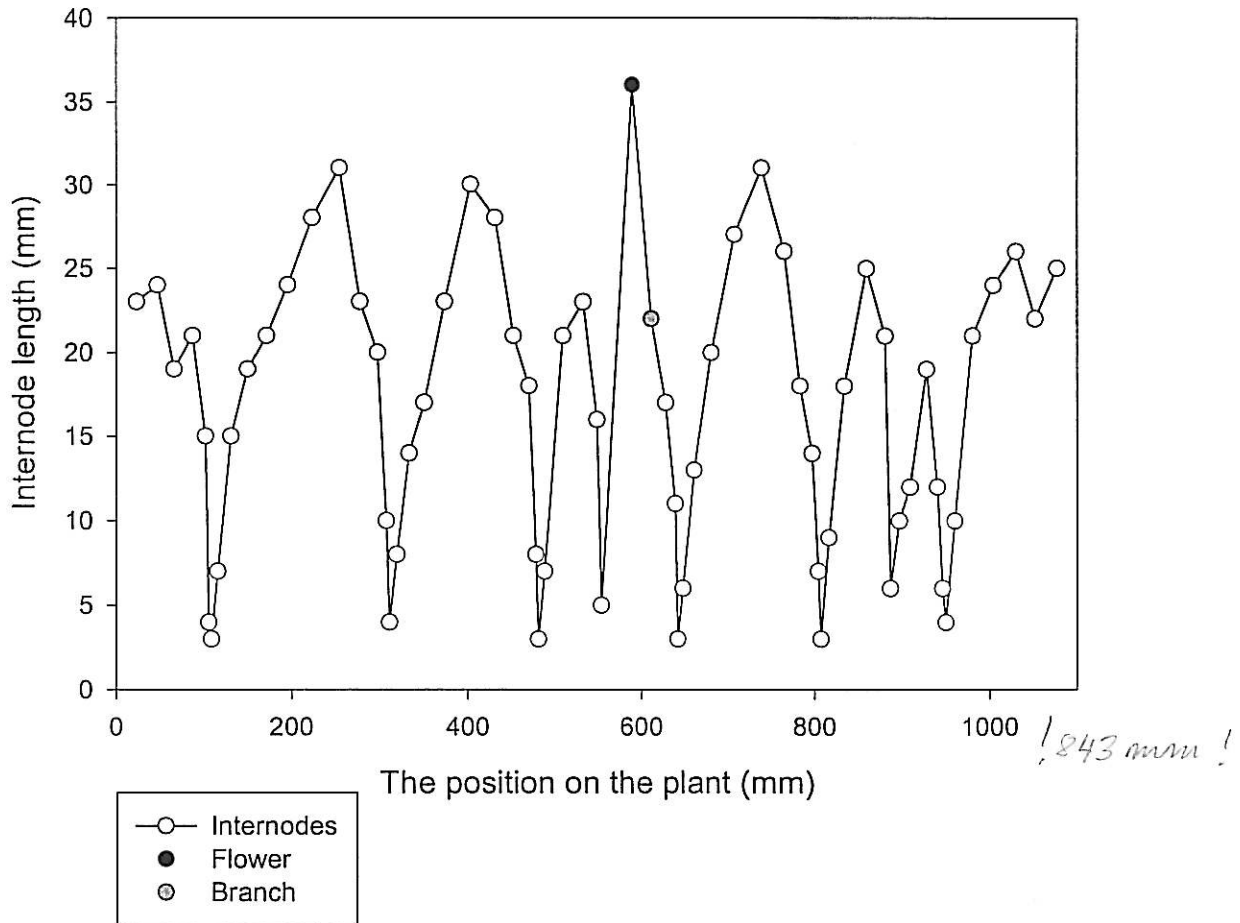
Fig. 16. The seasonal variation in internode length on location "Kvilda". The position on the plant is a distance of internode from the stolon tip. Note the different scales at both X and Y axes at Fig. 15 and Fig. 16.

The addition of fertilizer has significant positive effect on all measured growth characteristics (Table 3).

Table 3.

The t-test results showing the effect of fertilizer addition on measured growth characteristics. "p" are atteined significance levels.

	Mean Unfertilized	Mean Fertilized	df	p
Stolon length (mm)	94.4	147.6	16	0.016
Produced internodes	5.4	6.9	16	0.037
Mean internode length (mm)	14.6	19.5	16	0.023
Leaf area (cm^2)	17.6	22.6	16	0.002

Single plant growth simulations

Simulations of plant growth from different locations show mean prognoses of a single plant growth in future 15 years at each location. Plants at both "Medvědí" and "Kvilda" locations survived (Table 4).

Table 4.

The summarization of the results from 15 year clone growth simulations for plants at locations "Medvědí" and "Kvilda". The results from the excavation at location # 21 "Řásnice" are added for comparison. "na" means values not available.

	Medvědí	Kvilda	Řásnice
Age (years)	15	15	22
Produced internodes	1026	341	1500
Produced branches	86	9	84
Growing branches (alive)	20	5	16
Total plant length (m)	27.683	5.111	23.78
Most distant growing branches (m)	2.5	1.8	na
Clone extent (m)	3.7	2.0	3.6
Survival probability	0.235	0.767	na
Produced pseudo-individuals	10	4	10
Potentially covered area (m^2)	10.7	3.1	10.2

The typical plant representatives based on the mean values from the 3000 simulations for both locations, were then selected for visualization (Fig. 17 and Fig. 18). The growth of a plant at location "Medvědí" is much more vigorous, the plant is densely branched and the clone is extensive (Fig. 17). The simulated plant produced 1026 internodes and 86 branches on average, of which 20 were still growing.
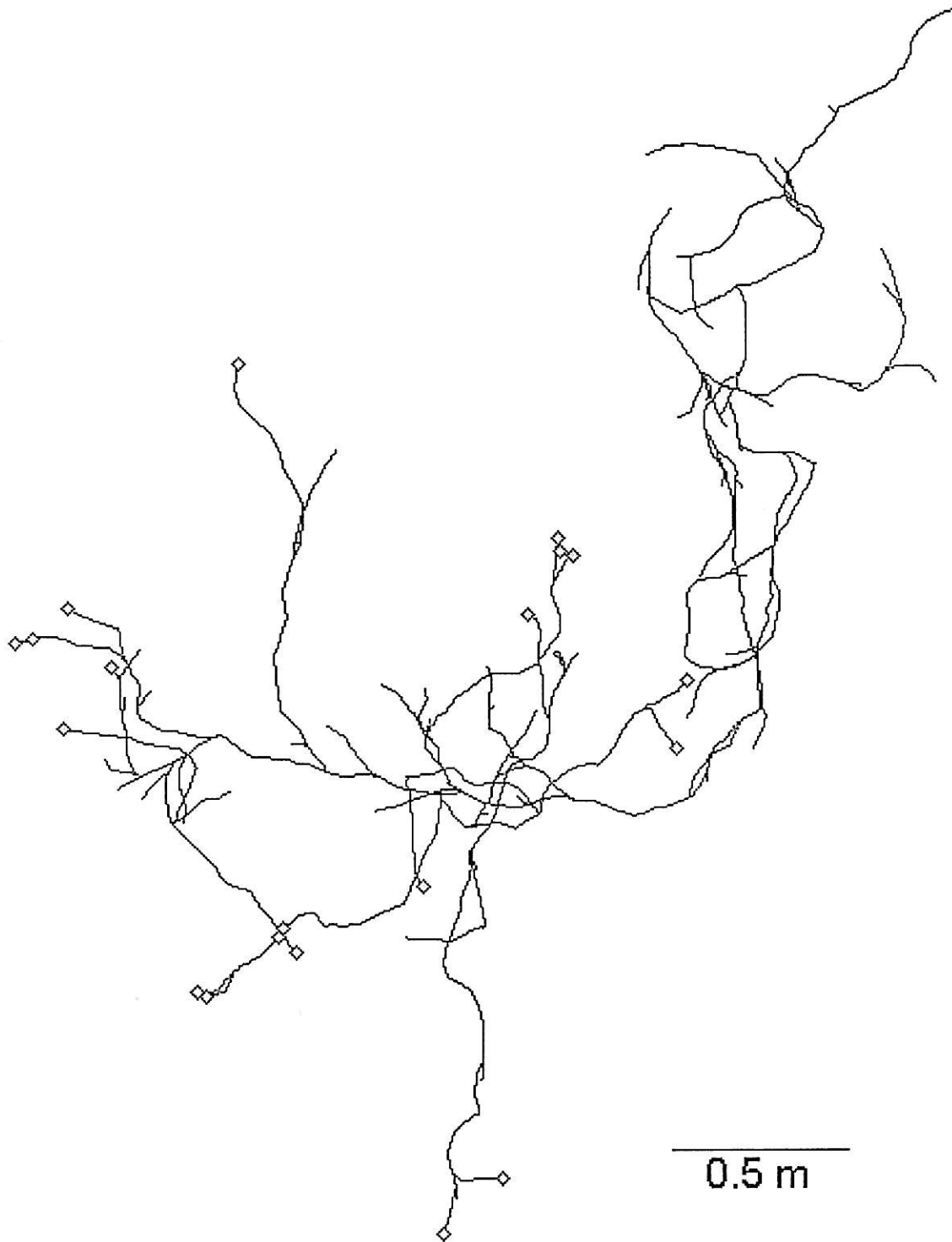
Fig. 17. The results of 15 year simulations of growth of the single clone. Growth parameters were estimated based on the field measurements on the location "Medvědí". The squared stolon tips represent living stolon. Note the different scales for Fig. 17 and Fig. 18.

At the opposite end of productivity lies the typical simulated plant from "Kvilda" location with 341 internodes, 9 branches, and only four of them are still alive (Fig. 18).
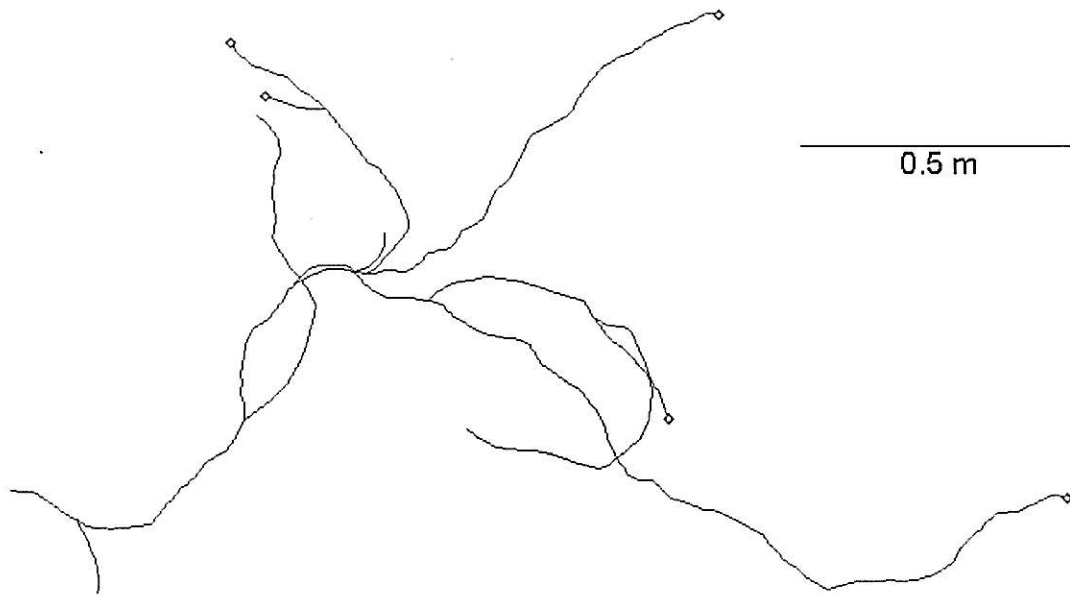
Fig. 18. The results of 15 year simulations of growth of the single clone. Growth parameters were estimated based on the field measurements on the location "Kvilda". The squared stolon tips represent living stolon. Note the different scales for Fig. 17 and Fig. 18.

Excavation of large *P. palustris* clones at location # 21 "Řásnice" provided two extensive clones, the larger one was 3.5 m long (Fig. 19).
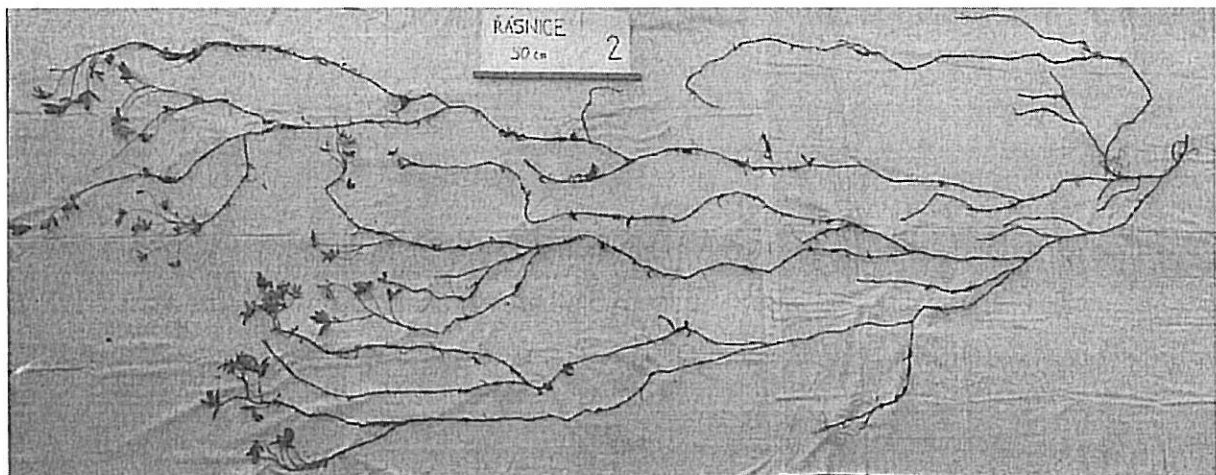
Fig. 19. The photo of excavated part of the clone from the location # 21 accomplished in June 2002. The scale bar at the figure is 50 cm long.

The larger clone consisted of 97 branches (16 of them alive) and from seasonal plant measures at this location the age was determined to be 22 years (Table 4).

Discussion

A general pattern in vegetation diversity and species richness follows the gradient of pH, sites with low levels of pH are relatively species poor (Peet et al. 2003, Tyler 2003). In peatlands with lower levels of pH and Ca content this trend is also noticeable and maximal species richness is found at moderate pH between 5 and 6 (Chytrý et al. 2003, Schuster & Diekmann 2003). The pH of the locations in this study ranged from 3.5 to 6.1 and number of recorded species significantly increased with pH. As the transitional fens were located predominantly at higher altitudes in this study, the number of recorded species decreased with the altitudinal gradient as well. The primary production in fens, similarly to species richness, decreases toward low values of pH, as reported by (Aerts et al. 1999), probably because of high toxicity of phenolic compounds limiting plant growth.

A second limiting factor is water saturation and consequently anoxic conditions in peat. Numerous plants are not capable to withstand toxic conditions after oxygen depletion in the soil (Brändle et al. 1996, Crawford 1996). In addition to high acidity, anoxia is a very strong limitation for plant growth. *Potentilla palustris*, a hydrophile species growing in a wide range of habitats, is well adapted to variation in both above mentioned factors.

Although the correlation between abiotic factors (e.g. light, nutrients, water level and pH) and growth characteristics of *P. palustris* was expected, the RDA did not reveal close relationships. The correlations were weak and non-significant. At the other hand, the nutrient content in soil influences the biotic factors (e.g. *Sphagnum* cover, vegetation cover, vegetation height and biomass) and these correlate well with growth characteristics of *P. palustris*. It seems the abiotic factors have an indirect effect on the growth of *P. palustris*. It is evident that physiognomy of the vegetation, namely vegetation height and density, explained the growth of *P. palustris* much better. Similarly, in many wetlands, plant mediated effects overrule the direct abiotic effects (Aerts et al. 1999). The exact species composition seem to be less important than vegetation physiognomy. This is in agreement with the equivalence of competitors hypothesis (Goldberg & Werner 1983).

Four main vegetation types with occurrence of *P. palustris* were distinguished for Czech Republic and similarly for my locations, but the species may be occasionally found in the other types also. First habitat type, mesotrophic to oligotrophic wet meadows ("A") experiences relatively low level of irradiance inside the vegetation. As altitude was highly correlated with irradiance, the meadows in my set that occur at lower altitudes, may experience light limitation. Without nutrient limitation, the vegetation height and biomass may increase and light becomes a strong limiting factor (Lepš 1999). However, without experimental testing the effect of individual factors (in this case not only nutrient and light),

deciding which factor is more limiting will be just a speculation. In the case of sites located within Šumava National Park, large experiments altering natural conditions would not be possible. The preliminary nutrient enrichment experiment had shown that nutrients are also limiting in such environment. The nutrient addition enhanced the growth of *P. palustris*, specifically it promoted growth of internode length and leaf area.

The conditions in the second vegetation type, alluvial ("C"), are probably similarly strongly limited by light. *Potentilla palustris* responded to lower light availability in both meadows and alluvial by slowing down the turnover of produced leaves and increasing the leaf area. Clonal plants behave differently from non clonal plants under shortage of resources in heterogeneous conditions. Non clonal plant always tends to invest more into resource acquiring organs for obtaining the scarce resource. Clonal plant possessing functional connection among ramets may afford to have "specialized" ramets, each of them producing mainly organs for obtaining the locally abundant resource (Alpert & Stuefer 1997, Price & Marshall 1999). The "division of labor" reported for various plant species (Alpert & Stuefer 1997, Charpentier & Stuefer 1999), however assume that the habitat is heterogeneous. When habitat is heterogeneous, but the distances between patches with suitable conditions are too high for transportation between ramets, the "division of labor" strategy is not efficient. Under those conditions, as well as in homogeneous conditions, the resource transportation is less advantageous than functional specialization of the ramet to scarce resource acquisition. Dense vegetation of meadows and alluvia has homogeneously low light levels. The clonal plant is, therefore, behaving similarly to a non clonal plant there, i.e., it increases its leaf area.

Besides nutrients and light, the growth of the plant can be also limited by water availability. Organic matter is able to retain a significant portion of water in the soil. In meadows, organic matter is rapidly decomposed and soils, if not flooded or fed by precipitation, may even dry out during the vegetation season.

On the contrary, in the alluvia and edges of water bodies habitat, where the groundwater is usually not deep below the soil surface, the limiting factor might again be light. Such species as *Lysimachia vulgaris*, *Phragmites australis* and *Carex acutiformis* present in alluvial habitat, formed taller and denser vegetation. The plant community was highly productive and therefore competition for light was probably very strong under dense biomass of tall graminoid species. The *P. palustris* plants in alluvia had two distinctly different growth forms: first, where the open water occured, the plant were very branched, some plants even formed the dense layer of overlaying interweaved rhizomes (e.g. at the locations # 6, 13 and 14). The opposite growth type was exhibited at sites with dense vegetation where stolons were unbranched, often with long internodes as at locations # 9, 12

and 21. In such conditions, the plants tend to escape by investing in linear unbranched growth (comp. Hutchings & Bradbury 1986, Routledge 1990).

The habitat with vegetation type "B", was represented only by one location (# 23). The soil was water saturated and contains high portion of organic matter. The N/P ratio revealed strong N limitation. The phosphorus content in plant tissue was the highest of all locations and nitrogen level was moderate. The growth was, however, not faster than in other locations, which implies that *P. palustris* was accumulating nutrients, without further growth response. Aboveground vegetation biomass, represented especially by *Sphagnum* species, was not high and did not impose the light limitation to other plants. The growth limitation might be caused by strong intraspecific competition in monodominant stand of *P. palustris* – thus limiting the vegetation height and irradiance itself. In such monospecific stands with relatively favorable conditions, the stolons were only moderately branched. Intraspecific competition is size independent and of symmetric mode (de Kroon et al. 1992). Therefore, there is a relatively greater possibility of growth for smaller shoots than for larger ones. The intermediate growth is thus an expected feature at monodominant stands (Hara 1994).

The last major habitat where *P. palustris* grows, transitional fens ("D"), had the optimum at higher altitudes of Šumava Mts., where precipitation is abundant. Water supply of these locations is also enhanced by usually nearby flowing water and consequently the soil rarely desicates. A nutrient N to P ratios indicated N limitation, but the values of N and P in plants were intermediately high. As the nutrients are predominantly incorporated in organic material, it is possible that they are efficiently recycled from senescing leaves of living plants. As reported by (Aerts et al. 1999), the nutrient flux through internal cycling exceeds external input by far. In addition, the plants from fens have higher nutrient use efficiency especially of P than species from other habitats and the nutrient resorption may be even less costly than obtaining nutrients from soil (Bedford et al. 1999). Nutrient resorption is not dependent on soil nutrient availability (Aerts 1996), which explains higher variability of nutrient content in peatland soils comparing to more stable values in plant tissue.

The irradiance under the sparse and low vegetation of transitional fens, represented by species *Carex lasiocarpa*, *Eriophorum angustifolium* and *Oxycoccus palustris* was much higher compared to other locations. It seems that at the fen habitat, the resource levels of nutrients, light and water were moderate to high and major limitation should be of other origin. As mentioned above, fens occur at the soils with low pH levels. The phenolic compounds present at highly acid sites, possibly prevent the optimal plant growth. *P. palustris* growth form was more condensed there (lower total length), with lower to intermediate stolon branching probability. The typical example of such environment include also location # 25, "Kvilda".

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The trend to invest resources in linear growth and therefore escape from tall dense stands was already suggested above. But in addition to this, branching probability was also higher at some locations with high vegetation. One explanation of enhanced both branching and linear growth may be similar to Roff's (1992): the vigorous plants do everything well. Furthermore, the stressful conditions of high vegetation enhanced not only keeping the leaves alive rather than reuse the nutrients from them, but also augmented the leaf size, both contributing to catch more of the remaining light inside high biomass of neighboring species. Higher leaf area may be also the compensation for lower photosynthetic activity of leaves growing in shade as in the case of *Calamagrostis canadensis* (comp. MacDonald & Lieffers 1993). In the case of *Potentilla anglica*, the reduced light availability did not enhance the leaf area, but petiole length increased (Huber 1995). This response type would not be probably of any use for *P. palustris* individuals, because the distance between the vegetation canopy and stolons of *P. palustris* is usually too high to reach more advantageous position by petiole elongation.

Any type of termination of the apical meristem has an impact on a plant growth form. Either the plant will die out or it will ramify its stem and it will continue its growth via lateral branches. In this study, three types of meristem termination were distinguished: death, herbivore grazing and flowering. When at least one of these types occurs, the plant had significantly higher branching than unaffected plants. It was a response of lateral meristems to lowering of auxin production.

Flowering has been shown to reduce the growth, as the energy is temporally allocated to sexual reproduction (Bouzillé et al. 1997). It may be true in a case of single ramet, but in the case of whole plant the opposite trend was revealed here. Contrary to other studies, where flowering reduced number of newly produced shoots (Carlsson & Callaghan 1990), *P. palustris* responded by increasing branching after flowering.

Similar effect was expected in response to herbivory, which is known to often dramatically change the plant form (Huntly 1991). The effect was however not so strong, most probably because herbivores removed noticeable part of the plant and also resources.

The death of the main stolon was of the lowest importance for new branching. The death usually happened as a consequence of the whole plant being in bad shape. In most cases, the plants had no resources to produce new branches close to the dying terminal meristem. In some cases, the death was caused by some external factor, such as flooding or local litter accumulation. If the plants were vigorous, they increased their branching afterwards as well.

In general, *P. palustris* quickly replaces single lost ramets by activating dormant meristems and branch formation (comp. Kenkel 1995). In contrast, the foraging theory regards branching to be a response to the increase of nutrients or light in good patches (de

Kroon & Hutchings 1995, Salemaa & Risto 2002). But those explanations are not mutually exclusive, and most probably, both occur in natural heterogeneous conditions.

Producing both flowering stems and branches together necessary results in trade off where to invest the energy. The quantity of ramets assure lowering of the genet death risk (Eriksson 1993), but any successfully established seedling lowers the extinction risk of whole population. The successful seedling establishment postulates recruitment at a good time and at a good site, conditions not frequently met. Plants compensate for low seedling establishment probability by high fecundity and seed dispersal ability (Eriksson 1993).

Many species, including *P. palustris*, have very limited seedling establishment in sites with dense vegetation, and particularly moss cover (Keizer et al. 1985, Špačková et al. 1998) and therefore their survival there must be attained by clonal growth. Nevertheless, the monodominant stands of some highly clonal plants, (e.g. *Rumex alpinus*), surprisingly originate from numerous successful seedling establishments (Klimeš 1992).

Although *P. palustris* has moderate seed production, seedling establishment was hardly observed at any location. It seems to be dependent on habitat type and the extent of eventual disturbance. If disturbance is small, vegetative growth is usually sufficient to cover the free space, but as disturbance gets bigger, clonal growth can not efficiently exploit the patch. Sexual reproduction becomes advantageous if disturbance patch is large and especially also distant from original site (Erikson 1992, Winkler & Fisher 1999).

Numerous seedlings of *P. palustris* were observed at a site where large patches without vegetation were formed by water fluctuation (Velké Dářko, Štech, pers. comm.), but their survival was very reduced by rising water (pers. obs.). But even such low seed establishment is of a great importance for maintaining the genetic diversity of a population and also it could be important in maintaining the metapopulation under changing environment (Eriksson 1993, Nishitani et al. 1999).

The different habitat conditions caused the plastic response of *P. palustris* main stolon length. The variability in internode length between locations was found to be much higher than the variability in internodes produced over growing season. The plastic response in internode length to diverse environment was also reported for *Maianthemum bifolium* (D'Hertefeldt & Jónsdóttir 1994). On the contrary, in other studies, the response in internode lengths of both *Potentilla anglica* and *Potentilla anserina* was more intermediate in different habitats, suggesting the rigid type of growth (Eriksson 1986, Huber 1995 respectively).

The production of an internode is probably of high costs, because the leaf and roots are also formed. Such production of biomass is also time demanding. The increase in internode number thus results in lower growth rate comparing to the production of small number of longer internodes. The longer stolon formation was mainly caused by internode elongation, which enhances its mobility under inconvenient conditions. Nevertheless,

Oborny's computer simulation found the internode elongation being never favorable, except in the case of intraclonal competition (Oborny 1994). This strong intraclonal competition was also the case of some locations with monodominant stands in my study.

The location "Medvědí" differed highly in annual stolon length increase from location "Kvilda" at each of the analyzed year. In addition, within each location, the annual increase also differed, which was, in fact, caused by outstanding increases in the year 2002. This year was exceptional in the amount of precipitation that reached 377.1 mm in Šumava Mts. during the month of August (data from meteorological station Horská Kvilda, Czech Hydrometeorological Institute). This exceptional stolon increase was a result of internode number increase and internode elongation together at both locations. Except the year 2002, the mean internode length stayed more homogeneous with minor fluctuations over years, but it differed between the locations. On the contrary, the number of internodes was similar at both locations with resembling trends in fluctuations. Again, the results from excavation measurements supported the theory of annual internode production similarity contrary to variability in internode length across the habitats. Major weather fluctuations may also affect internode production yet.

Relatively similar flowering activity at both locations might be caused by low investment into flowers under these conditions, but the annual variability in flower production might respond to weather fluctuation in opposite way than investment in vegetative growth. Similar seasonal variation in flowering was reported for *Carex bigelowii* (Carlsson and Callaghan 1990).

Seasonal measurements at different locations revealed that the short internodes are formed not only between two growing seasons, but are also found after flowering and consecutive branch formation. This feature is very important for "reading" the plant life history from internode sequences. The selected plants from both locations strongly differed in growth pattern, which resulted in different exploration habit of the surrounding environment. Contrary to Marshall & Price (1997), who suggested exploratory activity of individual stolon axes to be irrespective of local conditions, my measurements revealed plasticity in internode length and to less extent in internode number in response to the environmental conditions. But the branching pattern, as may be noticed in simulated plants, was also very responsive to different environment.

The solitary clone model is useful to study the lateral expansion of a clone without taking into account biotic conditions (Oborny & Cain 1997). I believe it is strongly dependent on the available data; if data are taken in natural conditions where density dependence and competition are affecting plant growth, the plant response is therefore included in the model. Simulated plants then behave as under natural conditions, but the neighboring individuals are not shown at the model. Simulated plants, especially these based on data from location

"Medvědí", behaved unrealistically when simulation took longer. It happened simply because the intraclonal competition and crowding overwhelmed the effects of interclonal and interspecific competitions. For these reasons, the simulations were restricted to 15 years only.

Simulated plants had greatly different total length, which was the result of difference in branching probability. On the other hand, death probability set in simulations was much higher for location "Medvědí" and the plants from there had short dead branches, which were not developed at the expense of others. This branching pattern resulted in the less than ¼ of living branches at location "Medvědí" comparing to more than ½ of living branches at location "Kvilda" at the end of 15 years simulation. The total simulated plant length (5 times higher at location "Medvědí") does not mean a lot, more important is a clone extent, which was roughly twice higher at location "Medvědí" than at location "Kvilda".

The growth positions at the end of simulations were best represented by the distances of the most remotely growing branches, which referred to the potential area covered by the clone. This area might be affected by branching angle, which is directing the stolon growth. The bigger the branching angle is, the easier is the 180° turn of the growth and potential cover of large areas (comp. Callaghan et al. 1986). Architectural pattern may also help place the ramets at a favorable places (Alpert 1995). Various species have greater branching angle (e.g. 60° for *Prunella vulgaris* and *Bellis perrenis*, Winkler & Schmid 1995). Comparing to these values, *P. palustris* had smaller branching angle around 30° at both locations, but the 180° turns still happened even in not highly branched location "Kvilda".

An interesting simulation outcome is also the number of "pseudo-individuals", the single ramet or groups of closely located ramets that would be in the field conditions considered as one plant individual (as the connections to other ramets in the clone is not easily observable). Surprisingly, if the growth will be allowed, the location "Kvilda" could accumulate more ramets per a 5m * 5m plot, but the time necessary for covering this area would be much longer than in location "Medvědí". If time since population establishment is sufficient, selecting several individual plants for field measurements may lead to partial selection of genetically identical individuals that might react to the environment similarly to each other. To found whether the population of one location is formed by single clone or more clones growing together would only be possible by molecular methods (see Pornon & Escaravage 1999).

Simulation model based on the field observations and field studies corresponded well to clone from natural conditions as was demonstrated by modeled plant comparison to excavated plant from location # 21. It showed that excavated plant had characteristics somewhat in between two simulated plants from extreme growth types, more close to location "Medvědí" in its extent and branch production, but 7 years older.

Conclusion

The stolons of *P. palustris* display growth variability irrespectively of general abiotic conditions, but the growth correlates well with physiognomy of the neighboring vegetation. The growth characteristics correspond well to the four main vegetation types, whereas the exact species composition of the community is less important. Branching was a stolon response to growth termination due to flowering or herbivory. The annual internode production across the habitats was more stable than the internode length, which exhibited high plasticity, nevertheless both were susceptible to fluctuations according to weather conditions. The short internodes were produced at both ends of the season and after branching. While it is not possible to assess the age of excavated stolons just from their absolute lengths, a reasonable estimate can be done by measuring the individual internodes along the stolon and reconstructing the seasonal dynamics over past years. Simulated plants corresponded well to the plants from natural conditions and simulations may be used to estimate medium term growth of *P. palustris* clones.

Acknowledgement

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Appendices:

Appendix 1

The area of distribution of species Potentilla palustris in the north hemisphere; (Hultén & Fries 1986).

Potentilla palustris
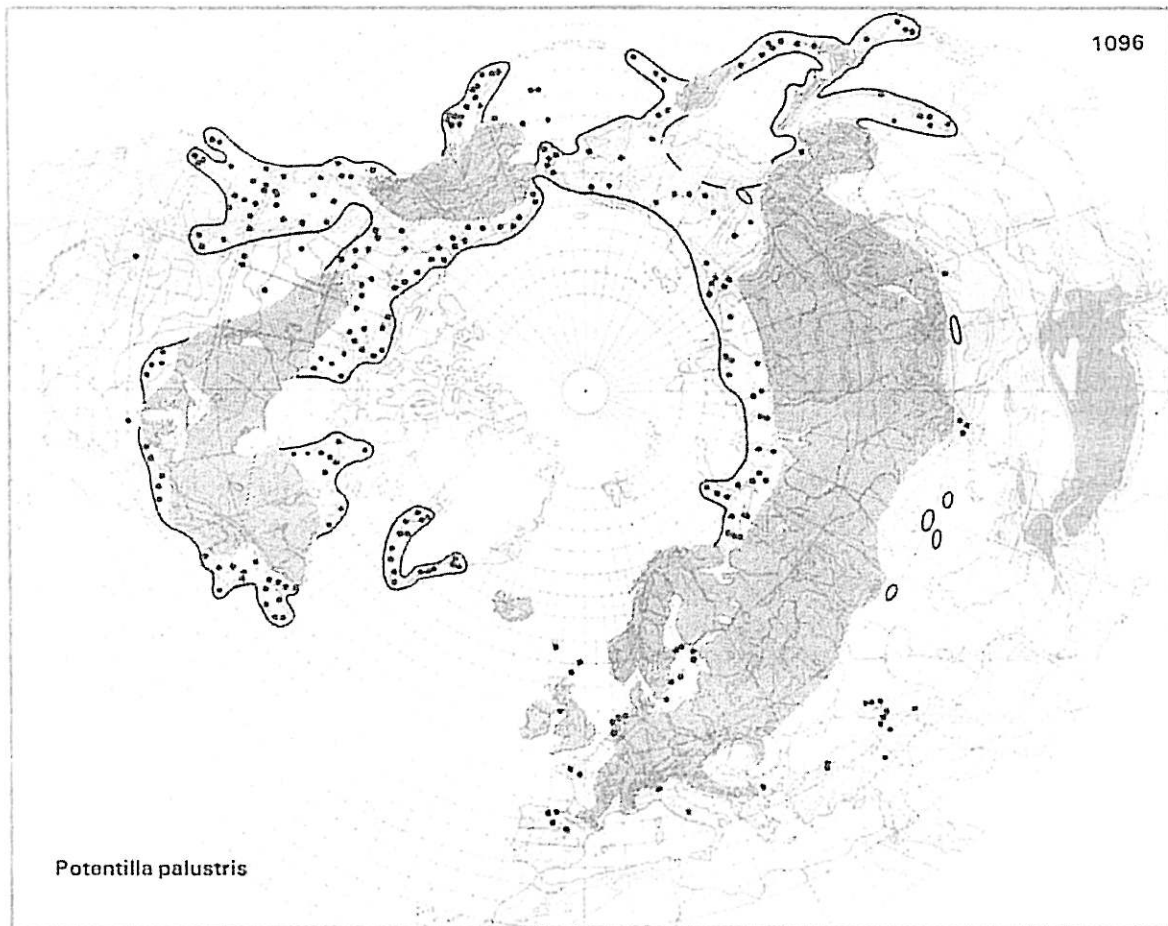
Appendix 2

The drawing of typical stolon of P. palustris selected for monitoring. Drawn by K. Houdková.

Appendix 3.

The list of locations, their geographical coordinates and altitudes. The mean values of all recorded variables at each location are also listed.

Location #		1	3	4	5	6	7
(North)	GPS position - Not included in analyses	48.71707	48.686111	48.68597	48.68783	48.68762	48.68639
(East)	GPS position - Not included in analyses	14.00789	14.060084	14.06149	14.03282	14.03313	14.03419
Altitude	Altitude (m a.s.l.)	770	725	725	735	735	735
Irradiance	Light intensity 5 cm above soil (%)	20,8	2,8	5,2	13,4	10,1	6,9
WD J	Water level in June 2002 (cm; soil surface = 0cm)	-9,5	-45	33	1	40	-15
pH	pH	3,8	5,9	5,9	4,8	5,7	5
Loss on ignition	Soil organic matter content (%)	90,2	33,1	49,3	87,6	83,9	19,9
H2O	Soil H2O content (%)	93	64	74	92	90	63
Soil N	Soil N content (%)	1,21	1,02	2,47	1,61	1,80	0,50
Soil P	Soil P content (%)	0,15	0,09	0,15	0,05	0,27	0,05
N ug/cm3	Soil available N (µg/cm3)	5,687	9,897	5,314	1,783	5,213	11,255
P ug/cm3	Soil available P (µg/cm3)	0,096	0,057	0,071	0,055	0,201	0,013
Biomass	Biomass of vegetation without P. palustris (g/0,1m2)	9,5	64,84	24,53	7,53	27,75	21,48
E1 cover	Cover of herbaceous layer (%)	55	65	85	60	60	95
Height	Height of vegetation (cm)	40	45	65	50	40	45
Sphagnum	Cover of Sphagnum species (%)	80	0	0	85	0	5
Tot cm	Total plant length including branch length (mm)	221	894	430	428	739	363
Tot me l	Plant mean internode length (mm)	11,4	20,7	16,1	17,6	18	14
Tot no l	Number of internodes on whole plant	19,4	43,3	26,7	24,3	41,2	25,8
Main cm	Main stolon length (mm)	209	447	348	360	440	339
Main me l	Main stolon mean internode length (mm)	11,7	22,2	17,2	19,3	23,6	16,2
Main no l	Number of internodes on main stolon	18	19,6	19,6	19,3	18,2	20,2
Main L	Number of leaves on main stolon	0,5	3,7	1,4	1,1	1,7	3,2
ln ML*LA	ln (Leaves on main stolon * Leaf area)	2,62	5,42	3,46	3,67	4,32	4,09
Flower	Number of flowers per flowering plant	5,8	0	2	8	7,3	6
Stem	Height of flowering stem (mm)	240	0	132	327	301	308
HerbL_p	Percent of herbivore grazed leaves (%)	0	0,16	0,06	0	0,11	0,14
Branch	Percent of growing stolons (%)	0,32	0,38	0,29	0,4	0,36	0,22
Dead p	Percent of dead stolons (%)	0,1	0,45	0,26	0	0,17	0,14
Flow p	Percent of flowering stolons (%)	0,45	0	0,05	0,4	0,38	0,15
Herb p	Herbivore pressure (Percent of grazed stolons)	0,03	0,08	0,04	0,07	0,24	0,18
Plant NP	Plant N to P ratio	10,2	9,6	8,4	7,5	6,7	7,8
Plant N	N content in leaves of Potentilla (%)	1,7	2,8	2,3	1,8	2,3	2,4
Plant P	P content in leaves of Potentilla (%)	0,2	0,3	0,3	0,2	0,4	0,3
Ash	Ash content in leaves of Potentilla (%)	5,7	7,4	6,5	7	6,1	6,3

Location	8	9	10	11	12	13	14	15	16	17	20	21	23
(North)	48.71303	48.73760	48.74164	48.74151	48.79476	48.85080	48.85194	48.85438	48.86164	48.86560	48.90166	48.91138	48.93966
(East)	14.01836	13.98236	13.98081	13.98079	13.90972	13.91953	13.89685	13.81311	13.79413	13.73658	13.78235	13.63439	
Altitude	765	775	775	775	765	730	730	730	775	800	800	760	970
Irradiance	16.7	1,4	23.5	11.6	4,4	30.3	40.3	9.9	12.7	6,3	6,3	9,3	12,1
WD J	0	0,3	2,8	2	-8,8	5	4,3	-50	-3,3	-6	20	-25	3
pH	5,6	5,3	6,1	5,4	5,3	4,9	4,7	5,3	5,9	5,8	5,1	4,8	5,8
H2O	64	70	76	86	89	92	92	77	78	64	84	84	92
Loss on ignition	16	36,4	57,9	81,5	78,3	50,1	42,9	20,9	59,8				90,7
Soil N	0,58	1,87	1,37	1,81	2,53	0,99	1,09	1,43	1,21	0,55	1,59	1,86	2,49
Soil P	0,07	0,29	0,09	0,28	0,24	0,15	0,22	0,14	0,36	0,11	0,12	0,16	0,40
P ug/cm3	0,072	0,226	0,041	0,039	0,719	0,217	0,173	0,312	0,289	0,51	0,185	0,241	0,255
N ug/cm3	8,08	10,753	5,359	5,331	2,756	2,194	3,816	5,551	7,896	10,904	16,236	7,485	
Biomass	29,23	40,94	23,48	23,41	13,42	7,72	24,57	11,04	19,56	20,17	13,76		12,22
E1 cover	95	95	80	80	85	35	40	75	95	60	60	65	65
Height	65	90	30	60	55	40	50	60	65	60	60	45	30
Sphagnum	0	10	0	0	10	85	80	0	0	30	30	0	75
Tot cm	556	1022	387	398	241	1276	847	621	548	413	753	335	409
Tot me l	14,2	18,9	16,8	15,3	14,4	14,7	18,8	15,8	15,6	12,9	21,1	14,9	13,9
Tot no l	39,3	54,1	23,1	16,8	26	16,8	45	39,4	35,1	32,1	35,6	22,6	29,4
Main cm	365	624	288	238	281	378	510	295	381	292	434	333	362
Main me l	16,8	25,8	16,5	17	14,9	21,2	22,2	19,4	17,1	14,6	25,7	15,6	16,9
Main no l	21,4	23,4	16,6	16,7	15,7	17,6	22,2	21,8	18,5	17	21,4		21,4
Main L	3,3	1,9	2,8	2,2	1,7	1,8	2,5	1,8	1,5	2,6	2,4	2,6	1,2
In ML*LA	4	3,69	5,14	3,62	3,31	3,93	4,13	3,9	2,92	4,3	3,91	4,1	3,13
Flower	10,8	11,3	1,3	6,2	4	7,4	0	9,8	3	6,8		9	7,5
Stem	400	633	161	317	233	256	0	344	209	507		290	284
HerbL p	0,01	0,12	0	0,08	0	0,06	0,01	0,06	0,08	0,05	0,18	0,17	0
Branch	0,63	0,52	0,19	0,23	0,15	0,45	0,38	0,48	0,31	0,09	0,49	0,57	0,57
Dead p	0,14	0,01	0,22	0,21	0,21	0,21	0,07	0,43	0,31	0,33	0,08	0,2	0,21
Flow p	0,35	0,33	0	0,35	0,29	0,26	0,03	0,19	0,13	0,36	0,55	0,34	0,34
Herb p	0,05	0,16	0,09	0,04	0,04	0,3	0,09	0,09	0,1	0,56	0,3	0,03	0,05
Plant NP	7,0	9,0	11,9	11,6	5,7	8,4	7,0	5,9	5,4	5,4	8,5	8,1	4,5
Plant N	1,6	2,7	2,5	2,0	1,7	1,5	1,9	2,2	2,0	1,8	2,7	1,7	1,8
Plant P	0,2	0,3	0,2	0,3	0,3	0,2	0,3	0,4	0,4	0,3	0,3	0,2	0,4
Ash	6	6,7	8	6,6	6	4,8	5,6	5,3	6,1	6,7	8	5,1	7,4

Location	24	25	26	27	28	29	30	31	32	33	34	35	36
(North)	49.04627	49.04714	49.03378	49.03447	49.02329	49.01143	48.96427	48.97163	49.10915	49.13548	49.14048	49.14011	49.12700
(East)	13.58210	13.58142	13.56949	13.56426	13.57822	13.57499	13.48578	13.45754	13.32506	13.38409	13.372251	13.36983	13.38621
Altitude	1070	1070	1055	1060	1050	1040	1140	1240	1085	820	835	835	820
Irradiance	43,3	36,2	54,9	45,6	58,2	30,7	31,2	47,2	37,1	9	11,3	28,2	11,8
WD J	1,5	-4,5	-5,3	0,8	2,8	-17,5	-5	-7,8	-1	5,5	10	-7,5	-1,5
pH	4,1	3,9	3,5	5,1	4,7	4,4	3,9	4,2	4,7	4,5	4,6	4,2	5,8
H2O	91,4	73	87,2	86,2	87,4	87,4	84,5	93,8	84,5	60,9	62,1	85,1	89,6
Loss on ignition	94	90	93	92	94	93	89	92	90	90	91	90	92
N ug/cm3	14.895	10.857	12.155	7.145	11.899	12.492	11.232	11.837	8.841	9.352	13.752	6.417	13.06
P ug/cm3	0,584	1,4	0,799	0,149	0,156	0,188	1,065	0,425	0,146	0,181	0,069	0,206	0,248
Soil P	0,33	0,24	0,20	0,21	0,19	0,12	0,11	0,09	0,11	0,12	0,05	0,08	0,17
Soil N	1,12	1,78	2,11	1,76	1,20	1,64	1,88	1,20	1,40	1,20	1,39	1,85	1,75
Biomass	13,92	17,81	13,56	10,59	9,92	7,33	9,04	7,59	13,06	33,89	20,76	6,31	31,96
E1 cover	55	75	55	50	55	60	50	55	70	80	65	25	85
Height	45	50	40	35	45	45	40	35	55	50	50	30	50
Sphagnum	95	5	70	85	80	70	30	85	25	60	85	85	20
Tot cm	625	387	268	207	401	246	544	166	793	493	333	277	508
Tot me l	19,3	11,5	12	12,1	16,9	11,5	13,8	9	18,6	16,4	13,4	12,3	15
Tot no l	32,3	33,7	22,4	17,1	23,8	21,3	39,4	18,4	30,1	24,9	22,6	22,6	33,8
Main cm	378	275	242	183	226	268	268	161	469	343	264	209	349
Main me l	20,4	13	12,1	12,6	17,6	11,7	18,4	9,5	22	20,5	15,4	12,6	21,9
Main no l	18,4	21,3	19,6	14,7	19,6	19,2	15,3	16,2	21	16,6	16,8	16,1	16,2
Main L	1,8	1,3	1,3	0,3	2,7	2	1,9	2	2,8	1,5	2,3	2,8	2,2
In ML*LA	2,61	3,51	3,27	1,69	3,87	2,68	4,22	3,62	4,92	3,34	3,89	3,97	3,65
Flower	1	5	5,2	3,7	5	5,8	9	5,3	7	5	2,5	2,5	5
Stem	123	207	190	168	308	233	300	296	550	252	348	330	330
HerbL_p	0	0	0	0	0	0,02	0	0	0,08	0,01	0,06	0,05	0,05
Branch	0,39	0,46	0,58	0,12	0,54	0,3	0,44	0,04	0,54	0,21	0,49	0,38	0,32
Dead p	0,06	0,22	0,07	0,1	0,11	0,19	0,18	0,12	0,11	0,15	0,03	0,25	0,22
Flow p	0,07	0,21	0,63	0,37	0,5	0,56	0,05	0	0,06	0,08	0,13	0,07	0,24
Herb p	0,45	0,14	0	0,15	0,06	0	0,25	0,08	0,2	0,49	0,22	0,28	0,21
Plant NP	6,0	9,7	5,8	8,1	5,2	7,0	8,5	8,9	6,6	6,7	6,7	6,1	7,0
Plant N	2,4	2,5	2,0	1,9	1,7	1,6	3,1	2,0	1,9	1,6	1,7	3,1	3,0
Plant P	0,4	0,3	0,3	0,2	0,3	0,2	0,4	0,2	0,3	0,2	0,3	0,5	0,4
Ash	7,3	5,4	5,9	6,1	6,5	5,9	6,9	5,7	8,7	5	6,1	7,4	6,9

Appendix 4.

List of species abbreviations and full names used in ordination analyses. The nomenclature follows Kubát et al. (2002).

| abbreviation	correct name	abbreviation	correct name
Agrcan	*Agrostis canina*	Junfil	*Juncus filiformis*
Agrsto	*Agrostis stolonifera*	Luzmul	*Luzula multiflora*
Alnglu	*Alnus glutinosa*	Lysvul	*Lysimachia vulgaris*
Antodo	*Anthoxanthum odoratum*	Lytsal	*Lythrum salicaria*
Antsyl	*Anthriscus sylvestris*	Mentri	*Menyanthes trifoliata*
Brimed	*Briza media*	Molcae	*Molinia caerulea*
Calcan	*Calamagrostis canescens*	Narstr	*Nardus stricta*
Calcus	*Calliergonella cuspidata*	Nauthy	*Naumburgia thyrsiflora*
Caracu	*Carex acutiformis*	Oxypal	*Oxycoccus palustris*
Carcan	*Carex canescens*	Peupal	*Peucedanum palustre*
Cardia	*Carex diandra*	Phaaru	*Phalaris arundinacea*
Carlas	*Carex lasiocarpa*	Phraus	*Phragmites australis*
Carlim	*Carex limosa*	Potere	*Potentilla erecta*
Carnig	*Carex nigra*	Potpal	*Potentilla palustris*
Carpan	*Carex panicea*	Ranacr	*Ranunculus acris*
Carros	*Carex rostrata*	Ranfla	*Ranunculus flammula*
Cirhet	*Cirsium heterophyllum*	Rumace	*Rumex acetosa*
Cirpal	*Cirsium palustre*	Scugal	*Scutellaria galericulata*
Equarv	*Equisetum arvense*	Senriv	*Senecio rivularis*
Equflu	*Equisetum fluviatile*	Sph_sp.	*Sphagnum sp.*
Eriang	*Eriophorum angustifolium*	Sphfle	*Sphagnum flexuosum*
Erivag	*Eriophorum vaginatum*	Sphpal	*Sphagnum palustre*
Fesrub	*Festuca rubra*	Sphter	*Sphagnum terres*
Galpal	*Galium palustre*	Spisal	*Spiraea salicifolia*
Galuli	*Galium uliginosum*	Trieur	*Trientalis europaea*
Hypmac	*Hypericum maculatum*	Valdio	*Valeriana dioica*
Juneff	*Juncus effusus*	Viopal	*Viola palustris*

Appendix 5.

The selection of some important simulation model parameter values including the parameter names and ranges for simulation runs at both locations "Medvědí" and "Kvilda".

Description	parametr	range	"Kvilda"	"Medvědí"
Density independent mortality of ramet	dens_indep	a/time	0,0125	0,0702
Mean internode length	r	0<a>1	0,0015	0,0027
Variation coefficient of the internode length	cv_r	0<a>1	0,6115	0,7986
Architectural constraint for branching (how many steps after an earlier branching it may branch again)	br_allowed	nodes	1	1
Probability of terminal branching after it is allowed	prob_term_br	0<a>1	0,0111	0,0911
Angle of rhizome growth after branching in degrees	branch_angle	angle	30,56	30,38
Standart deviation of the angle of rhizome growth in degrees	sd_angle	angle	14,98	18,13
Probability of a sleeping bud that may form a branch (meristem activation)	sleeping_bud	time	0,0005	0,000001

Appendix 6

Plants at locations "Medvědí" (a) and "Kvilda" (b) in July 2003, 14 month after their initial labeling for measurement.

a

b
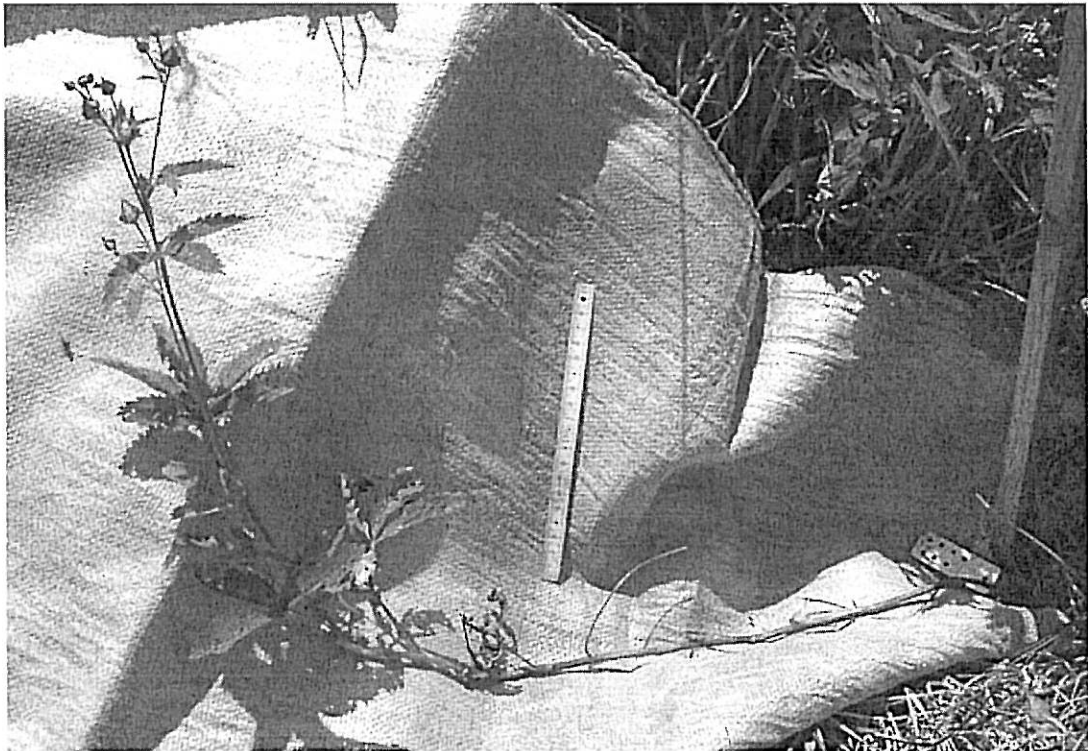
ffect of environmental heterogeneity on clonal behaviour of *Prunella* ~is L.

acek[1] and Jan Lepš[1,2,*]

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ed the response of a clonal herb, *Prunella vulgaris*, to its position in a gap, the identity of neighbouring d species, and simulation of competition for light. The growth characteristics, such as stolon length, e length and number of stolons were recorded in competitive environments with graminoid bunches of *caerulea, Juncus effusus* and *Nardus stricta* and in different types of gaps in a manipulative field ex-. Two pot experiments studied the effect of reduced light and of low red/far red ratio (R/FR) on the plant haracteristics. In both field and pot experiments we monitored stolon orientation in a treatment divided parts (competition/shaded or gap/unshaded). Methods of circular statistics were used to evaluate stolon on. The graminoid bunches had equivalent effects on plant vegetative growth – plants had longer stolons nodes than plants growing in gaps. The effects of treatments on other characteristics (amounts of stolons es) were not significant. In divided treatment, plants responded by accumulation of stolons and leaves in n removed part, and avoided the vegetated part. In the pot experiments the plant biomass and stolon lecreased in low R/FR and in low irradiance treatments, but the internodes in low R/FR were 26% longer l to the control. Centroids were uniformly distributed in divided low R/FR treatment contrary to low e treatment where they showed preference for unshaded part. No dependency of stolon length on its on was found in divided treatments of both experiments. *Prunella vulgaris* in heterogeneous environ-inguished favourable and less favourable conditions and produced more stolons with shorter internodes ourable conditions. This resulted in concentration of resource acquiring structures in favourable patches.

tion

ı anthropogenic meadows are plant commu-
h remarkable species richness, often contain-
than 50 species/m^2 (Kull and Zobel 1991).
man created communities have been main-
· a long time by extensive management, such
g and mowing. However, their species rich-
many cases endangered because the exten-
ıagement techniques have become uneco-
and meadows are either fertilised or
d (Špačková et al. 1998). These impacts

generally result in dominance by a few strong com-
petitors, increased biomass and decreased species di-
versity.

Many theories have been coined to explain the
ability of species to avoid competitive exclusion in
these diverse systems (Palmer 1994). The majority of
meadow species are clonal (Klimeš et al. 1997) and
understanding clonal growth is one of the clues to
explain species coexistence in species rich meadows.
We investigated the ecological behaviour of one of
their constituent clonal species, *Prunella vulgaris*.

l experiment was conducted in an oligotro-
meadow with high species richness in Ohra-
km southeast of České Budějovice, Czech
, 48°59′ N, 14°36′ E, 510 m a.s.l., and com-
·d other studies carried out there (Lepš
nd references therein). Mean annual precipi-
600–650 mm and mean annual temperature
C. The vegetation belongs to the Molinion
: meadow has been regularly mown (once to
·ear) since the early 1990s.

:econd part of this study was conducted in a
·owth facility with regulated day length (flu-
tubes Polylux XL F36W/830, GE Lighting,
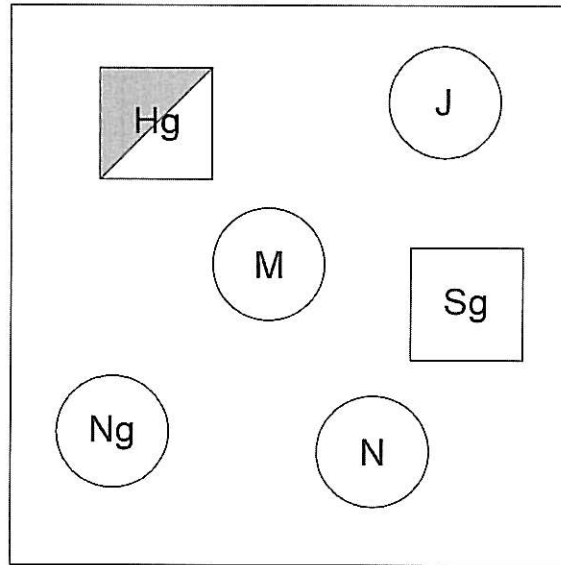ɔn flux rate was 95 µmol(photon) m^{-2} s^{-1}

Figure 1. Experimental design within the quadrats. Each quadrat contained six treatments: N = *Nardus stricta*, J = *Juncus effusus*, M = *Molinia caerulea*, Sg = Square gap, Ng = Natural gap and Hg = Half gap. For explanation see the text.

ental design

)eriment

experiment was established 5 June 1998 in
mown meadow with litter removed. We
ted 120 *P. vulgaris* seedlings (∼2 cm tall)
("Jiffy") pots to 20–1 m^2 quadrats. The ex-
al design of one quadrat is shown in Fig-
ich quadrat contained six microsites (treat-
These consisted of three types of gaps:
ʒap" (both above ground and below ground
n removed from a 20 cm × 20 cm square),
gap" (place without vegetation among the
and "Half gap" (above ground and below
egetation removed diagonally from half of
n × 20 cm square, seedling transplanted to
: of the square), and three graminoid species:
tricta, *Juncus effusus* and *Molinia caerulea*.
ninoid species differ mainly in the bunch
i.e., density of tillers. *Nardus stricta* forms
compact bunch with tillers close to each
. fine, dense, but relatively short leaves. *Mo-
rulea* and *Juncus effusus* have less dense
tems, but have taller shoots. The number and
stolons (in the "Half-gap" also the orienta-
olons) and number of leaves on each stolon
·rded five times (18 August 1998 and 9 May,
3 July and 12 August 1999). The presence of
n 1999 was recorded on 12 August. In all
s litter was removed for the second time in
ɔ9.

Pot experiments

The pot experiments consisted of two similar parts. The first part was established on 19 November 1998 by transplanting 84 starter pots with a ∼2 cm seedling of *P. vulgaris* into 10 cm × 10 cm pots. After two weeks, we covered the pots with aluminium foil of varying shapes ∼6 cm above the soil surface thereby decreasing the Photon Flux Density, PFD, (i.e., the total amount of light). The four treatments were: "A-f 1″ (the entire pot shaded by 10 cm × 10 cm square of foil), "A-f 3/4″ (three-quarters of the pot shaded by foil), "A-f 1/2″ (half of the pot shaded by a 10 cm × 5 cm foil rectangle) and "Control" (without foil). In the partially shaded treatments, the seedlings were positioned at the edge of the foil. The experiment was arranged in a randomised block design. The size of the first two completely developed leaves as a distance of tips of the leaves, number of leaves on each stem, stolon length, and the number of leaves of each stolon were recorded twice (17 December 1998 and 5 January 1999). Stolons shorter than 0.5 cm were not measured. The light regime was a 12 h day length.

In the second pot experiment, seeds were sown on 10 January 2000 and seedlings were transplanted into pots on 28 January 2000. In mid February we covered the seedlings with two types of foil, aluminium foil as in the first experiment and green plastic foil to

ι or no foil a one sample t-test was used: the
were transformed from a circular scale to a
cale. Only the X coordinates of tips were used:
ive value means an orientation to the side with
ion or foil, positive value the orientation to the
ιace. The one-sample t-test then tested the null
϶sis that the mean value of the X coordinate is
he last question investigated the difference be-
he vegetation and gap sides (or with and with-
l sides) in the stolon internode length using
Α. The centroids, or mean angles, were used,
of all angles, to avoid the mutual dependency
ηeasured angles within an individual (see Cain

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of different types of competitors and shading

field transplant experiment, three different
itors and three different gaps were used. Both
spreading and sexual reproduction of *P. vul-*
ansplants were affected by the treatment. The
of newly originated stolons was similar in all
tments (Figure 2). Individuals transplanted to
s of graminoid competitor had greater mean
ength (F = 7.85; p = 3 × 10⁻⁶) and the mean
le length (F = 9.13; p = 3 × 10⁻⁶) than in gap
nts (Figure 3, Table 1). The mean internode
n "Square gap" was only 60% of the "Nardus"
e average number of leaves per plant was al-
e same in all the treatments. There were no
ant differences among graminoid competitors
effect on any morphological characteristic of
ɡrowth of *Prunella*. The treatment "Half gap"
  in shorter internodes (85%) and higher
of stolons in the vegetation removed part
2). The average number of leaves in vegeta-
϶ part was three times higher than in the part
getation (27.1 versus 8.5). No plants flowered
rst season, and only a minority did during the
season. The frequency of flowering differed
the treatments (contingency table, chi-square
df = 5, p < 0.05). Most flowering plants were
ι "Nardus" (25%), then in "Molinia" (15%), in
gap" (10%), and "Half gap" (5%). No flow-
ants were found in "Juncus" and "Natural gap".
ie first pot experiment, aluminium foil was
simulate the lower availability of light in veg-
The important role of light quantity is appar-

ent in all of the ANOVA results (Table 2). All the
levels of shading significantly impacted growth of *P.
vulgaris* with the most shaded treatment being the
most impacted. The size of the two completely devel-
oped leaves was the highest in the "Control" and de-
creased with shading (F = 16.87; p < 10⁻⁶), as well
as the number of stolons (F = 14.35; p = 4 × 10⁻⁴)
and the total leaf number (F = 16.14; p = 3 × 10⁻⁴).
In the treatments "Control" and "A-f 1/2" the greatest
mean stolon lengths (F = 4.61; p = 0.005) and also
the largest mean internode lengths (F = 3.21; p =
0.028) were observed. The summary results from the
first pot experiment are in Table 2.

In the second pot experiment, we changed not only
the quantity but also the quality of light by changing
R/FR ratio using the green foil. Pronounced differ-
ences in above ground (Figure 4) and below ground
biomass were found (F > 40.88; p < 10⁻⁶ in both).
All treatments except "A-f 1/2" and "G-f 1/2" were
significantly different from each other (Tukey HSD
test). The size of the two completely developed leaves
decreased in order (C, G-f 1/2, A-f 1/2, G-f 1, A-f 1;
means are 15.6, 15.6, 14.9, 12.5, 4.9 cm; p < 10⁻⁶).
The number of leaves decreased in the same order (F
= 12.2; p < 10⁻⁴, means are 63, 51, 48, 37, 4). The
treatments also differed in the number of stolons de-
creasing in the same order (F = 122.89; p < 10⁻⁶,
means are 9.4, 8.2, 7.7, 6.6, 0.3). Mean stolon length
was about 4 cm and did not differ among treatments
(p = 0.8). The mean internode length was largest in
the treatment "G-f 1" (Figure 4, p = 0.05), the inter-
nodes in the "Control" were 80% of the length of
internodes in "G-f 1".

Angular analysis

Field treatment "Half gap" did not have centroids dis-
tributed uniformly around the circle (p < 0.02), ex-
cept for the measurement of 31 May (Table 3). The
non-uniform distribution of centroids is shown in Fig-
ure 5. Both mean angles and centroids were directed
toward the vegetation removed part (Table 4, Figure
5). No significant correlations between stolon growth
direction and their real length or mean internode
length were found, but the mean internode length in
vegetation removed parts was 85% of the part with
vegetation. There was no dependency of the length on
the angle. However, some preferences in stolon
growth orientation were observed. The number of the
centroids pointed to the side without the vegetation
was significantly greater (p < 0.05) in three measure-

...he average values of morphological characters from the first pot experiment. All the ANOVA results were highly significant (p <

Leaf size (cm)	Number of stolons	Number of leaves	Stolon length (cm)	Internode length (cm)
12.8	5.2	29.3	38.0	1.3
6.0	2.0	12.9	18.3	0.8
12.0	4.7	26.9	34.8	1.3
9.3	4.0	20.4	23.6	0.9
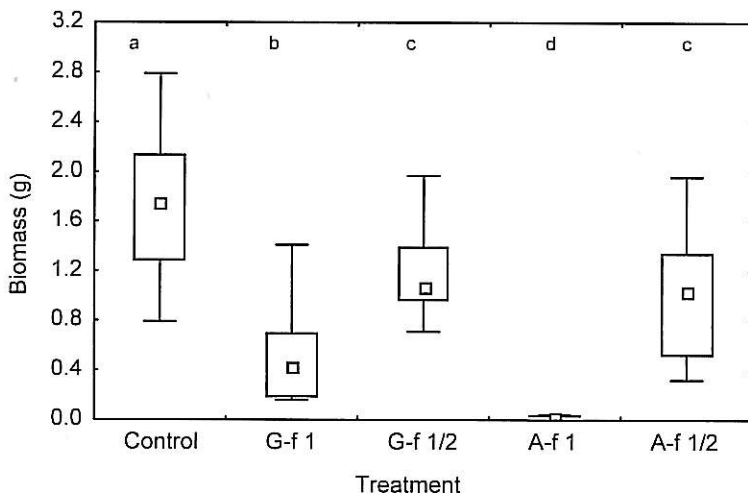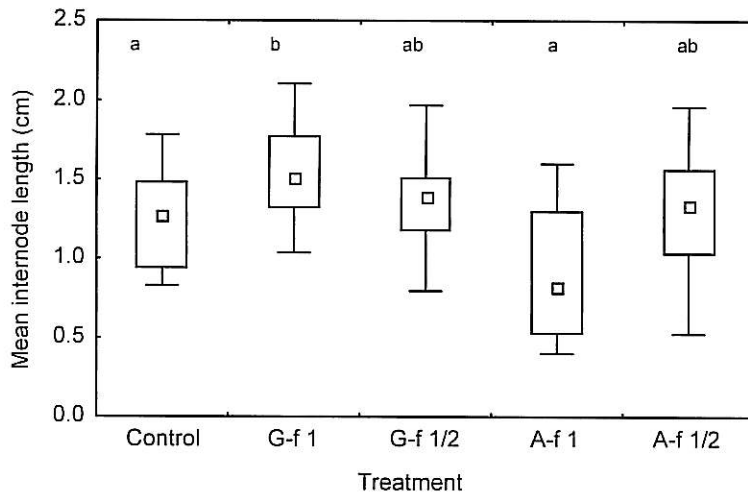
...Mean internode length and aboveground biomass of target plants in the second pot experiment. Identical letters on the top of the ...spond to nonsignificant ranges (p > 0.05) for the harvesting date measurement (Tukey HSD). Treatments: Control, G-f 1 = Green ...shading all the pot, G-f 1/2 = Green foil shading half of the pot, A-f 1 = Aluminium square foil shading all the pot, A-f 1/2 = ...foil shading half of the pot.

...wth chamber treatments ("A-f 1/2" and "G-f ...hypothesis of uniform centroid distribution ...ejected (Table 3). In addition we did not find a significant mean angle in the treatment with altered light quality "G-f 1/2", but in the treatment "A-f 1/2" we found a significant mean angle which indicates

The existence of mean angles, their corresponding values and the results of Parametric one-sample second-order analysis of angles criterion (Zar (1996), significant values (p < 0.05) are shown in bold). Comparison of values of mean angles, centroid angles and .e., distances from the plant centre) in the divided treatments ("Half gap", "A-f 1/2" and "G-f 1/2") in the field and pot experiments. etation free/unshaded part is 0–180°.

	Treatment	F Criterion	Mean angle (if it exists)	Centroid Angle	Centroid length (cm)
999	"Half gap"	**6.95**	113°47'	110°24'	3.24
1999	"Half gap"	**5.93**	121°50'	102°52'	3.06
)99	"Half gap"	**19.96**	122°45'	127°36'	4.85
st 1999	"Half gap"	**7.05**	119°40'	115°07'	4.39
h 2000	"G-f 1/2"	0.96		96°44'	1.67
h 2000	"A-f 1/2"	**4.17**	118°04'	98°41'	1.70
2000	"G-f 1/2"	0.58		39°34'	4.30
2000	"A-f 1/2"	**4.08**	105°34'	73°11'	4.24

Side preference of centroids. Significant results mean a
:e for the vegetation removed/unshaded part. One sample
s used to test results. "p" are significance levels.

	Treatment	p
999	"Half gap"	**0.007**
1999	"Half gap"	**0.000**
)99	"Half gap"	**0.000**
st 1999	"Half gap"	**0.001**
h 2000	"G-f 1/2"	**0.024**
h 2000	"A-f 1/2"	**0.035**
2000	"G-f 1/2"	0.286
2000	"A-f 1/2"	**0.016**

. The competitors appeared to be equivalent, ly as in Goldberg and Werner (1983). Visualy, ied that the long stolon growth form was par- y well developed within *Nardus stricta* which y dense root and shoot systems with hardly)s which would enable *P. vulgaris* to root there. hes of graminoids, the plants invest energy in growth rather than in root production. Not only establishment in a turf be difficult, but also the ts would probably be depleted by the grami- Evans and Cain 1995). Similar behaviour was d for *Elymus lanceolatus*, which, in response dense root system of *Agropyron desertorum*, long stolons crossing over the barrier (Huber- ald et al. 1998). Evans and Cain (1995) docu- the faster spreading of *Hydrocotyle bonarien-* ' stolons veering away from a grassy iment. ontrast to the bunch grass environment, *P. vul-* ı gaps had a more condensed growth with short and dense foliage. This growth pattern appar-

ently reflects the lack of aboveground competition and mechanical root and shoot obstructions in the gaps. Inconsistent results in the "Natural gap" can be explained by higher retention of water there or by the influence of neighbouring grass patches. Although the total number of stolons in the field experiment was roughly constant over the treatments, in the split treatment, where the seedling was transplanted on the border between favourable and unfavourable part, three times more stolons ended up in the favourable part. Consequently, the vast majority of leaves was placed into the vegetation free part of the habitat. This could be again considered as a foraging behaviour, also reported for *P. vulgaris* by Schmid (1985b).

In our field experiment, the internode length under favourable light condition was only 60% of that under competitive environment. Based on the model of Sutherland and Stillman (1988), de Kroon and Hutchings (1995) argue that the shortening itself in this range is not sufficient to place a significant amount of ramets or resource acquiring structures in the good patches. In our opinion, this conclusion is dependent on parameters of the model, particularly on the patch size and on the proportion of favourable and unfavourable area. If the area is perceived as a relatively favourable matrix with small unfavourable spots (bunches of competitive grasses), then the elongation of spacers under unfavourable conditions could be a very efficient tool of escape from the unfavourable patches.

The ability to forage is an important part of species' strategies. The creeping *Prunella vulgaris* is an inferior competitor for light. However, its ability to escape from unfavourable conditions by horizontal growth is probably one of the means that enable it to

Influence of competitor and decreased light quality and/or quantity on the growth characteristics of *Prunella vulgaris*.

Factor investigated	Light quality or quantity decrease	Graminoid competitor
size of leaves	little decrease	Not measured
total number of leaves	decrease	None
internode length	little increase (except "A-f 1")	Increase
number of stolons	decrease	None or decrease
mean stolon length	none (except "A-f 1")	Increase
Biomass	decrease	Not measured

lons accumulated in certain sectors of the cir-
2. a few very long stolons occur in certain sec-
s can be seen in Figure 5, the majority of sto-
eferred the stripped part of the treatment and
ᵤently the mean angle was found there. This
nce was not necessarily due to high nutrient
ility in the areas where vegetation was re-
or due to the low R/FR ratio on the other side.
l be simply caused by mechanical obstruction
stolon penetration into the vegetation, and/or
: interactions between *P. vulgaris* and neigh-
; species (see also Huber-Sannwald et al.
. The combination of all the three factors was
·obable.

situation in the pot experiment was slightly
ıt. We were not able to reject the hypothesis of
ıity of centroid distribution, but in the treat-
A-f 1/2", the mean angle was significant, re-
that plants responded to the low light by
accumulation of stolons on the side without
:. However, no side preference was revealed in
ır treatment with green foil; low R/FR ratio did
vent the stolons from growing to the shaded

sions

ects of treatment type on the clonal growth
ᵉristics of different plant organisation levels
ımarised in Table 6. It seems that *P. vulgaris*
inguish between favourable and unfavourable
in heterogeneous environments and is able to
by changing its morphology – stolon and
le length, stolon production and orientation.
ａ *vulgaris* assumed a penetrating guerrilla
growth in the presence of any graminoid com-
while in their absence, plant growth was more
;ed with shorter internodes. In the pot experi-
ıe number of stolons decreased under shading.

In heterogeneous treatments, *P. vulgaris* was able to place the majority of its stolons in the favourable parts of its surrounding environment. Two strategies are used to reach out of unfavourable spots – prolongation of vegetative spacers, and increased generative reproduction.

Acknowledgements

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