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Ecology of *Rumex alpinus* – a retrospective studies using annual growth markers on rhizomes

PhD. thesis

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Annotation

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I studied the species *Rumex alpinus* by reviewing the literature on the taxonomy, morphology, population biology, genetics, chemistry, physiology and ecology. Herbchronological studies on growth parameters of rhizomes were done on the *Rumex alpinus* plants in relation to altitude and to the climatic fluctuations, specifically to the snow accumulation.

Declaration – *Prohlášení*

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

I declare that in accordance with the Czech legal code § 74b, law no. 111/1998 in its valid version, I consent with the publication of my PhD. Thesis (in an edition made by removing marked parts archived by the Faculty of Science) in an electronic way, specifically, in the public access to the STAG database run by the University of South Bohemia in České Budějovice on its web pages, with the preservation of my copyright to the submitted text of this qualification thesis. I agree also with publishing by an electronic way according to a Czech legal code § 74b law no. 111/199 of opponents' and supervisor's references and the record of the course and the result of the PhD. defense. I also agree with comparing of qualification thesis text with the databases of qualification thesis Theses.cz running by National register of university qualification thesis and by a system for uncovering of plagiarisms.

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České Budějovice, September 15th, 2011

Author contribution statement

I hereby declare that Petra Šťastná contributed to preparation of the following papers:

Šťastná P., Klimeš L., Klimešová J. 2010. Biological flora of the Central Europe: *Rumex alpinus*. Perspect. Plant Ecol. 12: 67-79.

- review of literature, substantial part of writing

Šťastná P, Klimešová J, Doležal J. Altitudinal changes in growth and allometry of Rumex alpinus. submitted

- data collection and preparation for analyses, preliminary analyses, substantial part of writing

Klimešová J, Doležal J, Šťastná P, Klimeš L. Response to climatic fluctuations is modulated by snow accumulation on alpine clonal herb *Rumex alpinus* L. ms

- review of literature, preparation of data for analyses, preliminary analyses and participation on writing

Jitka Klimešová

supervisor

13th September 2011

Author contribution statement

Co-author statement

I would like to confirm that as a co-author of two research papers of Petra Štastná - *Altitudinal changes in growth and allometry of Rumex alpinus* (submitted to Alpine Botany) and *Response to climatic fluctuations is modulated by snow accumulation on alpine clonal herb Rumex alpinus L.* (in manuscript), I have contributed with the analysis of collected data. But the definition of sampling design, data collection and transcription, as well as the preparation of manuscripts were done by the other authors.

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Jiří Doležal

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To memory of Leoš Klimeš.

Content

General introduction

Alpine ecosystems and clonal plants

Clonal plants are important components of a range of communities at many latitudes and altitudes. Some are among the most successful species in terms of their geographical distribution and colonizing ability, many of them form extensive monodominant stands for considerable periods, resisting invasion by other species (Hutchings & Bradbury 1986). Specific biotope, which has been considered as typically dominated by clonal plants, is the mountain environment. Although proportion of clonal to non-clonal species is not higher than in surrounding habitats (Klimešová & Doležal in press) the clonal plants are here more abundant.

The occurrence of mountain organisms is driven by a complex of factors connected with altitudinal gradient, presented by a combination of temperature, snow regime and wind, modifying and interacting with temperature and snow at all points along the gradient (Bowman et al. 2001). Arctic and alpine permanent vegetation types are very stable communities and resistant to past and recent climate changes (Grabherr & Nagy 2003). The main reason for this appears to be longevity of the mainly vegetative reproducing members of such communities, reinforcing the hypothesis that long-lived clonal plants can enhance community and ecosystem resilience (Guisan & Thuiller 2005, de Witte & Stöcklin 2010). Several clonal species include representatives with the longest recorded life-spans of the plants (Cook 1983); the age of individual genet can even reach up to 10 000 years (White 1979). For example mapping of individual genets of *Carex curvula* revealed that clones spanning one square meter could be several thousands of years old (Steinger et al. 1996, Körner 1999).

Extreme longevity of clonal plants inhabiting mountainous areas makes population studies difficult as successful establishment of seedlings can be extremely rare. Ecological studies thus focus on growth parameters of established plants, which are however inevitably much affected by high spatial and temporal environmental variation in mountains. There are two possible approaches how to measure plant growth in such conditions, either follow marked individuals in consecutive seasons or to rely upon retrospect methods.

Plant chronology

Chronology of woody species, called dendrochronology, is based on counting of the annually produced tree-ring wood from the radial secondary thickening of trunk, and has been abundantly used as well-established method (e.g. Schweingruber 1996). Therefore a dendrochronology enabled description of the relationships between growth and climate for periods extending back up to 8200 years (Fritts 1976). This method is used frequently for an age-estimation of historical wood relicts and for the description of community dynamics of forests and population structure of woody species (Schweingruber 1996).

Presence of annual growth rings in perennial herbaceous plants, described for example by Molisch (1929, 1938), Vidal (1906) and Zoller (1949) was for many years neglected or even ignored until it was “rediscovered” recently (Schweingruber & Poschlod 2005). Numerous herbaceous perennials from temperate regions of Europe and North America exhibit annual growth rings of xylem in their root collar or subterraneous stem (Dietz & Ullman 1997, 1998, Schweingruber & Dietz 2001, Dietz 2002, Dietz & Schweingruber 2002). Recently approximately 84% of Central European dicotyledonous plants in subalpine and alpine zones have been reported to show countable growth rings (Schweingruber & Dietz 2001). The potential of this method is large, but it is not used very frequently and only a few species were studied to date. Limitation of the method is that despite longevity of many herbaceous species their perennating organs are relatively short living.

The method analyzing growth-rings in roots of herbaceous plants has been called “herbchronology” (Dietz & Ullman 1997). The annularity of herbal growth rings has been repeatedly verified (Dietz & Ullman 1997, Dietz & Fattorini 2002, Schweingruber & Poschlod 2005, von Arx et al. 2006). Results showed close correlation of number of growth rings with age of plant individual. The method has been used for age determination in population studies (e.g. Dietz & Ullmann 1998, Dietz et al. 1999, Dietz 2002, Křivánek 2003, Perkins et al. 2006, Pergl et al. 2005, 2007, Kuss et al. 2008), for correlating plant growth and environmental characteristics (Dietz et al. 2004, Rixen et al. 2004, von Arx et al. 2006, Friedmann 2009) and for dating of colonization processes at moraines (Kuen & Erschbamer 2002, Erschbamer & Retter 2004).

Another possibility to evaluate plant growth is based on morphological markers such branching, leaf and inflorescence scars, resting buds which are preserved in some species on perennial plant organs like woody stems of shrubs or rhizomes of herbs (Schweingruber & Poschlod 2005). Obtained information from the morphological markers, is in many cases wider, than from annual growth-rings analysis. It is possible, beyond the estimation of age identify the number of annually produced leaves (Pergent et al. 1997), flower stalks (Kron & Stewart 1994, Calvo et al. 2006), branching frequency (Hutchings & Slade 1988, de Kroon et al. 1991, Kron & Stewart 1994, Klimeš 2000), the angle of branching (Hutchings & Slade 1988, Kron & Stewart 1994, Klimeš 2000) and annual production of dormant buds (de Kroon et al. 1991, Tybjerg & Vestergaard 1992). The method therefore allows addressing complex ecological questions. Species of genus *Polygonatum* are often shown as typical example, with rhizomes where the growing season is defined by the scars – remnants of aerial shoot which delimit year increments (Troll 1937, Tybjerg & Vestergaard 1992, Hasegawa & Kudo 2005). Other studies were done for example on *Podophyllum peltatum* for which effect of fertilization and severing on activation of dormant buds was studied by de Kroon et al. (1991) and flexibility of development of the preformed buds to current conditions by Jones & Watson (2001). Growth parameters preserved on rhizomes of *Phragmites australis* were used for development of architecture model (Klimeš 2000), for evaluation of the effect rhizome age on tissue concentration of mineral nutrients, and storage carbohydrates (Čížková & Lukavská 1999, Klimeš et al. 1993) and for elucidation of resource-translocation patterns between rhizomes and the aboveground organs (Asaeda et al. 2005). Growth markers on rhizomes of *Typha latifolia* enabled evaluation of effect of fluctuating water table on growth and performance of species (Sharma et al. 2008) and on rhizomes of *Iris variegata* for developing of the growth model (Kron & Stewart 1994). Rhizome growth of sea grasses of *Posidonia* genus was used for assessment of belowground biomass (Short & Duarte 2001), for modeling the relationship between sexual reproduction and rhizome growth (Calvo et al. 2006) and for evaluation of interspecific differences (Pergent et al. 1997). Using morphological markers on rhizome of *Carex bigelowii* Carlsson & Callaghan (1991) estimated the age of the clonal fragments. The long-term growth dynamic of *Rumex alpinus* by stochactic model studied Klimeš (1992), the anatomical and morphological responses of different depths of burial on the rhizomes observed Klimeš et al. (1993), and the allocation of carbon to non-structural carbohydrates at two levels of nutrient availability was analyzed at Klimešová & Klimeš (1996).

Classical studies of morphological markers on woody shrub stems were done on *Cassiope tetragona*. Each row of evergreen leaves of the species has a wave-like appearance due to a marked pattern of leaf-lengths associated with small leaves produced in autumn and spring, and alternating with large leaves which expand in summer (Warming 1908). Length of stem annual increment was found to correlate with climatic conditions and therefore evaluating of stem annual increments from different localities or from experiment with manipulated temperature enabled to test interesting ecological hypotheses (Callaghan et al. 1989, Havström et al. 1993, 1995, Rozema et al. 2009). Also annual increments of the sporophyte of *Lycopodium annotinum* are distinguishable and were used for age determination of clonal fragments (Callaghan 1980).

The above overview shows potential of usage of morphological markers on perennial plant organs. In some areas, such as the Arctic, due to absence of trees and presence of shrubs with extremely small annual rings, is analyzing of morphologiacal markers very useful (Callaghan et al. 1989). Many species in northern latitudes are amenable to retrospective growth analysis because (i) clear innate markers of annual growth are often identifiable in the plant’s morphology due to the marked seasonality in the growth caused by prolonged winter dormancy, (ii) decomposition rates are often slow and records of past growth may remain for many years, and (iii) modular clonal growth is common and large networks of interconnected modules are formed (Callaghan & Collins 1976). The climatic conditions of tundra are in many ways similar to high mountain environment; hence many of plant characteristics would be applied in both places.

Ecology of *Rumex alpinus* L.

Rumex alpinus is perennial clonal species which originally occurred in tall herb communities in alpine zone and secondarily spread into areas affected by pasturing in above as well as below alpine timberline on deforested places enriched by nutrients and disturbed by resting animals. Thanks to the expansion of the distribution area the species is now widespread and form vast stands. It can be found along geographical and altitudinal gradients and in different microhabitats. As *Rumex alpinus* is very persistent even long time after cessation of pasturing, understanding its ecology is of high importance from theoretical as well as from practical point of view. For example, the species changed character of mountain meadows in the Krkonoše Mts., Czech Republic; therefore Administration of National Park took measures (chemical control) to suppress its dominance. For such management the good knowledge of the species is necessary. As ecological, chemical and physiological characteristics of the species has been studied by many authors, the first aim of the theses was to collect all available data about the taxonomy, morphology, population biology, genetics, chemistry, physiology and ecology of *Rumex alpinus* **(Chapter 1)**.

Rumex alpinus has potential to be analyzed by herbchronological method as was already shown in preceding chapter (see Klimeš 1992, Klimeš et al. 1993, Klimešová & Klimeš 1996). The species form epigeogenous monopodial rhizome (Fig. 1) perennating for about ten years and then decaying, so thus preserved traces after leaves and flowering stems are countable for this period. The size of annual increments (length and width), branching and number of resting buds can be also assessed. Therefore growth of plant in different environments can be studied by retrospect method.

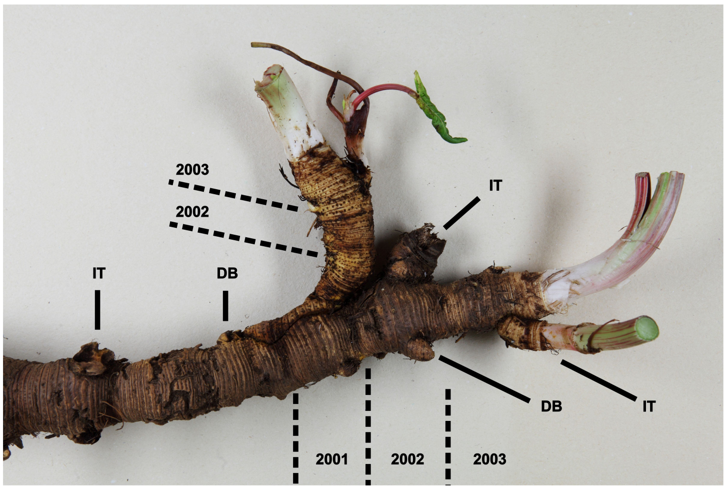

***Fig. 1:** Terminal part of the monopodial rhizome of Rumex alpinus as viewed from above. IT – inflorescence scars, DB – dormant buds. Numbers refer to the year in which the segments were produced. Stripes within the segments are leaf scars.* (Photographed by K. Antošová.).

The second aim of the theses was to study growth of *Rumex alpinus* with usage of morphological marks on rhizomes along altitudinal gradient and find out optimum for species growth. We expected that optimum of growth will be characterized by large biomass production and abundant flowering; on the other hand, suboptimal localities will be characterized by the reduced growth and flowering but with enhanced branching of rhizomes (clonal growth). Further the variability in growth parameters should increase along a gradient from optimal to suboptimal conditions (**Chapter 2).**

Despite effect of altitudinal gradient also local factors like type of bedrock, amount and composition of soil nutrients, water supply, duration of snow cover, exposition to sun and winds surely affect plants growth. These characteristics of locality are spatially or temporarily limited and often are also connected to specific climatic conditions of particular growth season. The third aim of the theses was to reveal an effect of one ecological factor on small spatial scale – snow duration – on growth of *Rumex alpinus* (**Chapter 3)**.

Studied area

All experimental field work was conducted in Štiavnica Valley in the Nízké Tatry Mts., West Carpathians, Slovakia (Fig. 2). The studied species is common along whole 1000 m long altitudinal gradient that the valley is named according the species ("Štiav" is common name for *Rumex* in Slovak language).

The Nízké Tatry Mts. form more than 80 km long, east-west directed mountain ridge, and are a part of Inner West Carpathians extended mainly in the territory of Slovakia (Brandlová 1993, Gaál & Bella 2008). The mountains were created during Alpine orogeny at the end of the Mesoic and the beginning of the Tertiary Age. Geological structure is complicated, but in general the crystalline core is built by Palaeozoic igneous rocks – various types of granites, granodiorytes (Ďumbierský type), migmatites, gneiss, mica-shists, phyllites and amphibolites. These rocks today create upper parts of the main ridge and south-face parts of mountains. Cover series presented by secondary sedimentary deposits as calk dolomite and marlstone, are unevenly distributed in the periphery of mountains, but markedly are more abundant at the north-face of the mountains. For example localities as the Demänovská dolina valley or the Kozie chrbty ridge contain large karst systems (Žák et al. 2009). During the Pleistocene, the mountains were covered by several mountain glaciers and thus the typical glacier georelief was formed (U-shape valleys, glacial caldrons, cirques, morenas, rocky seas and varied types of little selective weathering forms) (Gaál & Bella 2008, Gajdoš & Klaučo 2010). The altitudes of mountains range from 360 m (Bánská Bystrica) to 2043 m a.s.l. (the highest peak the Ďumbier Mt.).

The hydrological system is created by numerous springs and several lakes of glacial origin. The climatic situation is closely connected to specific altitude and place; mean November temperatures can decrease to -6°C, and in June increase up to 18°C. The annual precipitations in the top mountain parts exceed 1400 mm (1600 mm on the Chopok Mt.), but in valleys is less than 900 mm (Holý 1997).

The vegetation types alternate due to geological substrate, altitude and regional character. Forests cover 70% of the mountain area: mixed beech forest is found in lower altitude and coniferous forest at higher altitudes up to alpine treeline in about 1500 m a.s.l. where it is replaced by belt dominated by *Pinus mugo* krumholz. The highest parts are vegetated by alpine grasslands (Sillinger 1933).

The mountains were used for the pasturing for many centuries till about 1950. Consequently the timberline is at many places decreased as the forests were partly changed to pastureland and most sites enriched by nutrients are covered by vast stands of *Rumex alpinus* (Sillinger 1933). The mountains range is protected (the Low Tatra Mts. National Park) and alpine zone is recently used only for tourism.

Fig. 2. *View to the Šťiavnica Valley, the treeline.* (Photographed by J. Šubrt.)

The Šťiavnica Valley where field work was conducted is 8 km long and its altitude range from 882.4 to 1727.9 m a.s.l. It lies on the north side of the mountain ridge. The highest neighboring peaks are the Mt. Ďumbier (2043.4 m), Štiavnica (2021.3 m), and Malý Gápeľ (1807.4 m). At the bottom of valley runs the spring with the same name – the Štiavnica. Upper part of the valley under the Ďumbier Mt. opens into a cirque. In lower parts of the valley spruce forest grows up to 1400 m a.s.l. In the forest zone abandoned meadows and pastures overgrown by *Rumex alpinus* can be found. In higher altitude, large stands of krumholz spread creating a mosaic with alpine grasslands which totally dominate above 1620 m. The upper part of the valley is characterized by snow accumulation in winter and thus avalanches affect this part of valley. The highest studied locality of *Rumex alpinus* is at the top of ridge (1900 m a.s.l.) on the south-east slope of the Mt. Ďumbier.

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Biological flora of Central Europe: *Rumex alpinus* L.

Šťastná, P., Klimeš, L. & Klimešová, J. (2010). Biological flora of Central Europe: *Rumex alpinus* L. *Perspectives in plant Ecology,Evolution and Systematic*, 12/1, 67–79.

Abstract

Rumex alpinus L. (Polygonaceae) is a rhizomatous perennial plant inhabiting stream banks, spring areas, nutrient-rich and mesic to wet abandoned pastures and meadows. It is native in the mountains of Central and Southern Europe but its current distribution has been partly affected by its utilisation as a vegetable and a medicinal herb in the past. This article reviews the literature on the taxonomy, morphology, population biology, genetics, chemistry, physiology and ecology of this species.

Abstrakt

Rumex alpinus L. (Polygonaceae) je vytrvalá rostlina s podzemními oddenky, osidlující břehy toků, prameniště a živinami bohatá stanoviště od vlhkých po mokré opuštěné pastviny a louky. Jejím domovem jsou hory centrální a jižní Evropy, ale její současná distribuce je částečně ovlivněna i jejím historickým používáním jako zeleniny a léčivky. Tento článek obsahuje dostupné informace z literatury k taxonomii, morfologi, populační biologii, genetice, chemii, fyziologii a ekologii k tomuto druhu.

Následující pasáž od strany 16 až do 53 obsahuje utajované skutečnosti a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě JU v Českých Budějovicích.

Podíl studenta: cca 50%

Stav publikace: publikováno 2010

Chapter 2

Altitudinal changes in growth and allometry of *Rumex alpinus*

Šťastná P., Klimešová, J. & Doležal, J. (submitted).

Abstract

Alpine plants growing along altitudinal gradients have been traditionally considered to have reduced flowering and growth and enhanced clonality toward higher altitudes. This pattern, however, has seldom been studied for multiple characteristics in one plant species and over several years, and thus its generality is uncertain. In the present study, we used annual growth markers on perennial rhizomes (herbchronology) to analyse the longterm growth of *Rumex alpinus*. By determining rhizome segment (annual increment) width, segment length, and numbers of leaf scars, inflorescence scars, dormant buds, and branches preserved on rhizomes, we analysed past growth on seven sites along an altitudinal gradient (950–1900 m a.s.l.) in the Low Tatra Mts., West Carpathians, Slovakia. We determined where growth was optimum on the gradient, and we hypothesized that: (1) at the growth optimum, *R. alpinus* plants will be characterized by large biomass production and abundant flowering whereas at suboptimal localities the growth and flowering will be reduced but branching of rhizomes will be enhanced; and (2) the variability in growth parameters will increase along a gradient from optimal to suboptimal conditions. Although *R. alpinus* is a light-demanding species occurring preferentially along small streams above the tree line, the most vigorous growth (highest number of leaves and inflorescences) occurred at low altitudes in forest clearings. The lowest variability in growth parameters, however, occurred in the middle of the altitudinal gradient. Herbchronology was determined to be a useful tool for the retrospective study of plant growth.

Abstrakt

Horské rostliny se vyskytují podél výškových gradientů. Tradičně se u těchto rostlin předpokládá snížení frekvence kvetení a růstu směrem k vyšší nadmořské výšce a naopak zvýšení klonality. Nicméně, tato skutečnost byla zřídka studována na více charakteristikách jednoho rostlinného druhu po dobu několika let. Obecná platnost je této domněnky se však jeví jako nejistá. V předložené studii jsme použili roční přírosty na vytrvalých oddencích *Rumex alpinus* (herbchronologie) k dlouhodobé analýze růstu. Určením charakteristik ročního přírůstku (šířka a délka přírůstku, počet jizev po listech, počet jizev po květenství, počet dormantních pupenů a celkový počet větví zachovaných na oddenku) jsme využili ke zjištění růstu v minulosti u rostlin na sedmi stanovištích podél gradientu nadmořské výšky (950–1900 m n. m.) v Nízkých Tatrách, v Západních Karpatech na Slovensku. Snažili jsme se odhadnout růstové optimum, kde naše hypotéza zněla, že zde se budou vyskytovat rostliny *Rumex alpinus* s největší biomasou a budou často kvést, kdežto na méně optimálních lokalitách bude jejich růst a frekvence kvetení snížena, ale bude posíleno větvení oddenků. Dále, že variabilita růstových parametrů se bude zvyšovat podél výškového gradientu z optimálních do méně optimálních podmínek. Ačkoli je *R. alpinus* světlomilný druh vyskytující se převážně podél malých toků nad horní hranicí lesa, nejvíce vyvinutý růst (nejvyšší počty ročně vytvořených listů a nejvyšší frekvence kvetení) se objevila na lokalitách v nižší nadmořské výšce v lesních světlinách. Nicméně nejnižší variabilita růstových charakteristik se projevovala u rostlin ve střední části výškového gradientu. Herbochronologie se ukázala jako vhodný nástroj pro retrospektivní studium rostlinného růstu.

Následující pasáž od strany 56 až do 73 obsahuje utajované skutečnosti a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě JU v Českých Budějovicích.

Podíl studenta: cca 40%

Stav publikace: zasláno k publikování a obdržení recenzí

Chapter 3

Response to climatic fluctuations is modulated by snow accumulation on alpine clonal herb *Rumex alpinus* L.

Klimešová, J., Doležal J., Šťastná, P. & Klimeš L. (manuscript).

Abstract

Understanding an impact of climate variation on plant performance in cold regions is complicated by a fact that in cold period of year, precipitations fall as snow and further modify effect of temperature and moisture on plant growth. We conducted retrospect study using morphological markers preserved on rhizome of *Rumex alpinus* so that we were able to analyze growth parameters in snowbed and control plants during 12 years period in alpine zone of the Low Tatra Mts., West Carpathians. We analyzed effect of snow accumulation and mean monthly temperatures and precipitation in preceding and current season on annual leaf production, length and width of annual rhizome increment, its flowering and branching. We also experimentally established snow accumulation in continuous *Rumex alpinus* stand. The only growth characteristic responding consistently to natural as well as experimental snow accumulation was number of leaves, other growth parameters showed year to year fluctuations. The snow accumulation shortened growing season for the plants, thus climatic events causing further season shortening reduced plant vegetative growth (high precipitation in previous October and current April) whereas events causing prolonging of growing season (warm September) supported plant growth in snowbed site. While snowbed plants were more affected by actual weather, plants from outside of snowbed were more dependent on preceding year weather. For example flowering was supported by warm August of preceding year in control plants while it was enhanced by warm May and August of current year in snowbed plants. Our study revealed that growth parameters of the plant can be affected differently by snow accumulation according their driving factors. While some are tightly connected with snow cover duration (in our case number of leaves) others are controlled by different signals but snow cover may further modulate their developmental trajectories (flowering). For future studies of climate fluctuations effects on growth of plants from cold (alpine and arctic) areas it will therefore be necessary to disentangle driving factors for key lifehistory parameters.

Abstrakt

Porozumění vlivu klimatických výkyvů na chování rostlin v chladných oblastech je komplikované díky skutečnosti, že v zimních obdobích roku ovlivňuje růst rostlin kromě teploty a vlhkosti také sněhová pokrývka. Provedli jsme retrospektivní analýzu využívající morfologické znaky zachované na oddencích *Rumex alpinus,* takže jsme byli schopni zjistit růstové charakteristiky u rostlin vyskytujících se na sněhovém výležisku a u rostlin nacházejících se mimo během dvanácti let. Tyto rostliny se nacházely v alpinské zóně Nízkých Tatrer, v Západních Karpatech na Slovensku. Zjišťovali jsme efekt sněhu a průměrných měsíčních teplot a srážek v předchozím a následném roku na roční produkci listů, na délku a šířku ročních přírůstků, na frekvenci kvetení a větvení. Také jsme experimentálně vytvořili sněhové výležisko v další části stanoviště. Růstová charakteristika, které jako reagovala k přírodní nebo experimentální sněhové akumulaci byl pouze „počet ročně vytvořených listů“, ostatní růstové charakteristiky vykazovaly meziroční výkyvy. Sněhová akumulace zkrátila růstovou sezónu dotčených rostlin, nicméně další faktor způsobující zkrácení vegetační sezóny představovaly klimatické výkyvy. Konkrétně, snižovaly vegetativní růst (hojné srážky v říjnu loňského roku a letošního dubna). Naopak teplý podzim způsobil prodloužení růstové sezóny u rostlin na sněhovém výležisku. Obecně,

rostliny ze sněh. výležiska byly více ovlivněny počasím aktuálního roku, a naopak rostliny mimo byly více závislé na počasí v předchozím roce. Například kvetení bylo podpořeno teplým srpnem předchozího roku u rostlin mimo sněhové výležisko, ale u rostlin rostoucích ve sněhovém výležisku rozhodoval o kvetení teplý květen a srpen současného roku. Naše studie odhalila, že charakteristiky růstu rostlin můžou být kromě svých hybných faktorů rozdílně ovlivňovány také v závislosti na přítomnosti vyšší sněhové pokrývky. Některé z těchto charakteristik jsou těsně svázány s délkou sněhové pokrývky (v našem případě počet ročně vytvořených listů), jiné ovlivňují jiné faktory, ale přítomnost sněhové pokrývky může navíc modulovat jejich vývojové trajektorie (kvetení). Pro budoucí studie klimatických výkyvů na růst rostlin z chladných oblastí (alpinské a arktické pásmo) bude nutné pro rozklíčování životně-historických charakteristik oddělit tyto vlivy.

Následující pasáž od strany 76 až do 95 obsahuje utajované skutečnosti a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě JU v Českých Budějovicích.

Podíl studenta: cca 20%

Stav publikace: rukopis pro plánované opublikování

General conclusions

Rumex alpinus with its large shading leaves and robust rhizomes tend to dominate wet alpine and subalpine meadows and form nearly monospecific stands. Only few shade-tolerant species or tall-herb species can persist in these closed communities. Through epigeogenous rhizomes, growing horizontally shallow under soil surface, plants continuously shuttle in the stand. Although spread of *Rumex alpinus* was enhanced by pasture in past, the species is still persisting nearly 50 years after pasture cessation in Central European mountains. This is probably due to ability of the plant to recycle effectively nutrients.

In closed canopy stands *Rumex alpinus* reproduce only by clonal multiplication – the oldest parts of rhizome, after 10 to 20 years decay and consequently branches of rhizome can separate and form physically independent clonal fragments. The plants do not flower every year, but in the case of flowering, the number of produced seeds is several thousands per one inflorescence. Vacated achenes germinate only in full light conditions and under the closed canopy stay dormant for many years forming seed-bank. Establishment of new genetic individuals from seeds in monospecific stand is possible only after disturbance; seeds, however, are important for colonization of new habitats **(Chapter 1)**.

Rumex alpinus is distributed along whole altitudinal gradient found in studied site, Štiavnica Valley in the Low Tatra Mts., West Carpathians and ranges from 950 to1900 m a.s.l. Using growth markers on perennial rhizomes we were able to assess variation of growth along the altitudinal gradient **(Chapter 2)**. Plants with superior growth (i.e. plants with the largest annual rhizome increments, the highest number of leaves produced per year, and the highest flowering frequency) were found at the low altitude. These plants were also characterized by the lowest persistence of rhizomes. On the other hand, plants with the lowest variability in growth parameters occurred in the middle of the gradient, and plants with the most branching and with highest number of dormant buds occurred at high altitude sites. The most vigorous growth of the *Rumex alpinus* in the lowest altitude is probably a reason for ability to spread into deforested habitats in forest zone (former pastures and meadows) **(Chapter 1)**.

Except for large scale environmental gradients like altitude in the case of Chapter 1, growth of *Rumex alpinus* is affected by local factors, for example by the snow accumulation. Snow conditions vary on small spatial scale being mutually affected by precipitation, topography and wind **(Chapter 3)**. While some plant parameters were tightly connected with snow cover duration in our study (e.g. number of leaves produced per year), others were controlled by different signals but snow cover further modulated their developmental trajectories (flowering). Specifically, the snow accumulation shortened growing season for the plants, thus climatic events causing further season shortening reduced plant vegetative growth (high precipitation in previous October and current April) whereas events causing prolonging of growing season (warm September) supported plant growth in snowbed site. While the snowbed plants were more affected by actual weather, plants from outside of snowbed were more dependent on preceding year weather **(Chapter 3).**

Perspectives

Despite the fact that *Rumex alpinus* has been extensively studied, as was shown in the first chapter, there still remain many challenging questions. Especially the retrospect method using growth markers on rhizomes is promising tool for future studies focused, for example, on effect of climate variation and hence climate change on growth of the species. We can for example repeat measurements from eighties and check whether correlation of growth with climate remain the same in snowbed site. Similarly, we can use our data from altitudinal gradient for correlation of *Rumex alpinus* growth with climate and moreover we can compare variation in growth of *Rumex alpinus* with growth of surrounding trees (using annual rings) along the same altitudinal gradient.

With usage of the herbchronology we can ask also questions concerning life-history trade-offs, like: What is a relationship between branching and flowering? What is effect of flowering on vegetative growth?

The method of herb-chronology was proved to be a very useful tool for the retrospective study of the *Rumex alpinus* plant growth providing highly valuable data of long-term growth responses of the studied species to environmental conditions.