

Razvoj rastlinske ekologije v Sloveniji: Rastline skrajnih rastišč

The development of plant ecology in Slovenija: Plants of extreme habitats

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Uvod

Rastline naseljujejo različne habitate, od rastišč, kjer so razmere za življenje optimalne, pa do takšnih, kjer na njih delujejo različni stresi in motnje. Območje Slovenije je zelo raznoliko, kar je posledica raznolike geomorfologije (apnenec pokriva več kot 40 % celotne površine), razgibane topografije in klime, od submediteranske, alpske do zmerne celinske, kar se odraža v gradientu padavin. Na območju Slovenije pa se srečujejo tudi štiri biogeografske regije: mediteranska, alpska, panonska in dinarska (ATLAS SLOVENIJE 2005). Posledica raznolikosti slovenske krajine je velika raznolikost habitatov, med katerimi so tudi območja s posebnimi razmerami za rastline. Posebne razmere lahko ustvarjajo skrajni okoljski dejavniki, kot so pomanjkanje ali prekomerna svetloba, visoke ali nizke temperature, poseben vodni režim, teptanje ter obremenjenost območja z določenimi snovmi. Takšni habitati so različna mokrišča, na primer visoka in nizka barja, presihajoči sistemi, prodišča, mrazišča, slane površine, s težkimi kovinami obremenjena območja ter skrajno senčna rastišča, kot so vhodi v jame. Rastline se na skrajne razmere prilagajajo na vseh nivojih, morfološko-anatomskem, biokemijskem in fiziološkem, in prav pomen rastlin in njihove prilagoditve so glavni pred-

Introduction

Plants thrive in variety of habitats, from that with optimal life conditions to those with extreme conditions and disturbances. Slovenia is characterised by heterogeneous geomorphology with carbonate rocks presenting over 40% of its surface. The same holds true for climate ranging from submediterranean, alpine and temperate continental, resulting in a gradient of precipitation rate. The territory of Slovenia is divided into four biogeographic regions: mediterranean, alpine, panonic and dinaric (ATLAS SLOVENIJE 2005). A consequence of that diversity is a number of different habitats including extreme environments for plants. Extreme environments might occur due to extreme environmental conditions such as lack or insufficient radiation, low or high temperatures, floods, low nutrient availability, high content of heavy metals as well as due to different disturbances like trampling, grazing and wind. Such habitats are different wetlands like peat bogs, intermittent aquatic systems, saline areas, soils loaded with heavy metals, riparian zones and extremely shaded habitats as cave entrances. Plants of extreme environments evolved numerous adaptations and mechanisms that enable their survival in these habitats (LARCHER 2002). Due to their special character they became a frequent

met raziskav rastlinskih ekologov po svetu, pa tudi v Sloveniji (LARCHER 2002). Raziskave rastlin skrajnih rastišč pa niso pomembne samo z vidika razvoja znanosti, ampak so ključnega pomena tudi z vidika vedno večjih in hitrejših sprememb v okolju zaradi globalnega ogrevanja in vpliva človeka. Ker so te rastline razvile vrsto mehanizmov in prilagoditev, ki jim omogočajo preživetje v skrajnih razmerah, so pomembne za naseljevanje izpraznjenih, kontaminiranih, zaslanjenih in motenih rastišč. Članek podaja razvoj rastlinske ekologije v Sloveniji s poudarkom na skrajnih rastiščih.

Razvoj rastlinske ekologije

Rastlinska ekologija združuje različna področja z različno tradicijo in razvojem. Korenine segajo v prazgodovino, ko je bilo človekovo preživetje neposredno odvisno od poznavanja rastlin in njihovega okolja. Kasneje se zametki ekologije rastlin pojavljajo v delih Aristotela in Teofrasta (SMITH & SMITH 2001). V 18. stoletju najdemo opise rastlin in njihovega okolja v delih Buffona in Humbolta, v 19. pa Darwina, Cowlesa in Heckla, ki je prvi uporabil in opredelil besedo ekologija (GUREVITCH & al. 2002). Heckel je vključil v ekološko znanost različna področja poznavanja organizmov kot so fiziologija, morfologija in horologija, ki so nujno potrebna za razumevanje okoljskih razmer in prilagajanja (SCHULZE & al. 2002). To so tudi izhodišča za glavne smeri ekologije, ki so se kasneje razvile. Zaradi skromne tehnologije, ki je bila na razpolago za raziskave, je bilo sprva težišče raziskovalnega dela na proučevanju okoljskih dejavnikov rastišča in njihovega vpliva na rastlinstvo. Nastali sta prvi dve panogi rastlinske ekologije: autekologija, ki je proučevala vpliv okolja na posamezne rastline/vrste, in sinekologija, ki se je usmerila v proučevanje rastlinskih združb. Ker pa problematika rastlinskih združb ni samo ekološka, se je v tridesetih letih 20. stoletja sinekologija preimenovala v fitosociologijo in kasneje v fitocenologijo. Autekologija se kasneje razvila v ekofiziologijo, katere razvoj je omogočil hiter razvoj merilnih tehnik, s katerimi lahko spremljamo odvijanje življenjskih procesov pri rastlinah v naravnem okolju. Ekofiziologija

object of interest for researchers in Slovenia and worldwide. Studies of plants in extreme environments are essential from the point of view of global changes as these plants are potential candidates for revegetation of polluted, salt affected and disturbed areas.

This contribution presents an overview of plant ecology in Slovenia stressing the ecology of plants in extreme habitats.

Development of plant ecology

Plant ecology comprises different subdisciplines with different traditions and developments. It was of practical interest very early in human history, because the knowledge of environment was essential for survival of primitive society. The ecological science developed gradually throughout the history. The works of Aristotle and Teofrast in ancient Greece already contained some important ecological principles (SMITH & SMITH 2001). In 18th century different aspects of plant ecology can be found in writings of Buffon and Humbolt, and in 19th century works of Darwin, Cowles and Heckel. The latter first proposed and defined the word ecology (GUREVITCH & al. 2002). Heckel included in the science of ecology the areas physiology, morphology in chorology to understand environmental conditions for existence and adaptations of organisms (SCHULZE & al. 2002). Those areas were the basis for further development of ecology. Early studies of plant ecology were limited by modest technology. The majority of researches concentrated on the effects of environmental factors on plants. Two subdisciplines developed: autecology which was directed to the single species and their response to environmental factors and synecology comprising the studies of plant communities. The study of plant communities is not only an ecological issue that is why the term phytosociology appeared in the 30-ies of the 20th century, which latter on became phytosociology. Autecological research was upgraded by ecophysiological studies, which were enabled by quick development of measuring techniques. Ecophysiology presents an important subdiscipline of plant ecology, comprising the measurement of environmental parameters and their effect on life processes and structure i.e.

predstavlja pomembno vejo rastlinske ekologije, saj združuje raziskave okoljskih dejavnikov na rastišču rastline in njihov vpliv na zgradbo in funkcijo oz. proučuje funkcionalne prilagoditve rastlin na okolje na morfološko-anatomskem, biokemijskem in fiziološkem (ekofiziološkem) nivoju (LARCHER 2002). Danes rastlinska ekologija poleg vseh omenjenih področij vključuje tudi proučevanje strukture in dinamike rastlinskih populacij in globalne vplive na rastline (CRAWLY 1997, CRAWLY 1997, GUREVITCH & AL. 2002). Rastlinska ekologija pa ima pomembno vlogo tudi v agronomiji, gozdarstvu ter na področju varstva okolja in ohranjanja narave.

Pouk rastlinske ekologije na Univerzi v Ljubljani

Pouk rastlinske ekologije na Univerzi v Ljubljani se je pričel dokaj pozno. V študijskem letu 1965/66 je bil za 2. letnik študija Biologija uveden eno-semesterški predmet Ekologija rastlin, ki ga je predaval prof. Miran Vardjan. V polnem obsegu pa se je organizirano pedagoško delo – predavanja, vaje, terenske vaje – pričelo šele v študijskem letu 1968/69, ko je nastopil docent Andrej Martinčič. Rastlinska ekologija je bila sprva vključena v predmet Geobotanika, skupaj s Fitogeografijo in Fitocenologijo. Kasneje je bil predmet Geobotanika razdeljen na predmeta Ekologija rastlin ter Fitogeografija in fitocenologija. Tako je postala rastlinska ekologija eden izmed osnovnih predmetov v študiju biologije. Področje ekologije rastlin je postajalo v raziskovalnem pogledu vse bolj obsežno in kompleksno, kar se je odrazilo tudi na pedagoškem področju. V 80.-tih so bili uvedeni nekateri novi predmeti, npr. Primarna produkcija, z določenim deležem pa je bila problematika ekologije rastlin vključena tudi v predmete Ekosistemi ter Onesnaževanje in varstvo okolja, ki se je kasneje preimenoval v Varstvo okolja in naravne dediščine. Pred nekaj leti se je na podiplomskem študiju Varstvo okolja se je oblikoval nov predmet Spremembe okolja in rastline. Vsebine predmetov so se vseskozi posodabljal. Dolga leta se je izvajal študij rastlinske ekologije samo na Oddelku za biologijo Biotehniške fakultete Univerze v Ljubljani. Šele v devetdesetih se je začel izvajati tudi na nekate-

studying plant adaptations at functional, anatomical, morphological and biochemical levels. (LARCHER 2002). Today beside above mentioned areas plant ecology covers also the researches of plant populations' structure and dynamics and global impacts on plants (CRAWLY 1997, GUREVITCH & AL. 2002).

Plant ecology has also an important role in agronomy and forestry as well as in environment protection and nature conservation.

The study of plant ecology at University of Ljubljana

The study of plant ecology at University of Ljubljana started rather late. In the school year 1965/66 one semester Plant ecology course was organised in the 2nd year of the study of Biology. The lectures were given by profesor Miran Vardjan. Plant ecology gained more importance during the school year 1968/69, when assistant professor Andrej Marinčič started his work. At the beginning plant ecology was a part of the course of Geobotany together with phytogeography and phytocenology. Some years later two separate courses were organised; namely Plant ecology and Phytogeography and phytocenology. Plant ecology became one of the basic courses in biology study.

The plant ecological research became more and more complex what had reflected also in courses. In 80-ties a new course Primary production was introduced at the Department of Biology, and some aspects of plant ecology became a part of the courses Ecosystems and Environment pollution and protection, later becoming Environment and nature protection. Some years ago a course Environmental changes and plants was established at the post-graduate study Environment protection. All the courses were continuously updated. For a long time the study of plant ecology in Slovenia took place at the Dept. of Biology, only. In nineties the courses of Plant ecology started also at the Department of Agronomy (Biotechnical Faculty) and at the University of Maribor.

rih drugih oddelkih Biotehniške fakultete ter na Univerzi v Mariboru.

Razvoj raziskav v Sloveniji

V slovenskem prostoru so se s tovrstnimi raziskavami ukvarjali številni raziskovalci. Najprej, še pred uvedbo rastlinske ekologije v študijski proces na Oddelku za biologijo, so se tovrstne raziskave in ugotovitve pojavljale deloma v florističnih, nekoliko bolj pa v fitocenoloških raziskavah. Obsegale so analizo nekaterih okoljskih dejavnikov na rastišču določenih vrst ali združb. Analize so bile sicer zgolj deskriptivne, vendar jih lahko štejejo za predhodnico kasnejših raziskav na področju rastlinske ekologije, kjer je izhodišče merjenje okoljskih dejavnikov in morfološko-anatomske, biokemijske in funkcionalne prilagojenosti rastlin. Prav tako kot pri izobraževanju je tudi pri raziskavah dal slovenski rastlinski ekologiji pomemben pečat A. Martinčič. Ukvarjal se je s florističnimi in ekološkimi raziskavami skrajnih rastišč: mrazišč, vhodov v jame in jam z umetno osvetlitvijo, visokih in nizkih barij ter presihajočega Cerkniškega jezera. Svoje delo je predstavil v prispevkih o ekologiji mrazišč (MARTINČIČ 1977), flori jam z umetno osvetlitvijo (MARTINČIČ & al. 1981) in o morfološko-anatomskih prilagoditvah rastlin v njih (MARTINČIČ & BATIČ 1979), skupaj z M. Piskernikom je napisal monografijo o visokih barjih v Sloveniji (MARTINČIČ & PISKERNIK 1985) in v Monografiji o Cerkniškem jezeru objavil dva ekološko obarvana prispevka o flori in vegetaciji tega posebnega ekosistema (MARTINČIČ & LESKOVAR 2002, MARTINČIČ 2002). Z razvojem rastlinske ekologije v svetu so se začele razvijati tudi tehnike in pripomočki, ki so omogočali meritve delovanja rastlin v naravnem okolju. Rastlinska ekologija je bila bogatejša za novo smer, ekofiziologijo. A. Martinčič je že v osemdesetih letih začel proučevati funkcionalne (fotosintezo, transpiracijo, učinkovitost izrabe sevanja) in morfološke prilagoditve rastlin različnih skrajnih rastišč. S tega področja je nastalo precej člankov, ki povzemajo ekofiziološke raziskave šotnih mahov (GABERŠČIK & MARTINČIČ 1987) in rastlin v presihajočih razmerah (GABERŠČIK & MARTINČIČ 1992). Ekofiziološka problematika

The development of research in Slovenia

In Slovenia plant ecology became a subject of research for many scientists. Before the introduction of plant ecology in the pedagogical process, plant ecological research was part of floristic and phytocenologic research. They comprised the analyses of environmental parameters of habitats of some species and communities. Even though the analyses were mainly descriptive, they presented the basis for development of plant ecology studying environmental conditions and morphological, anatomical, biochemical and functional adaptations of plants. Like in the educational process, A. Martinčič had the most important role in plant ecology research development. He dealt with floristic and ecological research of extreme habitats: habitats subjected to low temperatures, cave entrances, caves with artificial light, raised bogs and fens as well as intermittent Lake Cerknica and on adaptations of plants growing there. His researches were published in scientific articles and monographs i.e. ecology of habitats subjected to low temperatures (MARTINČIČ 1977), contributions of flora in caves with artificial light (MARTINČIČ & al. 1981) and morphological and anatomical adaptations of plants in the entrances of caves (MARTINČIČ & BATIČ 1979), together with Milan Piskernik he wrote a monograph on raised bogs in Slovenia (MARTINČIČ & PISKERNIK 1985) in the Monograph on Lake Cerknica, he published articles on flora and vegetation stressing the ecological aspects of specific habitats (MARTINČIČ & LESKOVAR 2002, MARTINČIČ 2002). The development of plant ecology science resulted in different techniques and tools that enabled the measurements of plant activity in nature and the development of ecophysiology. In early eighties A. Martinčič started the researches of functional (photosynthesis, transpiration rate, light use efficiency, ...) and structural adaptations of the plants of extreme habitats. These researches resulted in many articles summarizing the ecophysiological studies of peat mosses (GABERŠČIK & MARTINČIČ 1987) and plants in intermittent habitats (GABERŠČIK & MARTINČIČ 1992).

Numerous plant ecologists started their work in the research group of professor Martinčič, completing their PhDs within the group and later on specialised for different applied and

je zastopana tudi v več diplomskih nalogah. V raziskovalni skupini A. Martinčiča so se kalili in zaključili svoja učna leta številni rastlinski ekologi, ki so kasneje razvijali nove smeri. Franc Batič se je posvetil bioindikaciji s pomočjo lišajev in proučevanju učinkov onesnaženega zraka na rastline (npr.: JERAN & al. 1995, BATIČ & al. 1999, AL SAYEGH-PETKOVŠEK & al. 2008, POLIČNIK & al. 2008). Danijel Vrhovšek se ukvarja z algami in remediacijo okolja (npr.: MULEC & al. 2007, VOVK-KORŽE & VRHOVŠEK 2007). Alenka Gaberščik se je posvetila ekofiziološkim raziskavam rastlin skrajnih rastišč in rastlin, rastočih v razmerah različnih stresov (UV-B sevanje in suša) (GERM & al. 2007, TROŠT SEDEJ & GABERŠČIK 2008) ter ekologiji vodnih rastlin (GERM & al. 2000, KU HAR & al. 2007, KRŽIČ & al. 2007, GERM & al. 2008), nadaljevala pa je tudi Martinčičeve raziskave na presihajočem Cerkniskem jezeru (GABERŠČIK 1989, GABERŠČIK & URBANC-BERČIČ, 2002A; GABERŠČIK & URBANC-BERČIČ, 2002B). V okviru skupine pa so svoje doktorsko delo zaključili še Aleksander Vukovič, ki se je ukvarjal z ekologijo bentosa, Nada Praprotnik, ki je postala kustodinja v Prirodoslovnem muzeju Slovenije, in Andraž Čarni, ki se ukvarja tako s fitocenološkimi, kot tudi z ekološkimi raziskavami.

Raziskave danes

Danes postajajo meritve v naravi oziroma raziskave rastlin iz naravnega okolja vse bolj pogoste, za razumevanje procesov in sprememb v naravi pa tudi nujno potrebne. Na takšen način danes raziskujejo tudi številni rastlinski fiziologi, katerih težišče raziskav je bilo do nedavna vezano na laboratorije in rastne komore. Z meritvami okoljskih parametrov pa podpirajo svoje raziskave tudi fitocenologi. Zaradi človekovega delovanja in globalnih sprememb mnoge površine niso več optimalne za razvoj obstoječe rastlinske združbe. Spremembe vodijo v propad vegetacije in dezertifikacijo, obremenjenost tal s težkimi kovinami, zasoljevanje, nepredvidljivost vodnega režima in presihanje. Zato postajajo študije rastlin, ki so sposobne uspevanja na takšnih območjih, vse bolj pomembne.

Slovenski raziskovalci so v presihajočih vodnih telesih ugotovili prevlado tako imeno-

scientific fields of plant ecology. Franc Batič dedicated his research work mainly to bioindication with lichens and effects of air pollution on plants (JERAN & al., 1995, BATIČ & al., 1999, AL SAYEGH-PETKOVŠEK & al., 2008, POLIČNIK & al., 2008). Danijel Vrhovšek deals with algae and ecoremediation (MULEC & al., 2007, VOVK-KORŽE & VRHOVŠEK, 2007). Alenka Gaberščik specialized for ecology of aquatic plants (GERM & al. 2000, KU HAR & al. 2007, KRŽIČ & al. 2007, GERM & al. 2008), ecophysiological research of plants and plants exposed to different stresses (UV-B radiation and drought) (GERM & al. 2006; GERM & al. 2007, TROŠT SEDEJ & GABERŠČIK, 2008) and she continued the Martinčič's research of intermittent habitats (GABERŠČIK, 1989, GABERŠČIK & URBANC-BERČIČ, 2002A; GABERŠČIK & URBANC-BERČIČ, 2002a). Within the research group also completed their PhDs Aleksander Vukovič, who dealt with the ecology of bentos, Nada Praprotnik, who became a curator in Natural History Museum of Slovenia and Andraž Čarni, who deals with phytocenological and ecological research.

Research of extreme habitats today

Nowadays plant research and measurements in natural habitats are becoming frequent, because they are of primary importance for understanding the processes and changes in environment. Such an approach is also used by many plant physiologists who used to work in laboratories and growth chambers. Ecophysiological approach is also important aspect of some phytocenological studies.

Due to antropogenic impacts and global changes many habitats usually do not offer optimal conditions for plant development. Changes lead to decline of plant communities and desertification, soil pollution with heavy metals, salinisation, unpredictability of water regime and intermittence. Therefore the outcomes of the studies of plants in extreme habitats are becoming of vital importance.

The studies of intermittent habitats revealed the dominance of amphibious plant species, possessing numerous adaptations, which enable plants to cope with changeable environment (KRŽIČ & al., 2007). Terrestrial specimens pro-

vanih amfibijskih rastlin (KRŽIČ & al. 2007), ki imajo številne prilagoditve, ki jim omogočajo preživetje v spreminjajočih se razmerah. Rastline na kopnem proizvedejo več snovi, ki absorbirajo UV-B sevanje, medtem ko se v vodi pred škodljivimi učinki sevanja zaščitijo s povečano količino karotenoidov in antocianov. Raziskave koreninskega sistema so pokazale razvitost aerenhima in prisotnost arbuskularne mikorize, ki ima pomembno vlogo pri privzemu hranil in vode iz mineralno revnih in občasno izsušenih tal. Pri nekaterih amfibijskih vrstah so prvič ugotovili kolonizacijo z mikoriznimi glivami. Tako kopne kot vodne oblike rastlin učinkovito izrabljajo svetlobo. Pojav heterofilnosti in različnih rastnih oblik omogoča nemoteno aktivnost v vodi in na kopnem (GERM 2002, GERM & GABERŠČIK 2003, KRŽIČ & al. 2005, KRŽIČ & al. 2007).

Halofilno vegetacijo slovenske obale raziskujeta KALIGARIČ in ŠKORNIKOVA (2006). Raziskave rastlin solin so prinesle novosti s področja kolonizacije korenin z mikoriznimi glivami (SONJAK & al. 2007). Stopnja mikorizacije rastlin in revegetacija pa so bili glavni predmet raziskav s težkimi kovinami obremenjenih območij (REGVAR & al. 2006).

Z vidika današnjih sprememb koncentracij CO₂ v ozračju so pomembne tudi raziskave rastlin v okolici vrelcev CO₂. S tovrstnimi raziskavami se ukvarjata raziskovalni skupini F. Batiča in M. Kaligariča. Povečane koncentracije CO₂ so izzvale različne fiziološke in morfološke učinke pri travniških vrstah (MARCHI & al. 2004, KALIGARIČ & al. 2008). Raziskave pa so obsegale tudi fotosintezne odzive in meritve potencialne respiracije korenin pri različnih vrstah (VODNIK & al. 2002, MAČEK & al. 2005). Učinki na anatomijo vrste *Juncus effusus* so predstavljeni v članku TURKA in sodelavcev (2002).

Posebne razmere pa lahko nastanejo tudi na nekaterih drugih rastiščih. To so gozdni robovi, katerih zgradba, ekologija in vrstna sestava je bila predmet raziskav ČARNIJA in sodelavcev (2005). Posebne razmere za Slovenijo so tudi v vodnih habitatih s povišano temperaturo v rokavu reke Save, kjer se je množično pojavila tropska vrsta *Pistia stratiotes*. Razmere za njeno preživetje in razširjanje je raziskovala ŠAJNA s sodelavci (2007). Zaostrene razmere s pogostimi motnjami so teptana rastišča, ki jih je proučeval ČARNI (2005).

duced more UV-B absorbing substances, while aquatic specimens cope with high light intensity by production of increased concentrations of anthocyanins and carotenoids. The research of root system gave an insight into aerenchyma development and mycorrhiza development, playing important role in nutrient and water uptake from mineral poor and occasionally dry soil. In some amphibious species the colonisation with mycorrhizal fungi was determined for the first time. The appearance of heterophylly and different growth forms enable the activity in water and on dry land (GERM, 2002, GERM & GABERŠČIK, 2003, KRŽIČ & al. 2005, KRŽIČ & al. 2007).

Halophile vegetation of the Slovenian sea-coast are researching KALIGARIČ and ŠKORNIK (2006). The researches on halophytes contributed new knowledge on mycorrhizal colonisation of roots (SONJAK & al. 2007). The level of mycorrhizal colonisation and efficiency of revegetation were the main topics of the researches of the habitats loaded with heavy metals (REGVAR & al. 2006).

From the aspect of greenhouse effect we should stress the importance of the researches of plants growing in the vicinity of CO₂ springs. Two research groups in Slovenia are involved in CO₂ research: the research group of F. Batič and M. Kaligarič. Increased concentrations of CO₂ exerted different effects at functional and structural level of meadow plants (MARCHI & al., 2004, KALIGARIČ & al., 2008). The study comprised the measurements of photosynthesis and potential respiration of plants in different species (VODNIK & al., 2002, MAČEK & al., 2005). The effects on the species *Juncus effusus* anatomy are presented in the article of TURK and co-workers (2002).

Outstanding conditions occur also in some other habitats. Among them we should mention forest edges. Their floristic structure and ecology is the interest of ČARNI and co-workers (2005). In Slovenia we found extreme habitats also in the oxbow of the river Sava, with enhanced temperature, which became the habitat of the tropic species *Pistia stratiotes*. The conditions for their survival and potential of spreading were examined by ŠAJNA and co-workers (2007). Extreme conditions with frequent disturbances occur also in trampled habitats, which were studied by ČARNI (2005).

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