

**Effects of
Experimental Disturbances**



**on Microsites
and
Plant Demography**

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**EFFECTS OF EXPERIMENTAL DISTURBANCES
ON MICROSITES AND PLANT DEMOGRAPHY**



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ANNOTATION: The thesis includes (I) studies of the effects of experimental disturbance treatments on microsites and demography of the endangered strict biennial *Pedicularis sylvatica* in Czech wet meadows, and consequences for species conservation and habitat management, and (II) studies of seedling recruitment in experimental gap microsites in Florida scrub, and the effects of mobile sand in gaps and roads on microsites and demography of herbaceous scrub plants.

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Martina Petřů

Martina Petřů

České Budějovice 17 April 2002

VĚNOVÁNÍ: Věnováno mým rodičům Věře a Milanovi Petřů.

DEDICATION: Dedicated to my parents Věra and Milan Petřů.

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Poděkování

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Introduction

Disturbances and their physical effects, varying in extent, frequency and intensity, widely influence spatial and temporal heterogeneity of many ecosystems (e.g. White 1979; Denslow 1984; Sousa 1984). Disturbances also affect microhabitats of component species in ecosystems, species' relative abundances, demography, life history traits, and population distribution and dynamics (e.g. Pickett & White 1985; Bowles et al. 1990; Quintana-Ascencio & Morales-Hernandez 1997; Löfgren et al. 2000; Lennartsson & Oostermeijer 2001). Large-scale natural disturbances, such as fires, droughts, floods, hurricanes, tornados, ice storms, landslides, etc., have important implications for structure of many natural habitats, often creating large openings in the canopy of dominant vegetation (e.g. White 1979; Denslow 1984; Sousa 1984).

Fires are examples of such disturbances in shrub- and tree-dominated ecosystems, creating canopy gaps (Wilczynski & Pickett 1993; Ehrenfeld et al. 1995; Connell et al. 1997). Gaps are often important microhabitats supporting populations of herbaceous understory species and providing favorable microsites for seedling recruitment (Menges & Hawkes 1998; Quintana-Ascencio & Morales-Hernandez 1997; Ostertag 1998). With time since fire, shrubs and woody plants encroach in large gaps, reducing gap area and finally closing gaps, while new gaps are created in the next disturbance event (Menges & Hawkes 1998; Young & Menges 1999). Fire-return intervals direct this small-scale gap dynamics of gap creating and closure, and alter the demography of gap-colonizing species (Quintana-Ascencio & Menges 1998; Quintana-Ascencio & Menges 2000; Menges & Quintana-Ascencio, in prep.). Also in grasslands, fires are important disturbances, creating gaps. Gap closure can be accomplished

by grasses, and shrub and tree encroachment can also occur with infrequent or no fire. The periodicity of fire-return intervals has changed since humans started to manage fire-prone ecosystems, regulating fire regimes by prescribed burning, suppressing fire and altering the seasonality of burns, or substituting mechanical treatments for fires (Forst 1998).

Natural disturbance regimes have been also altered by intensive habitat use, typical for European landscape, where anthropogenic disturbances have largely replaced natural disturbance regimes. Several natural habitats have been substantially modified. Examples of semi-natural habitats are grasslands and meadows, which nowadays occupy large areas of landscape after deforestation. These grasslands were historically maintained by mowing and grazing regimes, which limited the abundance of woody and shrubby plants. Being performed for centuries, the management regimes became traditional and many grassland species adapted their life histories to such disturbances (e.g. Bazzaz 1983; Pavlovic 1994; Lennartsson & Svensson 1996; Lennartsson & Oostermeijer 2001). Mowing periodically removed accumulated biomass and grazing and animal trampling created gaps, such as openings in vegetation and patches of bare ground (Eriksson 1996; Lennartsson & Svensson 1996) increasing microsite heterogeneity.

Gaps are common consequences of periodical disturbances such as mowing, grazing, or fire. Gaps vary substantially in size among habitats, depending on intensity and scale of disturbance effects. Gap sizes of several square meters are common in forests and shrublands (e.g. Hawkes & Menges 1998; Young & Menges 1999; Holeksa & Cybulski 2001; Coates 2002), while small gaps (several centimeters or decimeters) are typical of grasslands (Bullock et al. 1995). Variable gap sizes imply

variable mechanisms of creating favorable microsites for plants (Hawkes & Menges 1998). However, the general effects of gaps in favoring regeneration seem to be common across many ecosystems (Hawkes & Menges 1996; Menges & Hawkes 1998; Young & Menges 1999; Quintana-Ascencio et al. 1998; Sherman et al. 2000; Narukawa & Yamamoto 2001; Collins & Battaglia 2002).

Gaps are essentially microhabitats providing favorable microsites for seedling establishment of colonizing species (Grubb 1977 and e.g. Kelly 1989b; Weller 1989; Bullock et al. 1995; Quintana-Ascencio & Morales-Hernandez 1997; Kotorová & Lepš 1999), thereby affecting species demography (Morgan 1997; Fisher & Matthies 1998a, 1998b; Geisselbrecht-Taferner et al. 1997; Löfgren et al. 2000; Eriksson & Eriksson 2000). Plants utilize gaps by ramet ingrowth (Winn 1985; McConnaghay & Bazzaz 1987; Bullock et al. 1995) or recruit seedlings (Edwards & Crawley 1999; Kotorová & Lepš 1999; Menges and Kohfeldt 1995; Hawkes & Menges 1996; Menges & Hawkes 1998; Young & Menges 1999). Microsites for rare and endangered or endemic species are particularly important for species conservation efforts. Exploring the relationship between management regimes and microsite availability for seedling establishment may optimize sustainable management strategies for species persistence (e.g. Fisher & Matthies 1998a, 1998b; Quintana-Ascencio & Menges 1998; Lennartsson & Oostermeijer 2001; Menges & Quintana-Ascencio, in prep.).

To assess disturbance effects on microsites and plant demography requires experimental testing under field conditions (e.g. Křenová & Lepš 1996; Fisher & Matthies 1998a, 1998b; Kotorová & Lepš 1999; Kiviniemi 2001). Results of field experiments manipulating species' microsites or mimicking disturbance regimes often have implications for species'

demography (McEvoy & Rudd 1993; Löfgren et al. 2000; Lennartsson & Oostermeijer 2001) and consequently may influence management strategies to ensure viable populations.

This thesis integrates experimental studies of disturbance effects on microsites and plant demography in two distinct habitats, the xeric shrublands in Florida (Florida scrub) and wet meadows in the Czech Republic. Florida scrub is an ancient xeric shrub-dominated ecosystem inhabiting relict inland sand beaches and upland ridges. Florida scrub is periodically disturbed by large-scale fires, which may maintain small-scale gap dynamics. Also, anthropogenic disturbances such as firelanes, plow lines and sandy roads occur in Florida scrub and have been shown to host higher population densities of some herbaceous scrub species than in post-fire gaps within the shrub matrix. I studied disturbance effects on several endangered species endemic to Florida scrub, as well as common species widely distributed in the scrub habitats. I explored how disturbances create microsites for species regeneration in open gaps in Florida scrub and along roadsides and how dynamic microsites, such as mobile sands, are important for the demography of scrub herbs. Since many of the scrub species are endangered and endemic, understanding their microsite requirements is important for effective species conservation and management of the Florida scrub ecosystem.

Wet meadows in the Czech Republic represent semi-natural habitats largely affected by management regimes, such as mowing and grazing that promote co-existence of a many plants including several endangered species. I focused on the effects of experimental disturbances mimicking management regimes for an endangered species *Pedicularis sylvatica*. This species has been declining over the last 3-4 decades being sensitive to changes in habitat quality and management regime. I studied microsite

limitations of seedling recruitment and annual variation in species demography, and consequences of disturbances for population dynamics and species' performance under changing environmental conditions. I discuss effective management strategies, which allow persistence of this strictly biennial species.

Thesis organization

This thesis consists of two independent sections representing case studies of experimental disturbance effects on microsites and plant demography in the two ecosystems introduced above. Each section has two chapters. **Chapter 1** in **Section I** explores effects of experimental disturbances mimicking management regimes, on microsites for seedling establishment of *Pedicularis sylvatica* in wet meadows in the Czech Republic. This chapter is a rather short and introductory study to **Chapter 2**, which extends the previous text to annual variation in demography of *Pedicularis*, emphasizing the strictly biennial life cycle and experimental disturbance effects on species population dynamics. This chapter was submitted in full length as a Proceedings paper of the 44th International Association of Vegetation Science meeting in Germany in 2001, to *Journal of Vegetation Science* in March 2002. **Section II** includes studies from the Florida scrub. **Chapter 3** documents seedling establishment in natural and experimental gap microsites in variable weather conditions. This manuscript was prepared in collaboration with Eric Menges, and was submitted to *Journal of the Torrey Botanical Society* in January 2002. **Chapter 4**, an early manuscript draft, explores effects of dynamic microsites maintained by mobile sand for germination, seedling survival and demography of scrub herbs. A bilingual English – Czech **Summary - Souhrn** briefly integrates the major chapters' results in the broader

context of the thesis topic. Some general ideas and future perspectives are presented in **Concluding Remarks**. Chapters are written in standard format with tables and figures attached at the end of each chapter.

Poděkování - Acknowledgments and **References** are common for all chapters together (acknowledgments at the beginning of the thesis and references at the end. An **Appendix** includes list of oral papers and poster presentations of some of the chapters, and thesis related publications.

Úvod

Disturbancemi¹⁾, ve smyslu velkých přírodních katastrof, malo- či velkoplošného narušení přírodních podmínek ekosystémů a vnějších abiotických a biotických vlivů, včetně antropogenních, se zabývá rozsáhlá ekologická literatura (např. White 1979; Denslow 1984; Sousa 1984). Rozsah a frekvence disturbancí mohou význačně ovlivňovat strukturu, funkce a dynamiku ekosystémů, a také mikrostanovištní podmínky pro mnohé rostlinné a živočišné druhy, relativní abundance druhů, demografii, životní cykly a strategie, a distribuci populací a jejich dynamiku (např. Pickett & White 1985; Bowles et al. 1990; Quintana-Ascencio & Morales-Hernandez 1997; Löfgren et al. 2000; Lennartsson & Oostermeijer 2001). Velkoplošné přírodní katastrofy (požáry, sucha, záplavy, hurikány a tornáda, sněhové bouře, sesuvy půdy, aj.) mají velký význam pro strukturu mnohých ekosystémů.

Příkladem takových velkoplošných disturbancí jsou požáry v travinných, křovinných a lesních ekosystémech, zejména Severní

¹⁾ Vzhledem k mnohovýznamosti termínu jej zde používám v originálním znění bez českého překladu s bližším přiblížením významu v kontextu.

Ameriky. Fyzickým následkem požárů jsou rozsáhlé prostory zbavené vegetace, tzv. gapy (White 1979; Denslow 1984; Sousa 1984; Wilczynski & Pickett 1993; Ehrenfeld et al. 1995; Connell et al. 1997). Gapy jsou obvykle důležitými mikrostanovišti poskytujícími příhodné podmínky pro uchycení semenáčků mnohých bylinných druhů podrostu (Menges & Hawkes 1998; Quintana-Ascencio & Morales-Hernandez 1997; Ostertag 1998). S prodlužujícími se intervaly mezi jednotlivými požáry, křovinná a stromová vegetace zarůstá gapy od okrajů, plocha gapů se zmenšuje a gapy mizí, a jsou nahrazovány nově vytvořenými gapy při následujícím požáru (Menges & Hawkes 1998; Young & Menges 1999). Tuto maloplošnou dynamiku vzniku a zániku gapů usměrňují intervaly mezi jednotlivými požáry, a tyto intervaly mohou významně ovlivňovat demografii rostlinných druhů na gapy vázaných (Quintana-Ascencio & Menges 1998; Quintana-Ascencio & Menges 2000; Menges & Quintana-Ascencio, in prep.). S nástupem lidských aktivit do požárových ekosystémů, byla periodičita intervalů mezi požáry výrazně pozměněna (Forst 1998). Požárový režim byl v nedávné minulosti potlačen, sezonalita požárů narušena a v současnosti jsou požáry organizovány (tzv. prescribed burning) nebo nahrazeny mechanickými zásahy odstraňujícími naakumulovanou biomasu a opad. Požáry hrají významnou roli i travinných ekosystémech, kde také vytvářejí gapy, jejichž velikost a proporce jsou ovlivněny nepravidelným režimem požárů, nebo jejich vyloučením.

Přirozený režim disturbancí výrazně změnilo intenzivní využívání stanovišť, typické pro evropskou krajinu. Mnohá stanoviště byla zásadně pozměněna v důsledku jejich integrace do kulturní krajiny a antropogenní zásahy nahradily přirozený disturbanční režim. Klasickým příkladem takových polopřirozených stanovišť jsou luční společenstva, která v

současnosti osidlují rozsáhlé plochy v odlesněné krajině. Tato společenstva přetrvávají historicky udržována tradičním režimem kosení a pastvou, které zabraňují zarůstání keří a stromy. Management údržby luk kosením a pastvou byl provozován po staletí a mnohé rostlinné druhy se těmto režimům přizpůsobily svými životní cykly. Pro přežívání mnohých bylinných druhů se pravidelný režim obhospodařování luk stal kritickým (e.g. Bazzaz 1983; Pavlovic 1994; Lennartsson & Svensson 1996; Lennartsson & Oostermeijer 2001). Kosení periodicky odstraňuje vyprodukovanou biomasu a pastva a pohyb stád skotu či ovcí spásá biomasu a sešlapává substrát, čímž vytráří prohlubně, gapy – plošně nerozsáhlé prostory obnažené půdy zvyšující heterogenitu mikrostanovišť (Eriksson 1996; Lennartsson & Svensson 1996).

Gapy jsou běžným a frekventovaným následkem periodických disturbancí, managementu nebo požárů, jak byly zmíněny dříve. Velikost gapů se liší mezi stanovišti v závislosti na intenzitě a rozsahu disturbance. Gapy velikosti několika metrů čtverečních jsou běžnou součástí lesních a křovinných společenstev (např. Hawkes & Menges 1998; Young & Menges 1999; Holeksa & Cybulski 2001; Coates 2002), naproti tomu gapy velikosti několika centimetrů a decimetrů jsou typické pro luční společenstva (Bullock et al. 1995). Variabilní velikost gapů může ovlivnit mechanismy kterými se mikrostanoviště stávají příhodnými pro rostlinné druhy (Hawkes & Menges 1998), nicméně výsledný význam gapů pro regeneraci rostlinných druhů je zřejmě shodný v různých ekosystémech (Hawkes & Menges 1996; Menges & Hawkes 1998; Young & Menges; Quintana-Ascencio et al. 1998; Sherman et al. 2000; Narukawa & Yamamoto 2001; Collins & Battaglia 2002).

Gapy poskytují regenerační niky a umožňují vzcházení semenáčků kolonizujících druhů (Grubb 1977 and e.g. Kelly 1989b; Weller 1989;

Bullock et al. 1995; Kotorová & Lepš 1999), a mohou ovlivnit jejich demografické parametry (Morgan 1997; Fisher & Matthies 1998a, 1998b) a populační dynamiku (Geisselbrecht-Taferner et al. 1997; Löfgren et al. 2000; Eriksson & Eriksson 2000). Rostliny kolonizují gapy vrústem ramet (Winn 1985; McConnaghay & Bazzaz 1987; Bullock et al. 1995) nebo klíčí ze semen (Edwards & Crawley 1999; Kotorová & Lepš 1999; Menges & Kohfeldt 1995; Hawkes & Menges 1996; Menges & Hawkes 1998; Young & Menges 1999).

Gapy jako mikrostanoviště pro regeneraci jsou důležité pro vzcházení semenáčků ohrožených a endemických druhů a jejich následnou ochranu a management. Testování vztahů mezi režimy obhospodařování a regenerací druhů může výrazně přispět ke stanovení optimálního režimu obhospodařování na stanovištích a úspěšnou ochranu druhů in situ (e.g. Fisher & Matthies 1998a, 1998b; Quintana-Ascencio & Menges 1998; Lennartsson & Oostermeijer 2001; Menges & Quintana-Ascencio, in prep.).

Zhodnocení vlivu disturbancí na mikrostanoviště a demografii druhů vyžaduje experimentální testování v terénu. Řada experimentálních prací zabývajících se touto problematikou již byla prezentována (např. Křenová & Lepš 1996; Fisher & Matthies 1998a, 1998b; Kotorová & Lepš 1999; Kiviniemi 2001). Výsledky terénních experimentů, manipulujících mikrostanoviště nebo testujících režim managementu často dokumentují důležité parametry ovlivňující demografii druhů (McEvoy & Rudd 1993; Löfgren et al. 2000, Lennartsson & Oostermeijer 2001) a naznačují či doporučují taktiky managementu, které umožní přežívání těchto druhů ve vitálních populacích.

Tato diplomová práce zahrnuje experimentální studie vlivu disturbancí na mikrostanoviště a demografii rostlinných druhů ve dvou odlišných

ekosystémech; v xerickém křovinném systému na Floridě, U.S.A. (Florida scrub) a vlhkých loukách v České Republice. Florida scrub je původní společenstvo s dominantní křovinou vegetací, rozkládající se na reliktních vnitrozemských a přímořských písčinych dunách Floridy. Tato křovinná společenstva jsou periodicky narušována požáry, které regulují maloplošnou dynamiku vzniku a zániku gapů. Kromě požárů se v tomto ekosystému uplatňují také antropogenní disturbance, požárové linie, zákopy a cesty oddělující požárové jednotky, které zásadně ovlivňují distribuci bylinných druhů. Tyto druhy často osidlují okraje cest v mnohem větší abundanci než gapy po požárech. V tomto ekosystému jsem se zaměřila na vliv disturbancí pro několik ohrožených a endemických druhů a několik běžných druhů. Studovala jsem jak disturbance ovlivňuje mikrostanoviště pro regeneraci druhů v gapech a podél cest a jak je dynamický systém pohyblivého písčného substrátu důležitý pro mikrostanoviště a demografii druhů. Mnoho druhů tohoto ekosystému je ohrožených a endemických, tudíž objasnění druhových požadavků na mikrostanoviště je důležité pro efektivní ochranu druhů a management tohoto ekosystému.

Vlhké louky v České republice jsou polopřirozená stanoviště rozsáhle ovlivněná režimem obhospodařování, kosením a pastvou. Koexistuje zde velké množství rostlin, včetně mnoha ohrožených druhů. V tomto systému jsem se zaměřila na studium vlivu experimentálních disturbancí napodobujících režim obhospodařování pro ohrožený druh *Pedicularis sylvatica*, který v posledních třech až čtyřech desetiletích ubývá na svých stanovištích v důsledku citlivosti k změnám kvality stanoviště a režimu obhospodařování. Studovala jsem důležitost mikrostanovišť pro vzcházení semenáčků a variabilitu demografických parametrů druhu, a diskutuji jejich důsledky pro populační dynamiku a performanci druhu v

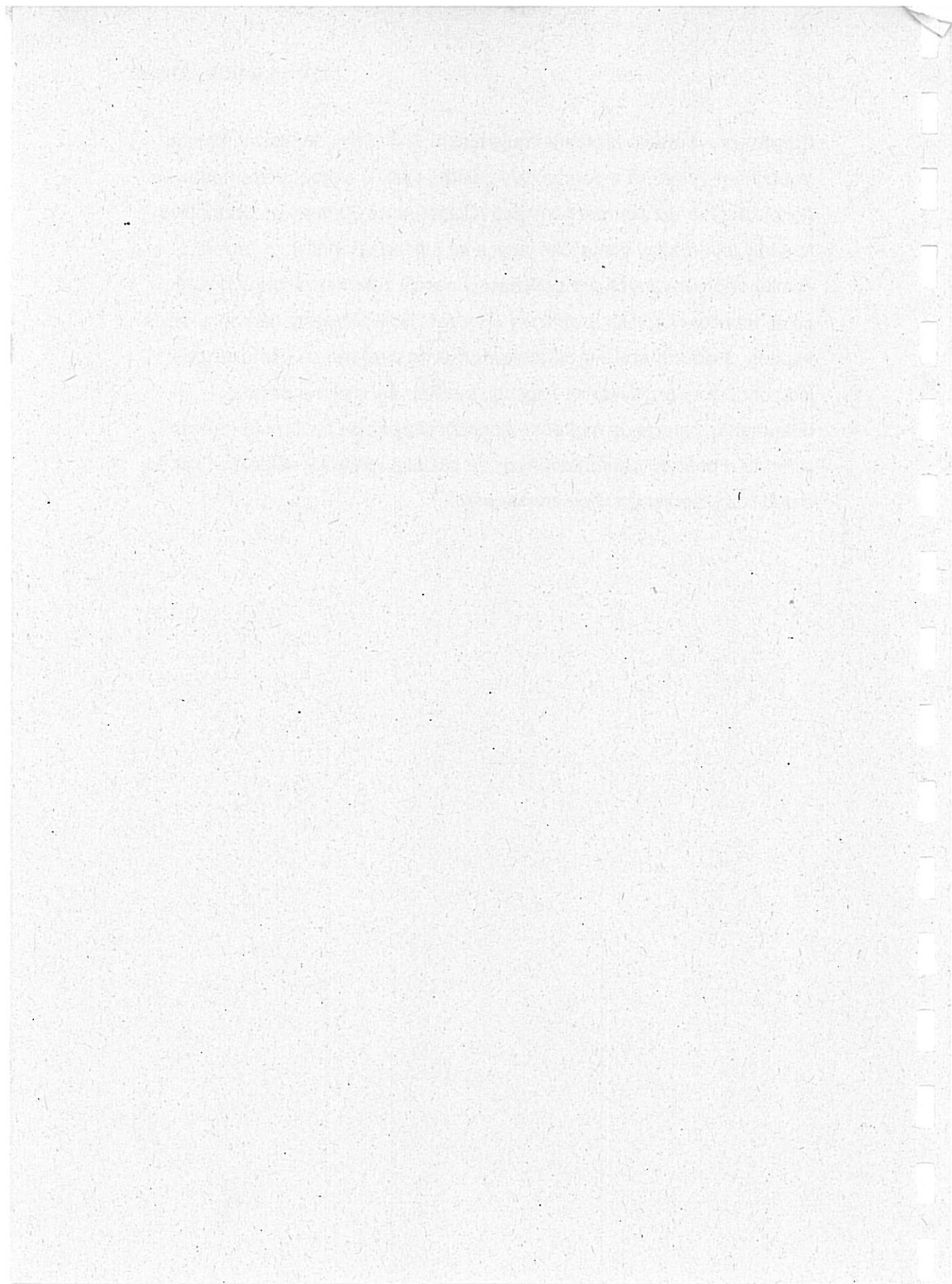
měnicích se podmínkách stanoviště, včetně efektivní strategie managementu pro tuto striktní dvouletku vlhkých luk.

Struktura diplomové práce

Tato diplomová práce se skládá ze dvou nezávislých sekcí prezentujících případové studie vlivu experimentálních disturbancí na mikrostanoviště a demografii rostlinných druhů v křovinném ekosystému Floridy a vlhkých luk v České Republice. Každá sekce má dvě kapitoly. První kapitola (**Chapter 1**) v první sekci (**Section I**) se zaměřuje na vliv experimentálních režimů obhospodařování a vytváření mikrostanovišť pro vzcházení semenáčků druhu *Pedicularis sylvatica* na vlhkých loukách v Čechách. Tato kapitola je krátkou úvodní kapitolou pro následující studii v kapitole 2 (**Chapter 2**), která rozvádí předchozí text a prezentuje meziroční variabilitu a vliv experimentálních režimů obhospodařování na demografii a populační dynamiku studovaného druhu s důrazem na striktně dvouletý životní cyklus. Tato kapitola byla v březnu 2002 poslána v plné verzi k posouzení pro publikaci jako proceeding paper 44th International Association of Vegetation Science meeting v Německu, konaného v roce 2001; proceedings konference jsou plánované jako hlavní téma nebo samostatné číslo *Journal of Vegetation Science*. Druhá sekce (**Section II**) zahrnuje studie z křovinného ekosystému Floridy. Třetí kapitola (**Chapter 3**) dokumentuje vzcházení semenáčků v přírodních a experimentálních gapech. Na tomto článku se spolupodílel Eric Menges, a společně jsme jej odeslali k posouzení pro publikaci v *Journal of Torrey Botanical Society* v lednu 2002. Poslední čtvrtá kapitola (**Chapter 4**) je ranou verzí článku, který se zaměřuje na vliv dynamických mikrostanovišť utvářených pohyblivých písčným substrátem v křovinném ekosystému Floridy na demografii tří bylinných druhů. Dvojazyčný anglicko-český

Introduction - Úvod

Summary - Souhrn krátce shrnuje hlavní výsledky jednotlivých kapitol. Zobecnění výsledků a perspektivy dalšího výzkumu jsou prezentovány v několika závěrečných poznámkách (**Concluding Remarks**). Jednotlivé kapitoly jsou psány v anglické jazyce ve standardním stylu a formátu článků připravovaných pro publikaci. Kapitoly zahrnují všechny běžné části, tabulky (Tables), a obrázky (Figures) jsou připojeny na konci každé kapitoly. **Poděkování – Acknowledgments** a reference (**References**) jsou souhrnné pro všechny kapitoly, poděkování stojí na začátku dokumentu, reference na konci. Appendix (**Appendix**) zahrnuje seznam referátů a posterů prezentovaných na základě výsledků některých kapitol a publikace spojené s diplomovou prací.



Chapter 1

Experimental microsites for *Pedicularis sylvatica*
seedlings in wet meadows



Experimental microsites for *Pedicularis sylvatica* seedlings in wet meadows

Abstract

Availability of favorable microsites is often an important requirement for seedling establishment of many herbaceous species. Microsites are frequently modified by disturbance regimes. I simulated the effects of management regimes on experimental microsites for seedlings of an endangered strict biennial *Pedicularis sylvatica*. In two populations in semi-natural wet meadows in the southern Czech Republic, I established a field experiment, manipulating *Pedicularis* microsites in five treatments. I created: (1) 'large gaps' (10 cm in diameter, 5 gaps per 0.25 m² plot with removed aboveground vegetation) to mimic cattle grazing and trampling. In the (2) 'small gaps' treatment, I removed the vegetation and created small gaps (5 cm in diameter, 5 gaps per plot) approximating the effects of sheep grazing and trampling. The (3) 'mowing and bryophyte removal' treatment had vegetation and 50% of bryophytes removed. In the (4) 'mowing' treatment, I removed aboveground vegetation, and the (5) 'control' remained undisturbed. The treatments were repeated every year in October 1997-2000. I monitored treatment effects on seedling recruitment in April/May 1998-2001. The seedling densities varied greatly among the years and differed significantly among treatments over the years. Gap plots had highest seedling densities in 1998 and 1999. Seedling recruitment varied between the two gap sizes. In some years, seedling densities in large gaps were higher than in small gaps, but this pattern was reversed in other years. Mowing plots had highest seedlings densities in 2000 and 2001. Mowing plots with bryophytes removed often

had lower seedling densities than gap and mowing plots. In control plots, the seedling densities were consistently low. Experimental treatments mimicking mowing and cattle and sheep grazing enhanced seedling densities of *Pedicularis sylvatica* in some years. These results suggest that combination of grazing and mowing management regimes in wet meadows may favor successful seedling establishment of this species.

Key words: disturbance, regeneration niche, safe site, seedling establishment, strict biennial

Nomenclature: Rothmaler 1976; Oberdorfer 1992, 1993

Introduction

Seedling recruitment of many plant species in various habitats is often related to microsite conditions such as aboveground openings in vegetation and area of bare ground in gaps (e.g. Bullock et al. 1995; Morgan 1997; Narukawa & Yamamoto 2001; Winsa & Sahlen 2001). In European semi-natural meadows, these microsites are often modified by management regimes (e.g. Zobel 2000; Kupferschmid et al. 2000; Coulson et al. 2001).

The traditional management in meadows was manual mowing, which periodically removed aboveground biomass and prevented litter accumulation. In addition, cattle or sheep grazed in the meadows and created gaps by trampling. Depending on grazing type and intensity, gaps differ in size and consequently in their effects on seedling colonization by individual species (Williams 1992; Bullock et al. 1995; Morgan 1997).

Thus, experiments exploring effects of gap size on

species performance can help to select an optimal grazing regime for focal species.

Management practices usually cannot avoid disturbance of the bryophyte layer, which is a frequent meadow component. Experimental studies removing bryophytes have found variable species responses. Bryophyte removal enhanced seedling recruitment of some vascular plants (Rabotnov 1969; Keizer et al. 1985), but had no effect on other species (Keizer et al. 1985). Removal of bryophytes can reduce favourable microsites for seedling recruitment, and also cause losses of seeds (During & Van Tooren 1990).

Microsites in meadows control seedling recruitment, which is limited to safe sites sensu Grubb (1977). Favourable microsite conditions may provide regeneration niches for seedling establishment of several meadow species (e.g. Winn 1985; McConnaughay & Bazzaz 1987; Edwards & Crawley 1999; Kotorová & Lepš 1999). Defining recruitment requirements of rare and endangered species in experimental disturbance treatments helps to optimize sustainable management strategies for species conservation (e.g. Lennartsson & Svensson 1996; Křenová & Lepš 1996; Morgan 1997; Löfgren et al. 2000; Lennartsson & Oostermeijer 2001).

In this study, I focus on management-created microsites for *Pedicularis sylvatica*, a wet-meadow species, endangered through its sensitivity to changes in habitat quality and management regimes. *Pedicularis sylvatica* is a strict biennial with seedling establishment being the only mode of regeneration. The short life span makes this species particularly sensitive to unfavorable microsite conditions with high extinction risk in local populations. Over four years (1998-2001), I explored the temporal variation of seedling recruitment in experimental

disturbance treatments (large and small gaps simulating cattle and sheep grazing, mowing and bryophyte removal). These experimental treatments mimic management regimes and allow me to evaluate management effects on microsite quality and to evaluate management strategies that may allow species persistence.

Methods

Study species

I studied *Pedicularis sylvatica* ssp. *sylvatica* L. (Scrophulariaceae); for simplicity I refer to the subspecies by its generic name. *Pedicularis* is an obligate hemiparasite from acid and nutrient poor soils with high water tables, such as fens, bogs and heathlands, and wet meadows in an elevation range of 400-1200 m a.s.l. (Hartl 1975). In the Czech Republic, the species' habitats include disturbed and trampled grass-dominated areas, bombing ranges in military training areas or woodland paths (Ter Borg 1985, pers. obs.), and meadows with *Violion caninae* or *Molinion* communities (sensu Oberdorfer 1992, 1993), managed by mowing and cattle- or sheep grazing. *Pedicularis sylvatica* used to be continuously distributed through the Czech Republic (Hendrych & Hendrychová 1998), but many populations have declined or become extinct in the last few decades due to drainage, management changes or management abandonment.

The species is a strict biennial, characterized by a two-year life span and obligate flowering in the second year after germination, regardless of size. Seedlings germinate from a transient or short-term persistent seed bank (sensu Bakker 1980; Thompson et al. 1997), establish juvenile rosettes in the first year, survive winter in buds, and flower and produce seeds during the second and final year. (For more details about the life

cycle see Chapter 2). In this study I focused on seedling responses to experimental management treatments.

Study sites

I studied *Pedicularis* seedlings in two oligotrophic wet meadows (mosaics of Molinion and Violion-caninae), referred to as sites Javornik and Ruda, in the southern region of the Czech Republic. Javornik (49°07' N, 13° 39' W) is located on the E mountain slope, 850 m a.s.l., mean annual temperature is 6.0 °C and mean annual precipitation 847 mm; temperature and precipitation are 30 year means from nearest meteorological station. The population is large (about one thousand flowering individuals), and is mown once a year (June-July) with additional late season sheep grazing (August-September) of moderate intensity. The standing biomass in June prior to mowing was 159.9-208.1 g.m⁻². Ruda (49° 08' N, 14° 43' E, 420 m a.s.l. with mean annual temperature 7.7 °C and mean annual precipitation 610 mm) is a medium-sized population with several hundred flowering individuals, mown twice a year, in June-July and August-September. The biomass before the first mowing was 214.2-295.1 g.m⁻².

Experimental design and analyses

In August 1997, I established a field experiment in each site, manipulating *Pedicularis* microhabitats in treatments mimicking mowing and grazing regimes. I treated square plots of 0.25 m². In (1) 'large gaps' I manually clipped aboveground vegetation to 5 cm height and removed belowground biomass from 5 artificial gaps randomly positioned within each treatment plot. Each gap was approximately circular, 10 cm in diameter and was 3 cm deep. Large gaps mimicked trampling during

cattle grazing. In the (2) 'small gaps' treatment, I clipped aboveground vegetation to 5 cm height and created small gaps in the same way as large gaps, but the gaps were 5 cm in diameter, mimicking trampling during sheep grazing. In the (3) 'mowing with bryophyte removal' treatment I manually clipped vegetation to 5 cm height and removed 50% of bryophytes from clipped plots. In the (4) 'mowing' treatment I clipped the vegetation without additional disturbances. In (5) 'control' plots, the vegetation remained undisturbed. Each treatment had 5 replicates in each site, and was repeated in October 1998, 1999 and 2000. In April/May 1998-2001 I monitored spontaneous seedling recruitment in response to treatment effects.

For statistical analyses I used SPSS Version 10.0 Inc. The field experiment was arranged in a full factorial design (2 sites x 5 treatments with 5 replicates). I employed repeated measures ANOVA models (von Ende 2001) to analyze annual variations in seedling densities in 1998-2001 with within-subject factor year, and between subject factors site and treatment. Tukey's HSD test compared significant differences post-hoc. For analyses I log-transformed numbers of individuals ($y = \log(x+1)$) to normalize distributions and homogenize variances and back-transformed data to the original scale for graphical presentation.

Results

Seedling densities varied considerably in treatments (note large standard errors) and varied greatly over the years (significant effect of year, Table 1). Microsite treatments did not have consistent significant effect over the years on seedling recruitment, and seedling densities did not differ significantly between sites (Table 1). However, the seedling preferences

for treatments varied greatly over the years (significant interaction year*treatment, Table 1, Figure 1).

Plots with large gaps had the greatest seedling densities in 1999 (Figure 1a), but the gap sized was not significant in 1998. The effect of gap size was not consistent among years. Seedling densities were low in large gaps in 2000 (Figure 1c) and did not vary significantly in plots with large and small gaps in 1998 or 2001 (Figure 1a, d). Mowed plots with bryophytes removed had high seedling densities in 2000 (Figure 1c) but not in other years. Control plots often had lower seedling densities than other treatments (Figure 1a-d), but not significantly.

Discussion

Densities of recruited seedlings varied greatly over the studied years, and were substantially greater in even years than in odd years. The seedling densities may have reflected seed densities on sites, since the seed-bank longevity usually does not exceed a single year (Petrů, unpubl.). This great variation in seedling densities was related to annual variation in population structure of *Pedicularis*. High seedling densities reflected high flowering plant densities in the prior year (Chapter 2).

Gaps and mowing sometimes elevated seedling recruitment in this experiment. Also other studies show positive effects of vegetation removal during mowing on seedling recruitment of a target species (e.g. Křenová & Lepš 1996; Lennartsson & Oostermeijer 2001). Effects of artificial gaps can vary according to gap size, related to frequency and intensity of grazing regime. Bullock et al. (1995) found that larger gap sizes increased frequencies of some species but decreased frequencies of others in artificial gaps of three sizes in British meadows. Seedling recruitment of an endangered species *Rutidiopsis leptorrhynchoides* in

Australian grasslands was greatest in large gaps (Morgan 1997). In this study, seedling densities of *Pedicularis sylvatica* varied in two gap sizes over the four years. Years with low seedling densities in large gaps had high densities in small gaps, and the pattern reversed in the following year, thus in average seedling recruitment of *Pedicularis* did not appear to consistently depend on gap size over the years. These results imply that both cattle grazing (producing large gaps) and sheep grazing (producing small gaps) may provide recruitment opportunities for his species.

Seedling recruitment positively responded to mowing in some years. This treatment removed accumulated biomass at the end of vegetation season, rather than simulated traditional mowing regimes in June-July. Removal of biomass prevented litter accumulation, which often reduces the favorability of microsites for seedling recruitment in many species (e.g. Goldberg & Werner 1983; Špačková et al. 1998)

Bryophyte cover in meadows often negatively affects seedling recruitment (Zampfir 2000; Van Tooren 1988; Keizer et al. 1985). Removal of 50% of bryophytes in this experiment could not avoid disturbance of upper soil levels. Lower seedling densities in plots with bryophytes removed compared to mowing-only, suggest that seeds trapped in bryophyte layer may have been removed by this treatment. However, the contribution of these seeds to recruitment is arguable, since seeds trapped within bryophytes may become dry and lose viability (During & Van Tooren 1990).

Limited seed and microsite availability can have an interactive effect on seedling recruitment (Edward & Crawley 1999; Kupferschmid et al. 2000; Zobel et al. 2000). Management regimes may enhance seed availability contributing to seed dispersal. Mowing and grazing disperse

seeds of meadow species if practiced at the time of seed ripening (Coulson et al. 2001). Seeds of *Pedicularis sylvatica* are small and fall close to reproductive adults (Petrů & Lepš 2000) and may later be dispersed during grazing. Traditional mowing time corresponds with seed ripening and can translocate seeds during manipulations with hay. The *Pedicularis* seeds are also adapted to ant dispersal, and ants may contribute to short-distance dispersal (Berg 1954).

Management-mediated microsite heterogeneity appeared to be important for seedlings of *Pedicularis sylvatica*. Management regimes had positive effects on seedling densities in some years, but varied between years. This variation may be attributed to weather patterns or seed limitation and low germination rates. Effective habitat maintenance of *Pedicularis sylvatica* may use a combination of mowing and grazing regimes promoting seed dispersal and creating gaps for successful seedling recruitment, establishment of adult plants and overall population performance.

Table 1. Results of repeated measures ANOVA for number of *Pedicularis* seedlings in 1998-2001 in two sites (Javorník and Ruda) and in response to five treatments (large gaps, small gaps, mowing and bryophyte removal, mowing and control) in the field experiment.

Source	df	MS	F	p
Between Subjects				
Site	1	0.19	0.73	0.605
Treatment	4	0.17	0.69	0.398
Site *Treatment	3	0.16	0.61	0.614
Error	36	0.26		
Within Subjects				
Year	3	17.51	46.69	<0.001
Year* Site	3	0.83	2.20	0.092
Year*Treatment	12	0.76	2.02	0.029
Year* Site *Treatment	9	0.59	1.57	0.134
Error (Year)	108	0.38		

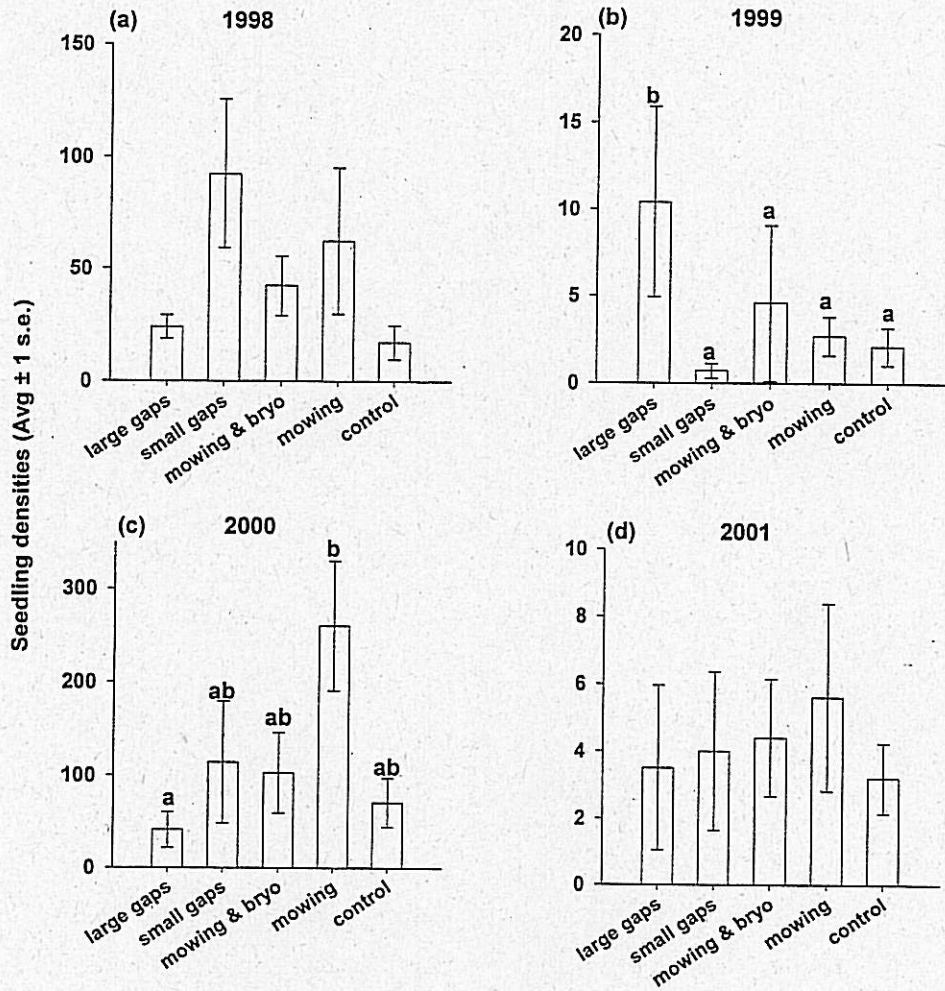
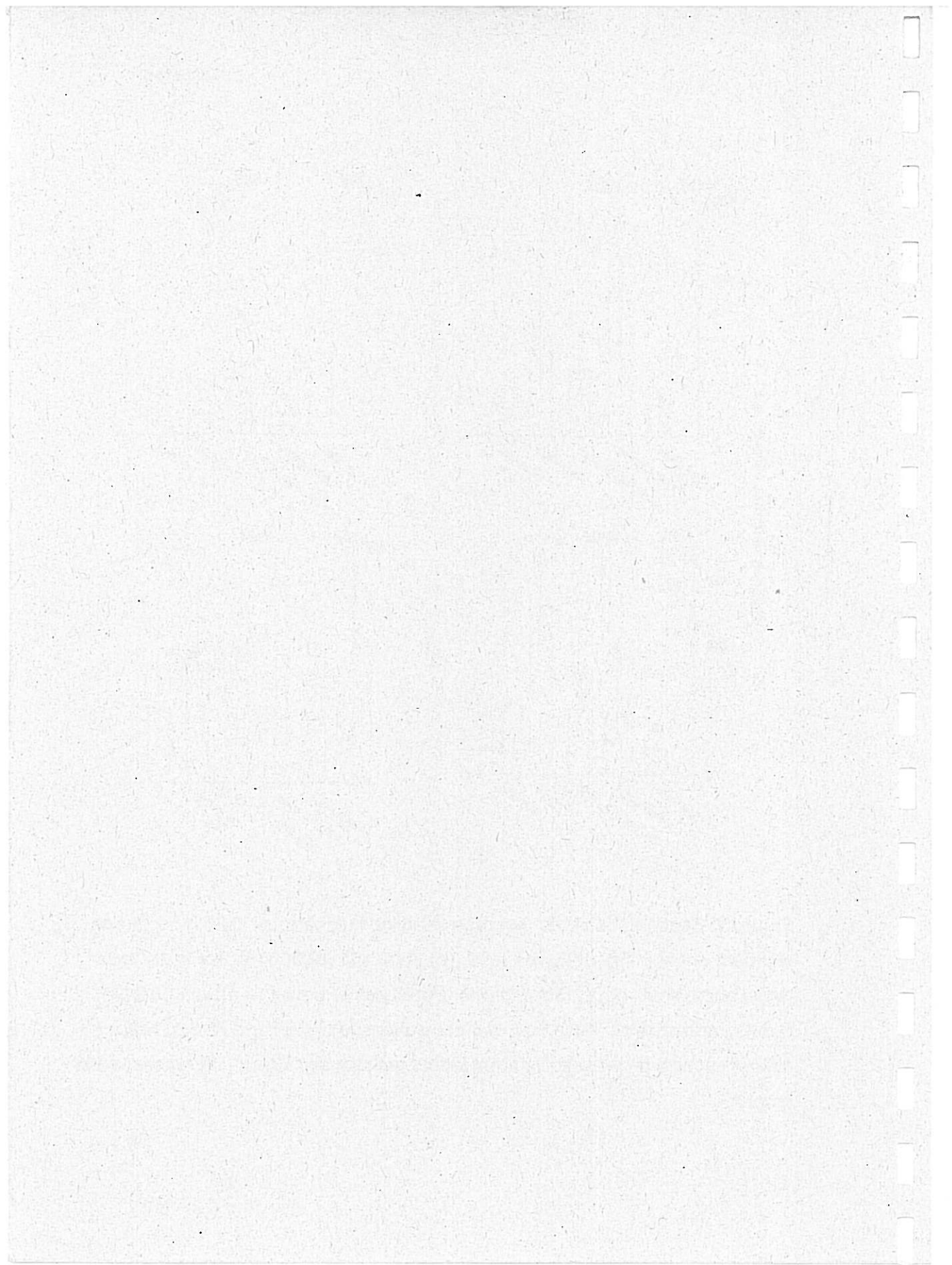


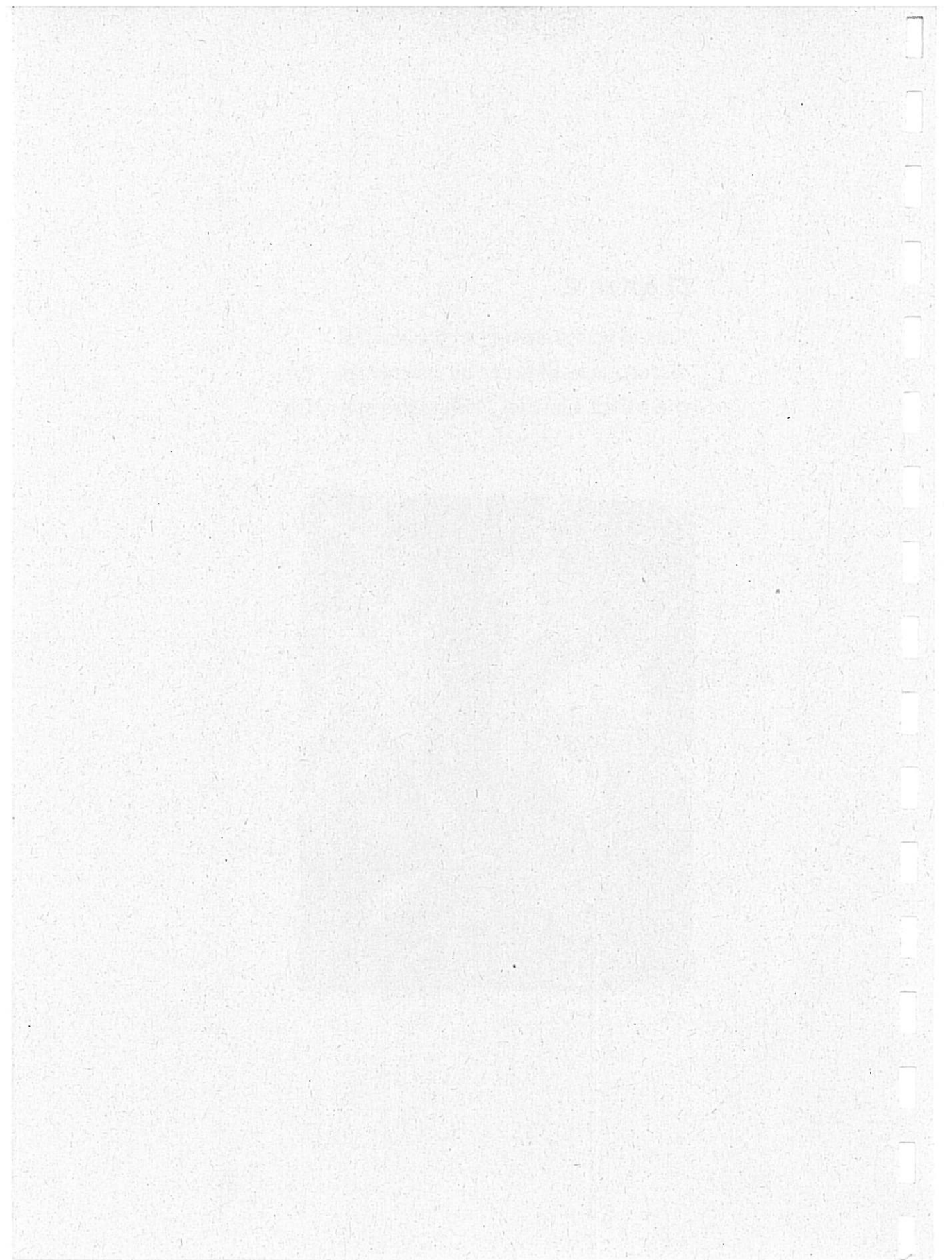
Figure 1. Seedling densities (average seedling numbers per 0.25 m² with one standard error) in (a) 1998, (b) 1999, (c) 2000 and (d) 2001 in five treatments (large gaps, small gaps, mowing with bryophytes removed (= mowing & bryo), mowing and control). Data from two populations (Javornik and Ruda). Note different scales on y-axes. Different letters indicate significant differences within graphs.



Chapter 2

Annual variation and experimental disturbance effects on demography of the strict biennial *Pedicularis sylvatica*





Annual variation and experimental disturbance effects on demography of the strict biennial *Pedicularis sylvatica*

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Abstract

Demography and population dynamics of short-lived perennial plants can be often determined by habitat quality and disturbance regime. In 1998-2001, I studied disturbance effects on population structure and dynamics of a grassland strict biennial *Pedicularis sylvatica*, and on demographic transitions (monthly dynamics of seedling recruitment in 1998 and within- and between-year survival in 1998-2000). In two Czech populations, I established three experimental disturbance regimes: (1) a gap treatment that simulated grazing management in *Pedicularis* habitats by clipping vegetation and creating small artificial gaps, (2) a mowing treatment where I clipped vegetation and removed litter, and (3) a no management treatment, where I left the vegetation untreated. The number of recruiting seedlings varied greatly by year, and demographic structure of populations showed significant annual oscillations in seedling numbers, from low (3.1 ± 0.7 average with one standard error per 0.25 m^2 plot) to high (102.9 ± 20.1). Inversely in the same years, adult numbers in populations oscillated from high (11.6 ± 2.3) to low (0.7 ± 0.3). Experimental disturbance effects on demographic transitions were not

significant, but there were significant site effects. In 1998, most seedlings recruited in April-May regardless the treatment, but most (86.8%) died before winter. Within- and between-year survival was not affected by disturbance regimes but fluctuated significantly among years. Between-year survival increased with increasing size of the winter bud. Since the oscillations in population structure and the demographic transitions did not significantly vary in response to experimental disturbance, individual population dynamics may be driven endogenously rather than by disturbance events. The lack of disturbance effects may also indicate population resistance to changes in habitat quality. However grazing or mowing regimes may favor population persistence, since long-term management abandonment often decreases habitat quality of grassland species.

Key words: artificial gaps, conservation, hemiparasitism, management, manipulative field experiment, microhabitats

Nomenclature: Rothmaler 1976; Oberdorfer 1992, 1993

Introduction

Modern landscape management emphasizing heavy mechanical equipment and fertilization can substantially modify sensitive habitats and affect plant and animal populations (e.g. Fisher & Matthies 1998a; Eisto et al. 2000; Mavraganis & Eckert 2001). Management regimes often determine the quality of habitats, such as semi-natural grasslands in Europe. Traditionally, European grasslands have been manually mown or grazed on regular schedules, forming nitrogen-limited habitats that can be extremely species rich. However, these grasslands are vulnerable to

species declines and local extinctions under modern intensive, or irregular management practices. If these habitats were abandoned, dominant grasses expand and shrubs and trees invade the community, suppressing and finally excluding competitively weak herbaceous species (Eriksson 1996; Lennartsson & Svensson 1996).

Many grassland plants are adapted to mowing and grazing, including small-scale animal trampling (Wells 1971; Kelly 1985a, 1985b; Silvertown 1983; Garcia 1992). These disturbances keep the grassland community open and provide opportunities for seedling recruitment in safe sites (Grubb 1977 and e.g. Kelly 1989b; Weller 1989; Fisher & Matthies 1998b; Kotorová & Lepš 1999), and consequently affect species demography and population dynamics (e.g. Löfgren et al. 2000).

Grassland management affects particularly short-lived monocarpic perennials, such as biennials (Viswanathan 2000). Although biennials are not very common, there has been a great interest in variation of their life span ('facultative biennials', de Jong et al. 1987; de Jong & Klinkhamer 1988a, 1988b; Schat et al. 1989; Klinkhamer et al. 1996; Bertin 2001). However, few studies focus on 'strict biennials' (Kelly 1989a, 1989b, 1989c; Fisher & Matthies 1998a, 1998b; Lennartsson & Oostermeijer 2001), where flowering occurs always in the second year regardless of plant size (Klinkhamer et al. 1987).

An example of a strict biennial species adapted to disturbed habitats is *Pedicularis sylvatica*, an endangered herb occupying semi-natural wet meadows in the Czech Republic. These meadows have been traditionally manually mown or grazed for centuries, however in the last 3-4 decades grazing has been widely abandoned, and mowing management has been mechanized and intensified. As a result, many historical populations have declined or become extinct (Hendrych & Hendrychová 1989). Thus,

current management trends may not maintain high-quality habitats for *Pedicularis* populations.

In this study I explored relationships between demography of the strict biennial *Pedicularis sylvatica*, and disturbance regimes, and consequences for species conservation and habitat management. I studied variation in population structure and disturbance effects on demographical transitions: seedling recruitment and survival. I also explored factors affecting survival. Finally I discuss populations' performance under changing environmental conditions.

Methods

Study species

I studied *Pedicularis sylvatica* ssp. *sylvatica* L. (Scrophulariaceae); for simplicity I further refer to the subspecies by the generic name.

Pedicularis is an atlantic and subatlantic species frequent in Western Europe, declining in abundance from west to east (Meusel et al. 1978).

The plant is limited to acid and nutrient poor soils, with high water table in an elevation range of 400-1200 m a.s.l. (Hartl 1975). Habitats include disturbed and trampled areas (bombing ranges in military training areas, woodland paths (Ter Borg 1985, pers. obs.); fens, bogs, heathlands, and mown, or grazed (sheep or cattle) wet meadows dominated by grasses *Nardus stricta* and *Molinia caerulea*. *Pedicularis* used to be continuously distributed through the Czech Republic in these meadows, but many populations has been affected by drainage and/or changes of management in the last 3-4 decades. The loss of many historical populations resulted in current scattered distribution of the species through the Czech Republic (Hendrych and Hendrychová 1998).

Pedicularis sylvatica is considered an endangered species, sensitive to

habitat quality changes. The species is an obligate non-specific hemiparasite with wide range of hosts. It is a hemicryptophyte with a winter bud (Ter Borg 1980, 1985).

Life cycle

I distinguished five stages in the strictly biennial life cycle of *Pedicularis*: seed, seedling, juvenile, plant overwintering in bud, and reproductive adult (Figure 1a). I studied all life cycle stages except seeds. I assumed the seed bank is transient or short-term persistent (sensu Thompson et al. 1997), and most of the seedlings germinate from seeds added to the seed bank during the previous year. Seedlings recruit in early spring and establish a juvenile rosette during the summer of the first year. Plants that survive winter flower in the following spring and produce seeds in the summer of this second and final year (Figure 1a).

Within one year, the population consists of two overlapping cohorts: plants in their first year (seedlings and juveniles) and plants in their second year (adults) (Figure 1a). I studied four cohorts of seedlings (plants born in 1998-2001) overlapping with three cohorts of adults (plants flowering in 1999-2001) (Figure 1b).

Study sites

I studied two populations in oligotrophic wet meadows (mosaics of Molinion and Violion-caninae sensu Oberdorfer 1992, 1993) in the southern region of the Czech Republic, and refer to the sites by the names Javornik and Ruda. Javornik (49°07' N, 13° 39' W, on the E mountain slope, 850 m a.s.l., mean annual temperature 6.0 °C and mean annual precipitation 847 mm; temperature and precipitation are 30 year means from the nearest meteorological station), is a large population with

about one thousand flowering individuals. The meadow is mown once a year (June-July) with additional late season sheep grazing of medium intensity (August-September). The standing biomass in June prior to mowing was 159.9-208.1 g.m⁻². Ruda (49° 08' N, 14° 43' E, 420 m a.s.l., mean annual temperature 7.7 °C and mean annual precipitation 610 mm), is a medium-sized population with several hundred flowering individuals, mown twice a year, in June-July and August-September, with 214.2-295.1 g.m⁻² biomass before the first mowing.

Experimental design and data collection

In August 1997, I established a field experiment within each site, excluding 0.25 m² experimental plots from the management performed on sites, and I treated them separately as follows: In (1) 'gaps' mimicking grazing/trampling, I removed aboveground biomass from the entire 0.25 m² plot and belowground biomass from 5 randomly located small circular gaps (5 cm diameter, 3 cm deep) within each treatment plot. In the (2) 'mowing' treatment, I clipped aboveground biomass and removed litter, and in (3) 'no disturbance' plots, the vegetation remained undisturbed. Each treatment had 5 replicates on each site. I repeated experimental treatments in October 1999 and 2000.

In 1998-2001 I evaluated the annual variation in population structure in census counts of adults and seedlings in April/May, and I counted juveniles in September/October in all disturbance regimes. I studied disturbance effects on *Pedicularis* demography: (a) monthly dynamics (April-September) of seedling recruitment in the first cohort in 1998, and (b) survival in the first year (within-year) and survival from the first to the second year (between-year) in 1998-2001. I explored the relationship between plant survival and bud size, measuring winter bud diameters of

160 plants in September 2000 and recording their survival in April 2001.

Statistical analyses

I completed all statistical analyses in this study in SPSS Version 10.0 Inc. The field experiment was arranged in a full factorial design (2 populations \times 3 disturbance regimes) with 5 replicates. To evaluate annual differences (1998-2001) in seedling, juvenile and adult numbers in population structure, I employed repeated measures ANOVA models (von Ende 2001) with between-subjects factors disturbance regime and site and within-subject factor year.

I analyzed disturbance effects on monthly seedling recruitment in April-September 1998, in repeated measures ANOVA with between-subject factors disturbance regime and site and a within-subject factor month. Within-year survival (number of juvenile plants at the end of the first year over the maximal number of recruited seedlings), and between-year survival (number of adult plants in the second year over the number of juvenile plants in the first year) in 1998-2001 were compared in univariate two-way ANOVAs with factors disturbance regime and site. The design for survival was necessary unbalanced due to zero recruitment in some of the experimental plots in the first year. A t-test and one-way ANOVA compared annual differences in within- and between-year survival, respectively. I compared the log-transformed winter bud diameter among disturbance regimes and between sites in two-way ANOVA with unbalanced design due to non-equal distribution of plants in experimental plots and between sites. In ANOVAs, I used Tukey HSD test for the post-hoc pairwise comparisons of significant differences. For all analyses I log-transformed numbers of individuals ($y = \log(x+1)$) to normalize distributions and homogenize variances. I used binary logistic

regression to explore the relationship between plant survival and winter bud diameter. A t-test compared sizes of winter buds, which died vs. survived.

Seedling and adult numbers in 1998-2001 differed greatly, thus their relative proportions are presented within a single graph on a logarithmic scale. I present means and standard errors of 1998 monthly seedling numbers back-transformed to the original scale.

Results

Annual variation in population structure in 1998-2001

Population structure oscillated greatly among years in relative proportions of seedlings, juveniles and adult plants (significant effects of year, Table 1). The seedling and adult numbers in populations varied greatly among years (Figure 2). In even years, the population structure consisted of high seedling numbers and low adult numbers (only in 2000). Inversely, in odd years, the population had low seedling and high adult numbers (Figure 2). Seedling numbers differed significantly among years and among disturbance regimes (significant interaction year*disturbance regime, Table 1, Figure 2). Numbers of juveniles and adult plants differed significantly among years between populations (significant interactions year*site, Table 1, Figure 2 for adults). The overall effects of disturbance regimes on seedlings, juveniles and adults were not significant (Table 1). Overall juvenile and adult numbers differed significantly between Javornik and Ruda sites (Table 1).

Disturbance effects on demography

(a) Dynamics of seedling recruitment in 1998

Monthly seedling recruitment in 1998 was not significantly affected by disturbance regimes (Table 2) and had similar patterns in both populations (Figure 3). Seedlings recruited spontaneously in spring but few seedlings survived until fall (Figure 3). The phenology of seedling recruitment differed between populations (significant interaction month*site, Table 2)

(b) Within- and between-year survival in 1998-2001

Within-year survival in 1998 and 2000 did not differ among disturbance regimes and between sites (Table 3a), and survival did not differ significantly between the two years ($t = 1.88$, $df = 51$, $p = 0.065$). In 1999, the number of recruiting seedlings was insufficient for analysis. The average survival (with one standard error) in 1999 was $21.0 \pm 7.3\%$. Average survival from 1998 and 2000 was $73.4 \pm 5.0\%$.

Between-year survival in 1998-99, 1999-2000 and 2000-2001 did not differ among disturbance regimes but differed between sites (Table 3b). Survival in 1999-2000 was significantly higher in Ruda, in 2000-2001 survival was higher in Javornik. Survival varied significantly among years (MS error term = 1.11, $df = 1, 61$, $F = 4.27$, $p = 0.018$). In 1998-99, average survival with one standard error was $72.7 \pm 10.5\%$. In 1999-2000, the survival was lower ($42.1 \pm 11.8\%$), however it increased to $62.1 \pm 13.1\%$ in 2000-2001.

Winter bud size was not affected by disturbance regimes, but differed significantly between sites (Table 3c); larger buds were in Javornik (average with one standard error was 3.22 ± 0.18 cm) than in Ruda (2.73 ± 0.24 cm). The interaction disturbance regime*site was significant (Table 3c). Winter buds were larger in gaps in Javornik, but in mowing treatment

in Ruda. Survival of winter buds was high (69.4 % of all marked plants survived). Buds were larger in plants, which later survived (average bud diameter with one standard error was 3.59 ± 0.18 cm) compared to plants, which died, where the bud size was 1.91 ± 0.17 ($t = 6.31$, $df = 158$, $p < 0.001$). Survival significantly increased with bud size (chi-square = 35.32, $df = 1$, $p < 0.001$).

Discussion

This study documents great annual oscillations in population structure of *Pedicularis sylvatica* over four years. This was a consequence of the strictly biennial life history (Kelly 1989c) not related to experimental disturbance treatments. The population always consisted of two spatially intermixed cohorts and their relative proportions within the population fluctuated inversely over the studied years. In years when the population had high seedling number, the number of adults was low, and this pattern was reversed in the following year.

These population dynamics were not affected by disturbance regimes and seem to be maintained endogenously in each population. Gaps have been documented to provide regeneration niches (Grubb 1977), and enhance seedling recruitment (e.g. Kelly 1989a, 1989b, 1989c; Fisher and Matthies 1998a; Petruš & Lepš 2000; Lennartsson & Oostermeijer 2001), but were not favored over other treatments in this experiment. Mowing was a traditional management regime favoring populations of grassland herbs (e.g. Lennartsson & Oostermeijer 2001) removing produced biomass and preventing accumulation of litter, which often has negative effects (e.g. Goldberg & Werner 1983; Špačková et al. 1998). In this experiment, effects of mowing were not significantly different from

disturbance exclusion in undisturbed plots. Four years without management in these plots may not represent the effects of abandonment. Longer-term detrimental effects of abandonment (e.g. invasion by woody plants) were not seen. Larger sample size and long-term monitoring in this experiment may reveal negative effects of abandonment on population structure and dynamics, as shown by Bakker et al. (1980) and Lennartsson & Svensson (1996), and significant disturbance effects (e.g. Löfgren et. al 2000; Lennartsson & Oostermeijer 2001).

Sites differed in juvenile and adult numbers, between-year survival, and survival of winter buds, perhaps reflecting differences in microclimate, soil conditions, or productivity between the two sites. Significant effects of site in interaction with disturbance regimes may represent different responses of populations to the local management regime. Gap treatment (simulating traditional grazing) on Javornik site created the most positive demographic responses, while in Ruda, traditional mowing had greater positive effects than gaps.

High seedling mortality is a great source of loss for many plant species including *Pedicularis*. Survival of the species may be related to density and the distribution of the hemiparasite's host plants. Unlike seeds that germinate independently of host plants (Růžička 1999), *Pedicularis* seedlings require functional haustorial attachments to host roots to successfully establish (Ter Borg 1985). *Pedicularis* often uses roots of different host species simultaneously, and the host species pool may influence *Pedicularis* demography. Plants grew faster and reached larger size in the first year when experimentally planted with certain host species (Petrů, unpubl.).

Pedicularis plant size in the first year affects survival to the next year.

In this study, the larger plants had higher survival to the next year. However, size of plants at the end of the first year did not limit reproduction in that year, as it was often found in 'facultative biennials', where flowering can be delayed until juvenile rosettes reach a threshold size (Werner 1975; Gross 1981).

Facultative and strict biennials differ in the length and variation of the life cycle, and also in patterns of population dynamic (Van der Meijden et al. 1992). Results of this study show *Pedicularis sylvatica* is a type of biennial with persistent populations, but fluctuating cohort abundances (Van der Meijden et al. 1992; Kelly 1989c). This type of biennial population dynamics shows variable survival patterns, and persistence in local patches drifting around the site responding to varying conditions, limited by suitable safe sites (Grub 1984; Van der Meijden et al. 1992). These fluctuations in cohort abundances and mobility of local patches in populations may represent a type of metapopulation dynamics (Van der Meijden et al. 1992). Data presented in this study support the temporal component for such a metapopulation model. Data on spatial structure are being gathered, but not presented here.

Pedicularis populations may exhibit 'cyclic stability' (Kelly 1989c) with recurring cycles of predictable changes in plant abundance. However, four-year data, presented in this study, were not sufficient to clearly demonstrate this pattern. The 'cyclic stability' may reduce extinction risk in populations of this biennial. Fluctuations in population size, generation overlaps and asynchrony of seedling and adult densities may buffer populations in catastrophic stochastic events in bad years, however only if these events do not affect simultaneously seedlings and adults. At certain level, *Pedicularis* populations may be resilient to temporal changes of environmental conditions.

Despite some demographic stability in *Pedicularis* populations (at least at larger spatial and temporal scales), there are likely to be negative consequences of long-term management abandonment on the populations. Both grazing and mowing regimes would benefit *Pedicularis* populations keeping grass and woody plant dominant in the species habitats low.

Table 1. Results of repeated measures ANOVA for number of *Pedicularis* seedlings and juveniles in 1998-2001 and adult plants in 1999-2001 as a function of disturbance regime (= Dist. regime: artificial gaps, mowing and no disturbance) and site (Javornik and Ruda).

Source	Seedlings				Juveniles				Adults			
	df	MS	F	p	MS	F	p	df	MS	F	p	
Between Subjects												
Dist. Regime	2	0.79	2.47	0.106	0.47	2.04	0.152	2	0.12	0.86	0.436	
Site	1	0.39	1.21	0.282	2.10	9.09	0.006	1	4.54	31.76	<0.001	
Dist. Regime*Site	2	0.25	0.78	0.466	0.25	1.08	0.355	2	0.14	1.00	0.382	
Error	24	0.32			0.23			24	0.14			
Within Subjects												
Year	3	14.60	42.60	<0.001	3.12	21.80	<0.001	2	4.36	28.45	<0.001	
Year*Dist. regime	6	0.80	2.51	0.029	0.15	1.08	0.384	4	0.16	1.01	0.411	
Year*Site	3	0.67	1.96	0.127	0.73	5.11	0.003	2	0.71	4.60	0.015	
Year*Dist. regime*Site	6	0.44	0.44	0.272	0.04	0.29	0.938	4	0.04	0.22	0.928	
Error (Year)	72	0.34			0.14			48	0.15			

Table 2. Results of repeated measures ANOVA for number of *Pedicularis* seedlings as a function of time (monthly census counts: April-September 1998), disturbance regime (= Dist. regime: artificial gaps, mowing and no disturbance) and site (Javornik and Ruda) in a field disturbance experiment in each study population in 1998.

Source	df	SS	F	p
Between Subjects				
Dist. regime	2	7.87	1.93	0.167
Site	1	1.69	0.83	0.371
Dist. regime*Site	2	0.55	0.13	0.876
Error	24	48.97		
Within Subjects				
Month	5	5.59	8.89	<0.001
Month*Dist. regime	10	1.06	0.84	0.592
Month*Site	10	5.01	7.97	<0.001
Month*Site *Dist. regime	20	1.35	1.07	0.390
Error	120	15.10		

Table 3. Results of ANOVAs for (a) within-year survival in 1998 and 2000 as a function of disturbance regime (= Dist. regime: artificial gaps, mowing, and no disturbance) in sites Javornik and Ruda in the field disturbance experiment in each population. In 1999 the number of recruited seedlings and their survival were insufficient for analysis. MS Error terms (for survival in 1998 df = 17; and for 2000 df = 24) are reported under their respective column headings. (b) between-year survival in 1998-1999, 1999-2000 and 2000-2001, MS Error terms (for survival in 1998-1999 df = 22; for 1999-2000 df = 6 and for 2000-2001 df = 17) are under their column headings. (c) Survival of winter bud in 2000-2001. Note that the design for survival was unbalanced.

(a)

Source	1998 (0.15)			2000 (0.08)	
	df	F	p	F	p
Dist. regime	2	0.63	0.407	1.13	0.710
Site	1	0.21	0.650	3.46	0.075
Dist. regime*Site	2	0.64	0.538	0.35	0.710

(b)

Source	1998-1999 (0.10)			1999-2000 (0.03)		2000-2001 (0.08)	
	df	F	p	F	p	F	p
Dist. regime	2	0.80	0.463	2.15	0.198	2.10	0.158
Site	1	0.23	0.639	29.96	0.002	4.97	0.040
Dist. regime*Site	2	0.29	0.781	2.15	0.198	0.26	0.774

Table 3 cont.

(c)

Source	df	MS	F	p
Dist. regime	2	11.99	3.04	0.051
Site	1	9.06	4.03	0.047
Dist. regime*Site	2	16.10	5.39	0.005
Error	154	2.97		

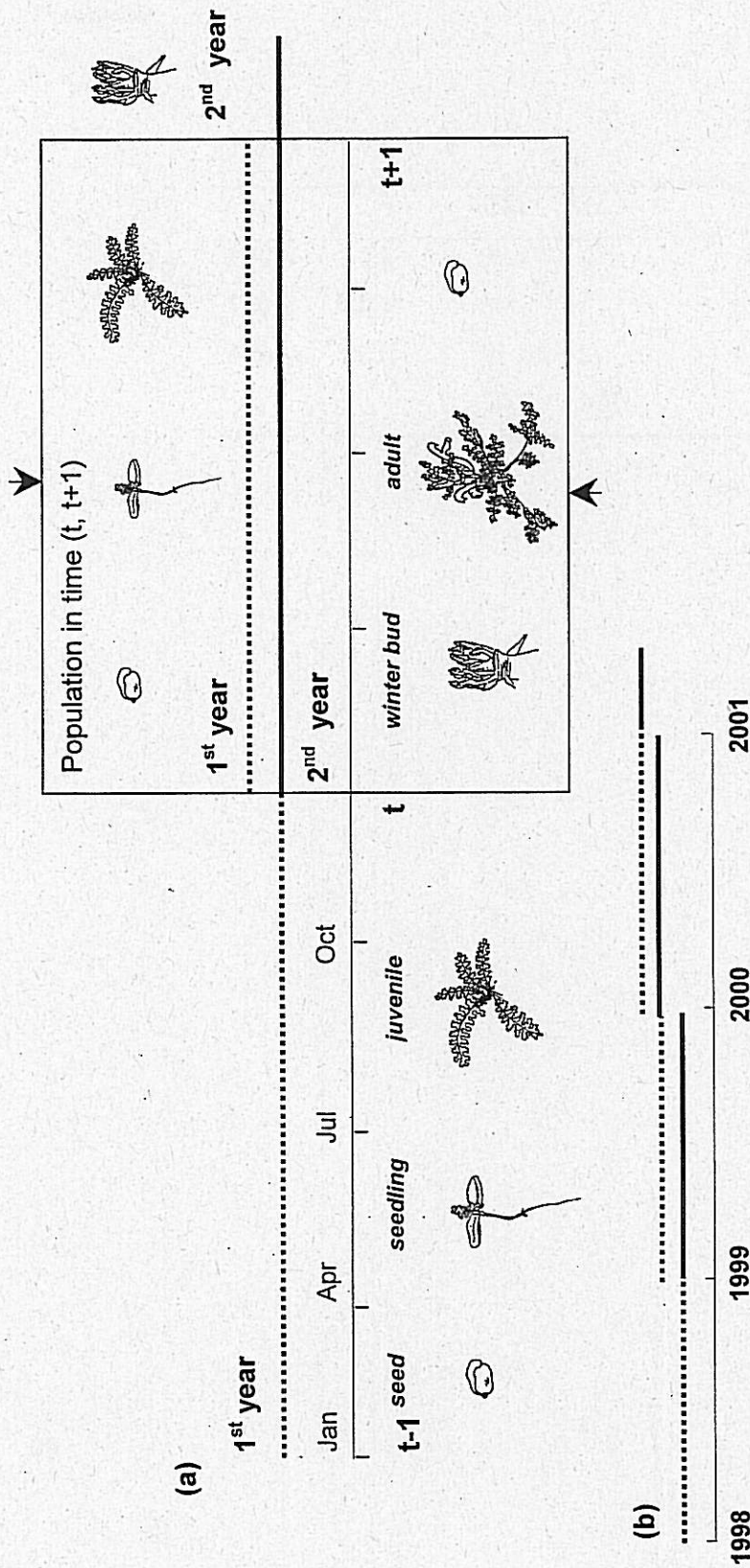


Figure 1. The strictly biennial life cycle of *Pedicularis sylvatica* ssp. *sylvatica*. **(a)** Time interval (t-1, t+1) of the species life span, dotted line for first-year stages (seeds, seedlings and juveniles), solid line for second-year stages (overwintering bud, reproductive adult and seeds). Within one year, e.g. time interval (t, t+1), cohort of plants in their 2nd year overlaps with plants in their 1st year. Size of stages: seed 0.2-0.3 cm, seedling 1-2 cm, rosette 4-10 cm, bud 0.5-3 cm, adult 9-30 cm. Arrows indicate studied cohorts of seedlings and adults and their overlap within population. **(b)** Overlaps of cohorts during the study period.

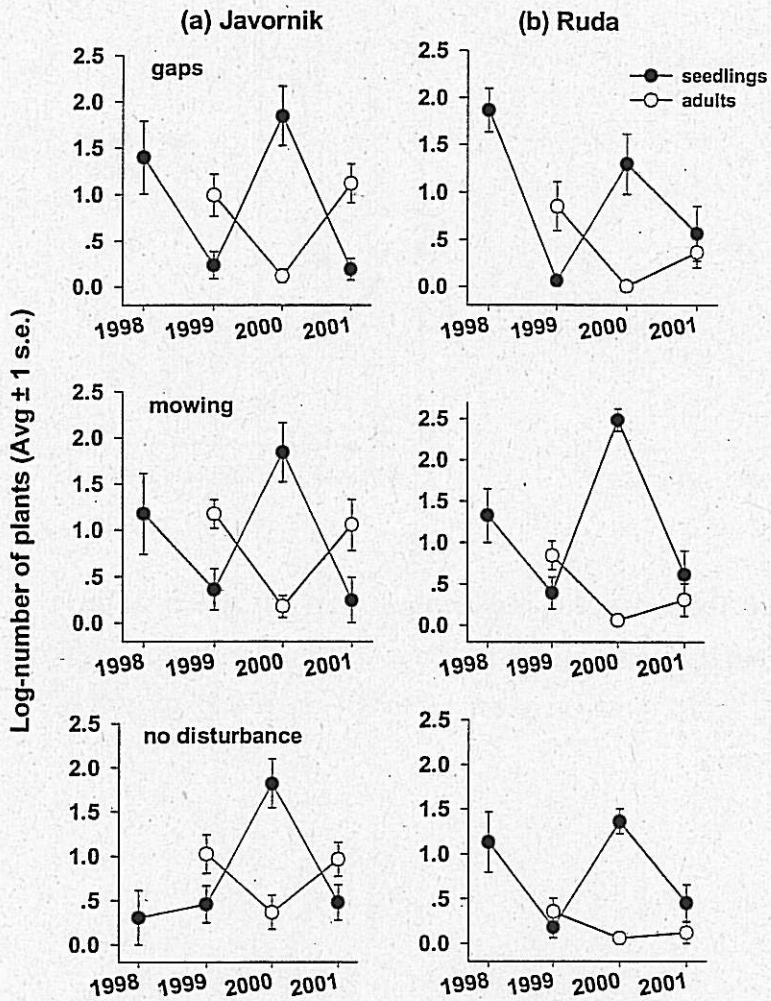


Figure 2. Inverse relationship of seedlings (close circles) and adults (open circles); means with one standard error of log-transformed numbers ($y = \log_{10}(x+1)$). Seedlings and adults in *Pedicularis* populations (a) Javornik and (b) Ruda in 1998-2001 with disturbance regimes: gaps, mowing and no disturbance. In 1998 only seedlings were recorded.

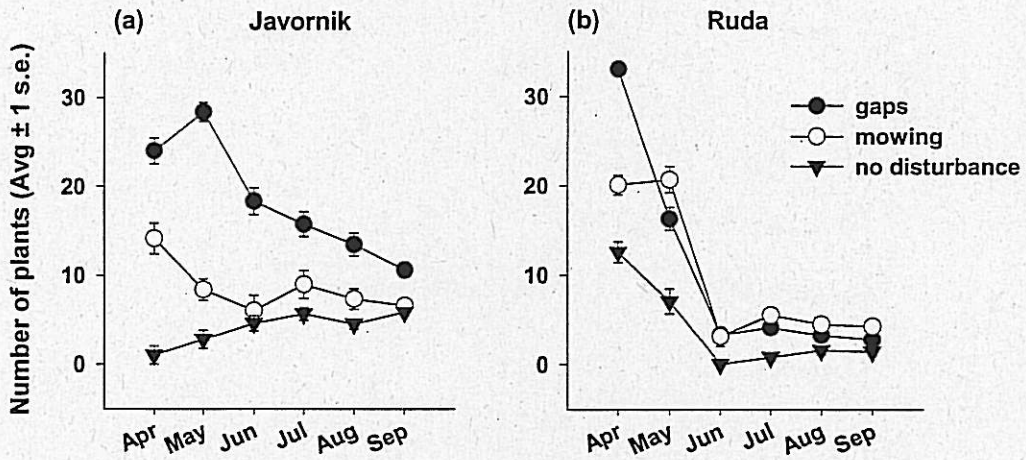
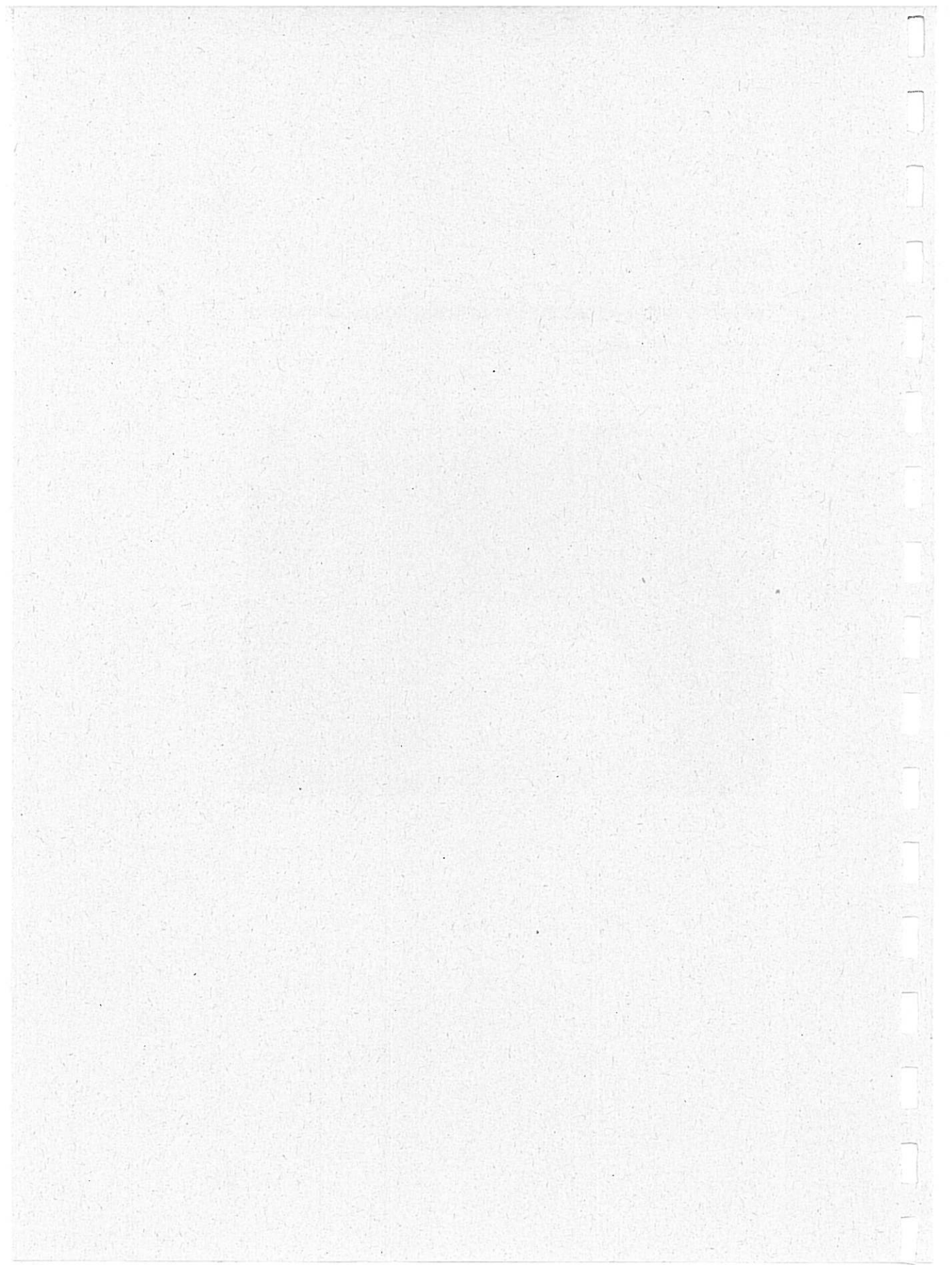


Figure 3. Dynamics of seedling recruitment, April-September 1998 in disturbance regimes: gaps, mowing and no disturbance and populations: (a) Javornik (b) Ruda. Average seedling numbers per 0.25 m² plot with one standard error.

Chapter 3

Seedling establishment in natural and experimental
Florida scrub gaps





Seedling establishment in natural and experimental Florida scrub gaps

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Abstract

Gaps are often important microhabitats for recruitment of herbaceous plants. In the Florida scrub, fires create gaps by top-killing resprouting shrubs. These natural gaps are aboveground gaps (without aboveground vegetation) that may also be complete gaps (if belowground roots and rhizomes are absent). Within three types of gaps (natural gaps, experimental aboveground and experimental complete gaps), we studied seedling recruitment and survival of spontaneous species and seven sown herbs for two years. We created aboveground gaps by clipping vegetation and complete gaps by removing shrub roots and rhizomes. These gaps occurred in two Florida scrub habitats: rosemary scrub and scrubby flatwoods. We also explored factors that can affect recruitment patterns in gaps, such as soil moisture, root water retention and light availability. In addition, we tested effects of supplemental watering on sown seeds in the field and on potted seeds in the lab. Drought in 2000 and 2001 suppressed natural seedling recruitment. Watering treatments increased recruitment in all types of gaps and in the lab experiment. Over half of all gaps were colonized, but seedlings were few. Recruitment was highest in watered, complete gaps in scrubby flatwoods, where the soil

moisture levels were higher and light levels lower than in the other gap types. Seedlings of a single spontaneously recruited species were more abundant than sown species. Locally common gap specialists were more abundant than generalists. Because many of these gap specialists are endangered plant species, understanding how disturbances create microsites for their regeneration is critical for conservation and management of the Florida scrub ecosystem. In small-scale conservation projects, artificially created gaps may substitute for post-fire gaps when prescribed burning is impossible.

Key words: artificial gaps, drought, endemic plant species, fire ecology, mechanical treatment

Nomenclature: Wunderlin 1998

Introduction

Disturbance is an important component of many world ecosystems, affecting their spatial and temporal heterogeneity, relative species abundances (e.g. White 1979; Sousa 1984; Denslow 1984) and population distribution and dynamics (e.g. Pickett and White 1985; Bowles et al. 1990; Quintana-Ascencio & Morales-Hernandez 1997; Lennartsson & Oostermeijer 2001). Many plant species are dependent on disturbances, including fires, ice storms, floods, droughts, landslides, or human-maintained management regimes, to create open spaces for colonization and microsites for regeneration (Grubb 1977; Petraitis et al. 1989; Hobbs & Huenneke 1992; Pavlovic 1994).

Fires are large-scale disturbances in shrub-dominated ecosystems such as the Florida scrub. Florida scrub plants have developed various

post-fire recovery mechanisms. Most dominant shrubs resprout and spread clonally, while many herbaceous species, including many endangered narrow endemics, recruit seedlings (Menges & Kohfeldt 1995). Fires create open patches (gaps) in the shrub matrix providing recruitment opportunities for obligate seeders (e.g. Hawkes & Menges 1996; Menges & Hawkes 1998; Young & Menges 1999).

Past studies have defined gaps in Florida scrub based on the distribution of the matrix shrubs. Gaps are defined as openings larger than 1 m² in the matrix of dominant shrubs taller than 0.5 m (oaks *Quercus chapmanii*, *Q. geminata* and *Q. inopina*, palmettos *Sabal etonia* and *Serenoa repens*, lyonias *Lyonia lucida*, *L. ferruginea* and *L. fruticosa* or rosemary *Ceratiola ericoides* (Menges & Hawkes 1998; Young & Menges 1999; nomenclature follows Wunderlin 1998). Post-fire gaps are large aboveground gaps, gradually closing filled by tall shrubs between fires. Long-term fire exclusion may cause gaps to become assimilated into the matrix. These aboveground gaps extend from one shrub canopy to the other but usually include herbs and lichens. In addition, shrub roots and rhizomes grow into aboveground gaps, making belowground gaps smaller than aboveground gaps. We are defining 'complete gaps' as the coexistence of above- and belowground shrub-free spaces; complete gaps have been documented in several studies from forest ecosystems (e.g. Wilczynski & Pickett 1993; Ehrenfeld et al. 1995; Connell et al. 1997; Ostertag 1998). In the Florida scrub, complete gaps have not been studied. Thus our investigation will help to establish their significance for Florida scrub plant populations.

Edges of sandy roads, firelanes and plow lines within scrub are essentially anthropogenic complete gaps. Roadsides have been shown to host higher population densities of some herbaceous scrub species,

compared to the population densities found in post-fire gaps in the scrub (Hartnett & Richardson 1989; Myers 1990; Hawkes & Menges 1995; Lambert & Menges 1996).

We focus here on gaps in two scrub habitats: rosemary scrub and scrubby flatwoods. Rosemary scrub, a phase of sand pine scrub (Abrahamson et al. 1984), is dominated by the Florida rosemary (*Ceratiola ericoides*, Empetraceae), often found in pure stands or intermixed with clumps of oaks (*Quercus inopina*, *Q. chapmanii* and *Q. geminata*) and sand pines (*Pinus clausa*). This ecosystem has low productivity and is found on acidic, nutrient poor, droughty and well-drained sandy entisols of St. Lucie or Archbold series (Abrahamson et al. 1984; Myers 1990; Carter et al. 1999). Rosemary scrub has a fire return interval of about 15 - 60 years (Menges 1999) and persistent large open gaps, where many narrowly endemic herbaceous species recover post-fire from seeds (Menges & Kohfeldt 1995). Scrubby flatwoods are commonly adjacent to or intermixed and integrated with rosemary scrub (Abrahamson et al. 1984). This community is dominated by the same oak species that occur in rosemary scrub, palmettos (*Sabal etonia*, *Serenoa repens*), lyonias (*Lyonia lucida*, *L. ferruginea*) and blueberry (*Vaccinium myrsinites*), (Abrahamson et al. 1984). This more productive vegetation grows on somewhat poorly drained, lightly textured fine sands with low clay content, such as Satellite, Duette or Zolfo series (Abrahamson et al. 1984; Myers 1990; Carter et al. 1999). In contrast to rosemary scrub, scrubby flatwoods are less open and disturbed by more frequent (5-20 years) fires (Menges & Hawkes 1998).

Many Florida scrub herbs are gap specialists (Menges & Kohfeldt 1995; Menges & Hawkes 1998; Quintana-Ascencio et al. 1998; Young & Menges 1999). These species vary from locally rare to locally abundant,

and from narrowly endemic (to the Lake Wales Ridge) to endemic (to central Florida ridges) to widespread species. In contrast to these gap specialists, gap generalists can often colonize both gaps and the surrounding shrub matrix (Menges & Kohfeldt 1995; Young & Menges 1999).

Gaps in rosemary scrub affect the demography of many gap specialized species (Hawkes & Menges 1995; Menges & Kohfeldt 1995; Hawkes & Menges 1996; Menges & Kimmich 1996; Quintana-Ascencio & Menges 2000; Hawkes 2000). However, the role of scrubby flatwood gaps for species regeneration has not yet been well demonstrated. Gap dynamics and the availability of open space differ between rosemary scrub and scrubby flatwoods. Gaps in rosemary scrub are more abundant, larger and persist longer compared to scrubby flatwoods, where gaps are smaller and more ephemeral (Hawkes & Menges 1996; Menges & Hawkes 1998; Young & Menges 1999). Several scrub herbs are specialized primarily for rosemary gaps. However, scrubby flatwoods gaps frequently share herbaceous species with gaps in rosemary scrub (Hawkes & Menges 1995; Menges & Kohfeldt 1995; Young & Menges 1999). In this study, we explored the species preference in colonizing rosemary scrub and scrubby flatwoods gaps.

In the excessively drained soils of Florida scrub, patterns of seedling recruitment may be influenced by periods of drought. Recent studies have shown the importance of water for seedling establishment and survival (Carrington 1996; Hawkes 2000; Quintana-Ascencio et al. in press) and also this study documents the effect of prolonged drought on seedlings.

Many of the Florida scrub herbs require fire management to maintain viability of their populations (Quintana-Ascencio et al. in press; Satterthwaite et al. in revision; Menges & Quintana-Ascencio in prep.).

However, prescribed burning is often difficult in the modern fragmented and populated landscape, and land managers may substitute mechanical treatments such as roller chopping, tree and shrub cutting for fire.

Mechanical treatments can mimic some fire effects and promote longer persistence of bare ground (Schmalzer 1992; Greenberg et al. 1994; Greenberg et al. 1995). We explored how creating gaps manually may affect seedling recruitment of scrub herbs.

This study evaluates how microsites in gaps and varying precipitation patterns affect seedling recruitment of Florida scrub herbs. Consequently, we address how important gap microsites are for species conservation. In small-scale post-fire gaps and experimentally created aboveground and complete gaps (with both aboveground and belowground components removed), we studied natural colonization and establishment of seven sown herbaceous species. We conducted watering experiments to test the importance of water for seedling performance in this xeric shrub ecosystem during periods of drought. We discuss the potential use of artificial gaps in small-scale conservation projects as a short-term substitute for fire, when burning is impossible.

Methods

Study site

We conducted the studies at Archbold Biological Station (ABS), at the southern end of Florida's Lake Wales Ridge (27° 11' N, 81° 21' W, Highlands Co., 13 km south of Lake Placid), comprising approximately 2000 ha of Florida scrub and other native plant communities. The climate, history, vegetation, and soils were described by Abrahamson et al. (1984). The present study focuses on rosemary scrub and scrubby flatwoods in the northern part of the Station, in rosemary scrub (the

southern part of rosemary patch 1) and adjacent scrubby flatwoods. At the time of this study, this part of Archbold had not been burned for about 37 years, since 1964.

Study species

We examined recruitment of seven species with diverse life history traits and post-fire recovery mechanisms (Table 1). Five species are gap specialists: the narrow (Lake Wales Ridge) endemics *Eryngium cuneifolium* and *Hypericum cumulicola*, the (central Florida Ridges) endemics, *Paronychia chartacea* ssp. *chartacea* and *Polygonella basiramia*, and the widespread gap specialist, *Balduina angustifolia*. Florida Ridges endemic *Liatis ohlingerae* and widespread *Palafoxia feayi* are generalists that occur both in gaps and in the scrub matrix. For simplicity we refer to each species by its generic name. We studied species recovery after disturbance from sown seeds. We also identified spontaneous recruitment of the widespread gap specialist *Lechea deckertii* (Table 1).

Field disturbance experiment

In January 2000 we installed a field experiment exploring seedling recruitment of seven scrub herbs into natural gaps and into experimental aboveground and complete gaps. In rosemary scrub and scrubby flatwoods, gaps were situated in an area smaller than 1 ha, gap types were randomly intermixed, and the inter-gap distances were greater than 3 m. To obtain the size distribution of natural gaps (openings > 1m²), we first surveyed gaps in two perpendicular belt transects 50 m long, 4 m wide through each vegetation type. We calculated the median gap diameter in the widest part of gap (2.5 m in rosemary scrub, 2.0 m in

scrubby flatwoods). We then randomly selected 10 median-sized natural gaps in each vegetation type for monitoring. We created two types of round experimental gaps in each vegetation type with the respective median diameters, each gap type in 10 replicates. In aboveground gaps, all aboveground parts of shrubs were hand-clipped. For complete gaps, shrubs were clipped and belowground shrub roots and rhizomes removed to a depth of 30 cm. The resprouted shrubs in experimental aboveground gaps were hand-clipped again in December 2000.

Shortly after gap establishment, seeds ($n = 20$) of five species, *Balduina*, *Eryngium*, *Hypericum*, *Polygonella* and *Palafoxia* were added to all 60 gaps, placed in the gap center. *Liatris* seeds ($n = 10$) were added at the same time into 10 randomly selected gaps in each vegetation type. Seeds of all species were collected locally as they matured in fall 1999. They were stored in the refrigerator and then collectively added to the experiment in January 2000. Gaps were scored for germination monthly until April 2000. We refer to this period as the 2000 germination season.

An extreme drought in 2000 (Figure 1) suppressed germination in the experiment. Subsequently we watered half ($n = 5$) of the gaps of each type from December 2000 until February 2001 (we refer to this as the 2001 germination season), supplying gaps with 2.5 mm of water twice a week, skipping the watering if the precipitation was > 2.5 mm in the last 3 days. The other gaps were left as non-watered controls. Both watered and non-watered gaps received rainfall during the experiment. We added additional seeds ($n = 30$) of *Balduina*, *Eryngium*, *Hypericum*, *Liatris* ($n = 15$), *Polygonella* and *Palafoxia* into each gap. *Paronychia* was added as a new species. Seeds were collected in the fall 2000 as they matured, and added to plots shortly after collection between November and December

2000. We monitored seedling recruitment and survival weekly from December 2000 until March 2001, during the 2001 germination season.

To explore microsite characteristics, we measured gravimetric soil moisture in gaps, water retained in roots, and percent open sky in gaps in July 2000 and February 2001. In July 2000, we measured soil moisture in all gap types, at random points in the shrub matrix and at random points at a roadside adjacent to scrub. In February 2001 we quantified the effect of watering by comparing soil moisture in watered and non-watered gaps. We expressed soil water content as a percentage of dry weight and calculated percent water retained in roots based on the difference between wet and dry weight of roots, cored to a depth of 5 cm from gaps. We also collected soil samples from the same gaps to examine gravimetric soil moisture and compare percent water in roots with percent soil water. Light conditions in gaps were estimated as percent open sky using a spherical densiometer. Only a subset of gaps ($n = 3$) of each gap type in each vegetation type was examined for abiotic conditions to reduce disturbance in gaps with added seeds.

We completed all statistical analyses in this study in SPSS Version 10.0 Inc. Originally (January-November 2000) the field experiment had a full factorial design (2 vegetation types \times 3 gaps types \times 6 species) with 10 replicates. In 2001, we modified the design by implementing the watering treatment and adding *Paronychia*, resulting in a new design (2 vegetation types \times 3 gap types \times 2 watering regimes \times 7 species) with 5 replicates. We employed a univariate ANOVA full factorial model, with factors watering, vegetation type and gap type, to analyze seedling establishment in the field experiment. We compared seedling numbers of sown species vs. spontaneously recruited species using a t-test and we

used a univariate ANOVA for comparison of seedling numbers among the species guilds. The numbers of seedlings recruited from sown seeds were insufficient to run separate analyses for each species. We analyzed the overall seedling establishment in gaps by pooling data of sown species and spontaneous *Lechea* in one group. *Hypericum* never recruited and so we excluded the species from all analyses. Seedling recruitment was low and resulted in a data set with many instances of zero germination. To normalize distribution and homogenize variances, we log-transformed data ($y = \log(x+1)$). Tukey's HSD test compared significant factors ($p < 0.05$) post-hoc. We analyzed seedling survival, the number of seedlings surviving over maximal number of seedling recruited (non-zero cells only), for species differences, where the design was necessarily unbalanced due to its dependence on initial recruitment.

In watered gaps we compared differences in soil moisture in July 2000 and February 2001 with a t-test. We compared soil moisture in gaps before and after watering using a paired t-test. With one-way ANOVAs, we compared soil moisture among gap types, random points at the shrub matrix and at the roadside, and light conditions among gap types, employing Tukey's HSD test for post-hoc pairwise comparisons of significant factors ($p < 0.05$).

Watering experiment on potted seeds

To test whether the level of water added in the field watering treatment in December 2000 through March 2001 was sufficient to induce germination, we conducted an outdoor watering experiment on potted seeds of six species: *Balduina*, *Eryngium*, *Hypericum*, *Paronychia*, *Polygonella* and *Palafoxia*. For each species, we planted 30 seeds into individual pots (8 by 8 cm by 9 cm deep). The experimental design (3

watering regimes \times 6 species) had 10 replicates resulting in a total of 180 pots. We placed pots outdoors in indirect light beneath an overhanging roof so that rainfall was excluded. Pots were supplied with 2.5 mm of water, the same amount used in the field watering treatment, and watering was applied at three treatment frequencies: once every two weeks, once per week and twice per week. We randomized the initial pot position, and switched the position of the three groups four times during the course of the experiment. We scored seedling recruitment and survival weekly from the end of December 2000 until the beginning of March 2001. With a non-parametric Kruskal-Wallis test we analyzed differences in proportions of seedlings surviving among the three watering levels.

Results

Field disturbance experiment

During the 2000 germination season, no seedlings recruited in the entire field experiment. During the 2001 germination season, 53.3% of all gaps were colonized and a total of 544 seedlings recruited in gaps. Seedling recruitment strongly responded to watering. Average seedling numbers were significantly higher in watered gaps (Table 2, Figure 2d) and seedlings recruited in 80% of watered gaps compared to 23.4% of non-watered gaps (Figure 2a). Both rosemary scrub and scrubby flatwoods gaps were colonized (56.7% of gaps in rosemary scrub had seedlings vs. 46.7% gaps in scrubby flatwoods, Figure 2b) and seedling numbers did not differ significantly between the two vegetation types (Table 2, Figure 2e). Gap types did not significantly differ in seedling numbers (Table 2, Figure 2f). Complete gaps were colonized most frequently (65% of complete gaps had seedlings) and also had the highest seedling

numbers, followed by natural gaps (50%) and experimental aboveground gaps (45%, Figure 2c). The number of recruited seedlings varied greatly among individual gaps (note the large confidence intervals in Figure 2). The impact of watering treatment depended upon vegetation type and gap type (significant interaction of watering*gap type and vegetation type*gap type, Table 2). Watering markedly increased numbers of recruiting seedlings in all types of gaps in both vegetation types, with the relative increase greatest in aboveground gaps in rosemary scrub and natural gaps in scrubby flatwoods. Absolute seedling numbers were greatest in complete gaps in scrubby flatwoods and natural gaps in rosemary scrub.

Spontaneous seedling recruitment was significantly greater than recruitment from sown seeds ($t = 4.02$, $df = 45$, $p < 0.001$; Figure 4c), but it was represented by only one species, *Lechea deckertii*. Sown species recruited in 51.6% of gaps compared to spontaneous recruitment of *Lechea* colonizing 26.7% of gaps (Figure 4a). Seedling recruitment among the species guilds differed significantly ($F = 4.35$, MS Error = 86.80, $df = 3, 416$, $p = 0.005$, Figure 4d). Seedlings of widespread gap specialists (*Balduina* and spontaneous *Lechea*) were the most abundant and frequent, and emerged in 46.6% of gaps. Endemic gap specialists (*Paronychia* and *Polygonella*) recruited in 25% of gaps and gap generalists (*Liatris* and *Palafoxia*) colonized 25% of gaps. Narrowly endemic gap specialists (*Eryngium* and *Hypericum*) were the least frequent (in 5% of gaps, Figure 4b).

Spontaneously recruited *Lechea* was the most abundant species in the whole study and colonized 26.7% of gaps. *Balduina* occurred in 35% gaps and was the most abundant of the sown species (Figure 5). Seedlings of *Hypericum* were never observed. Seedling survival from the

first recruitment in December 2000 through March 2001 was high, generally > 50% (Figure 6) with no significant differences among species ($F = 1.84$, MS Error = 0.04, $df = 6, 37$, $p = 0.117$). However, most surviving seedlings were in watered gaps.

Percent soil water in gaps decreased significantly between July 2000 and February 2001 ($t = 3.50$, $df = 34$, $p = 0.001$). Watering significantly increased soil moisture in gaps (paired t-test: $t = 4.02$, $df = 45$, $p < 0.001$). Soil moisture measured in July 2000 differed significantly among gap types, random points in the scrub matrix, and random points at the roadside ($F = 2.64$, MS Error = 0.43, $df = 4, 51$, $p = 0.044$). Experimental gaps and road points had higher percent soil water than natural gaps and random points in the matrix (Figure 7), but there were no significant pairwise differences. Measured in July 2000, roots contained $0.34 \pm 0.31\%$ water (average with 95% confidence interval) as compared to $0.008 \pm 0.004\%$ in soils. Complete gaps in the experiment received significantly lower light levels (the average with 95% confidence interval was $8.85 \pm 0.54\%$) compared to light levels in natural gaps ($33.41 \pm 18.13\%$) and aboveground gaps ($29.58 \pm 12.91\%$, $F = 5.95$, MS Error = 175.81, $df = 2, 15$, $p = 0.012$).

Watering experiment in pots

Germination of all species except *Polygonella* was very low under all watering regimes. *Eryngium* and *Palafoxia* never germinated in pots. Frequent watering supported germination of the other species but not enough for statistical analyses. *Balduina* seedlings recruited in 60% of pots in the high water treatment, a total of 12 seedlings with 75% survival. *Hypericum* germinated in 30% of pots in the high water treatment with 3 seedlings and 1 survivor, and *Paronychia* germinated in 40% of pots in

the high water treatment with 15 seedlings and survival of 26%.

Polygonella germinated quickly and in large numbers but germination did not significantly differ among levels of watering ($F = 1.65$, MS Error = 0.01, $df = 2, 27$, $p = 0.21$, Figure 8). *Polygonella* survival was significantly greater in the high watering regime compared to medium watering, but no seedlings survived in the low watering regime. (Kruskal-Wallis: $H = 6.54$, $df = 2$, $p = 0.038$, Figure 8).

Discussion

This study documents recruitment opportunities for herbaceous plants in natural and experimental artificial gaps in two Florida scrub habitats, rosemary scrub and scrubby flatwoods. Seedlings recruited in all gap types and in both vegetation types when promoted by supplemental watering. In scrubby flatwoods, seedlings recruited frequently in experimental complete gaps, perhaps in response to this novel disturbance creating complete openings in the dense shrub matrix. These gaps had specific moisture and light conditions compared to other gap types. Young & Menges (1999) documented rapid closure of natural gaps in scrubby flatwoods post-fire. Rosemary scrub is more open with persistent natural gaps. In our study, natural gaps were colonized primarily by rosemary scrub specialists rather than by non-specialists.

Seedling recruitment of species specialized to gaps predominated. Widespread gap specialist *Balduina* along with spontaneously recruited widespread gap specialist *Lechea*, and widespread gap endemics *Paronychia* and *Polygonella* were more frequent and abundant in gaps than narrow endemic gap specialists *Eryngium* and *Hypericum*. Gap generalists *Liatris* and *Palafoxia* showed little recruitment in our study. These species recover from fire mainly by resprouting rather than

recruiting many seedlings (Menges & Kohfeldt 1995; Carrington 1996). *Lechea deckertii* also resprouts following fire, although it has high levels of seedling recruitment from a persistent seed bank (Maliakal, unpubl.).

The reasons for gap specialization by so many Florida scrub herbs has not yet been well explained. Gaps may be important for herbaceous plants sensitive to shrub competition for light (Hawkes & Menges 1996). Light generally does not limit aboveground growth of established plants in gaps (Tilman 1982) however light levels may be limiting germination of some scrub herbs. Seedling establishment of *Eriogonum longifolium* var. *gnaphalifolium* was significantly higher in shaded microsites with supplemental watering, which elevated soil moisture levels and reduced extreme soil surface temperatures (Carrington 1996). Experimental complete gaps were more shaded compared to other studied gaps perhaps as an artifact of their experimental establishment within dense and tall shrubs. Supplemental watering in combination with partial shading in gaps may have provided favorable microsites for abundant seedling recruitment.

The removal of belowground competition in experimental complete gaps resulted in high seedling recruitment, consistent with observations of high population densities of some scrub herbs such as *Polygonella basiramia* (Hawkes & Menges 1995) and *Balduina angustifolia* (pers. obs.) along sandy roads, which are arguably artificial complete gaps. In complete gaps, belowground competition from shrub roots for space, water and nutrients is eliminated. Roots in scrubby flatwoods are very dense just below the soil surface. The percent water retained in live roots is relatively high compared to the amount of water in soil, thus roots may reduce amount of soil water available for seedlings in natural gaps in scrubby flatwoods. Experimental disturbances removing roots and

rhizomes from belowground gaps increased soil moisture potentially available for seedlings.

Many roots in rosemary scrub are distributed in upper soil depths (0-15 cm), where they are likely interacting with roots of many herbs. Rosemary root leachate was shown to impact recruitment and survival of gap specialists, particularly *Eryngium cuneifolium*, more than gap generalists (Hunter & Menges in press). Florida rosemary contains the novel compound ceratiolin, which is released from fresh Florida rosemary leaves by rain (Tanrisever et al., 1987). Ceratiolin is mildly allelopathic, but degrades to hydrocinnamic acid, which was found to have much stronger allelopathic properties (Fischer et al., 1994). Therefore removing roots from rosemary scrub eliminates allelopathic components from the shrub-herb interaction.

Litter inhibits germination and recruitment in many ecosystems (e.g. Goldberg & Werner 1983; Špačková et al. 1998). Soil surface disturbance and bare soils are important for seedling establishment of many species (e.g. Cantor & Whitham 1989; Parker et al. 1989). Also, in the Florida scrub, litter in the matrix may prevent seedling recruitment. Many rare scrub endemics are associated with mechanical disturbances to the soil such as firelanes, plow lines, sandy roads and gopher tortoise burrows (Hartnett & Richardson 1989; Myers 1990; Hawkes & Menges 1995; Lambert & Menges 1996). Disturbance may favor germination by removing litter and by providing appropriate conditions to break dormancy, or by burying seeds at appropriate depths.

Disturbance of the microbiological soil crust may also be important. Germination of herbaceous plants is improved when soil crusts remain intact (the situation in most natural gaps) or are physically disturbed (a situation similar to experimental aboveground gaps), while complete crust

removal suppresses seedling establishment (Hawkes 2000). Crusts in xeric ecosystems have been shown to influence soil water content, including water retention (Campbell et al. 1989, Johansen 1993, Verrecchia et al. 1995). Thus, crust removal can decrease moisture available for seedlings. We found improved seedling recruitment in complete gaps, where the crust was removed during gap establishment, but only if gaps were watered.

Species apparently differ in their germination responses to water. Some species have documented high recruitment rates in wet conditions, such as *Balduina angustifolia* (this study) *Polygonella basiramia* (Quintana-Ascencio & Menges 2000; Hawkes 2000) or *Paronychia chartacea* ssp. *chartacea* (Hawkes 2000). Many studies have found strong correlations of rainfall with germination in scrub and other systems prone to periods of drought (Guterman 1993; Menges & Weekley 1999; Hawkes 2000). *Hypericum cumulicola* seems to be particularly sensitive to the lack of rainfall, dramatically declining in field germination experiments since 1997 (Quintana-Ascencio & Menges 2000; Hawkes 2000), with no germination in the field part of this study. *Eryngium cuneifolium* recruited only in watered gaps in this study. Rainfall is a good predictor of *Eryngium* seedling emergence (Menges & Weekley 1999).

The 2000-2001 winter was the third consecutive drought year, unprecedented at Archbold Biological Station since 1932 (ABS weather records). Recent field germination experiments (Hawkes 2000) show continued low germination since 1997-98, an El-Niño year with high winter precipitation and high germination (Hawkes 2000; Quintana-Ascencio & Menges 2000). Similarly, low seedling recruitment was recorded for *Eryngium*, *Polygonella*, *Dicerandra frutescens*, *Dicerandra christmanii* and other scrub species in 2000 and 2001 in comparison to

wetter years (Menges, unpubl.). The drought in 2000 and 2001 strongly affected seedling recruitment in this experiment. The potential effects of small-scale gap disturbance on field seedling establishment were overshadowed by the drought. Improved recruitment associated with supplemental gap watering and high watering regime in the pot experiment in this study is consistent with Carrington (1996) and Hawkes (2000), confirming the importance of water for seedling recruitment of scrub plants in the drought period.

Drought years may induce more seeds to enter the seed bank rather than germinate. Of the herbs studied, all but *Polygonella* commonly delay germination and enter persistent seed banks (Quintana-Ascencio 1997; Quintana-Ascencio & Menges 2000; Nemeth & Menges, unpubl.). Lacking a substantial persistent seed bank, *Polygonella* seeds often germinate during the first winter, no matter what conditions exist. As an evidence of this strategy, seeds of this species are often viviparous, germinating on the maternal plant prior to dispersal. *Polygonella* germinated in the watering experiment in all watering regimes, but low germination occurred in the field experiment.

Rapid evaporation and infiltration dry out Florida scrub surface soils and limit water availability for germination. Gagnon et al. (in prep.) show that surface soil layer is often much drier than soils at 50 and 90 cm depths. Gaps have higher soil moisture than soil under shrubs (Gagnon et al. in prep., this study). During mild droughts this may restrict seedlings to gaps. With more severe droughts, no seedling recruitment may occur. At Archbold, percent soil moisture dramatically declined from 1997-98 through 2000-01 (Hawkes 2000; Gagnon et al. in prep.; this study).

Disturbances substituting for fire, such as mechanical treatments, help create patches of bare soil that promote open-site plants (Breininger

and Schmalzer 1990; Greenberg et al. 1994; Greenberg et al. 1995). However, they may leave scrub areas vulnerable to invasion by exotic and weedy species. These treatments alone, without subsequent fire, may leave abundant litter likely inhibiting recruitment of many plants. However, small-scale gap creation (with litter removal) could potentially serve as an alternative to fire-managed small-scale conservation projects, providing regeneration opportunities for some scrub herbs. Many endangered endemics of the Florida scrub are specialized for gaps. Therefore providing for seedling regeneration in gap microsites could be an important component of Florida scrub management.

Table 1. Study species used in the experiments (except *Lechea deckertii*, which recruited spontaneously), plant family, range, local habitat, local abundance, life history, mechanism of recovery after fire, and gap specialization guild.

<i>Species</i>	Family	Range	Primary Habitat (Secondary habitat)	Life History & Primary Recovery Mechanism	Gap Specialization (Guild)
<i>Balduina angustifolia</i>	Asteraceae	se NC, w-s SC, FL	Scrubby flatwoods, oak scrub, sandhills, roadsides	Biennial Seeds	Widespread gap specialist
<i>Eryngium cuneifolium</i>	Apiaceae	Endemic LWR, Hi Co, FL	Rosemary scrub	Perennial Seeds	Narrowly endemic gap specialist
<i>Hypericum cumulicola</i>	Hypericaceae	Endemic LWR, Hi and Po Co, FL	Rosemary scrub (oak scrub)	Perennial Seeds	Narrowly endemic gap specialist
<i>Liatris ohlingerae</i>	Asteraceae	Nearly Endemic to LWR, FL	Rosemary scrub, scrubby flatwoods	Perennial Resprouts	Endemic gap generalist
<i>Paronychia chartacea</i> <i>ssp.</i> <i>chartacea</i>	Caryophyllaceae	Endemic to s, c ridges of FL	Rosemary scrub, scrubby flatwoods, roadsides	Annual Seeds	Endemic gap specialist
<i>Polygonella basiramia</i>	Polygonaceae	Endemic to LWR, BRR FL	Rosemary scrub, scrubby flatwoods, roadsides	Perennial Seeds	Endemic gap specialist
<i>Palafoxia feayi</i>	Asteraceae	Endemic to FL	Scrubby flatwoods, rosemary scrub, flatwoods, roadsides	Perennial/ woody shrub Seeds and Resprouts	Widespread gap generalist
<i>Lechea deckertii</i>	Cistaceae	s GA and FL	Rosemary scrub, scrubby flatwoods	Perennial/ Woody base Seeds (Resprouts)	Widespread gap specialist

Most of the species are State or Federally endangered (*Eryngium*, *Hypericum*, *Polygonella* and *Liatris*) or threatened (*Paronychia*) (Coile 2000). Nomenclature and plant family follows Wunderlin 1998. Species range and local habitat taken from Menges et al. 2000 Life history, recovery mechanism, and gap specialization data taken from Hawkes 2000 (*Eryngium*, *Polygonella* and *Paronychia*); Hawkes & Menges 1995 (*Polygonella*); Hawkes & Menges 1996 (*Eryngium*, *Polygonella* and *Paronychia*); Hemdon 1999 (*Liatris*); Menges & Kimmich 1996 (*Eryngium*); Menges & Kohfeldt 1995 (all species); Quintana-Ascencio & Morales-Hernandez 1997 (*Hypericum*); Quintana-Ascencio et. al. 1998 (*Hypericum*); Quintana-Ascencio & Menges 2000 (*Eryngium*, *Hypericum* and *Polygonella*); Young & Menges 1999 (*Palafoxia* and *Lechea*); Quintana-Ascencio & Menges 1996 (*Balduina*, *Eryngium*, *Hypericum*, *Liatris* and *Polygonella*). LWR = Lake Wales Ridge, BRR = Bombing Range Ridge, Hi Co = Highlands County, Po Co = Polk County, s = south, e = east, w = west, c = central, ABS = Archbold Biological Station.

Table 2. Results of ANOVA for seedling establishment in gaps as a function of watering treatment, vegetation type (rosemary scrub and scubby flatwoods) and gap type (natural, artificial aboveground and artificial complete gaps) in the field experiment.

Source	df	SS	F	p
Watering	1	658.8	7.83	0.005
Vegetation type	1	192.0	2.29	0.132
Gap type	2	402.9	2.39	0.092
Watering*Vegetation type	1	200.2	2.38	0.124
Watering*Gap type	2	197.0	2.34	0.097
Vegetation type*Gap type	2	566.5	3.37	0.035
Watering*Vegetation type*Gap type	2	548.0	3.26	0.039
Error	408	34310.9		

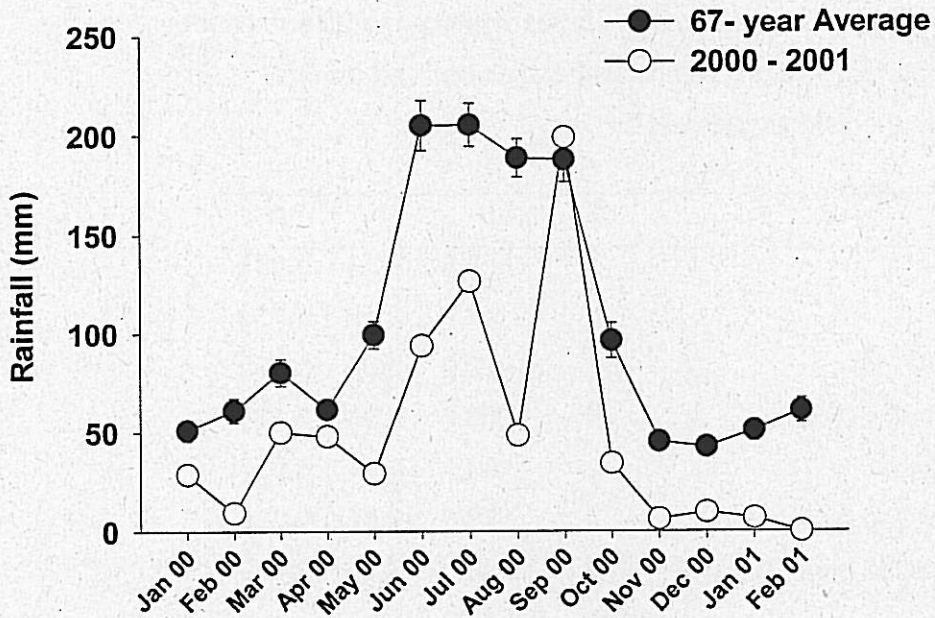


Figure 1. Pattern of monthly precipitation in 2000-2001 and 67-year average precipitation from 1932-1999 (with 95% confidence intervals) at Archbold Biological Station. All rainfall data are from Archbold Biological Station weather records.

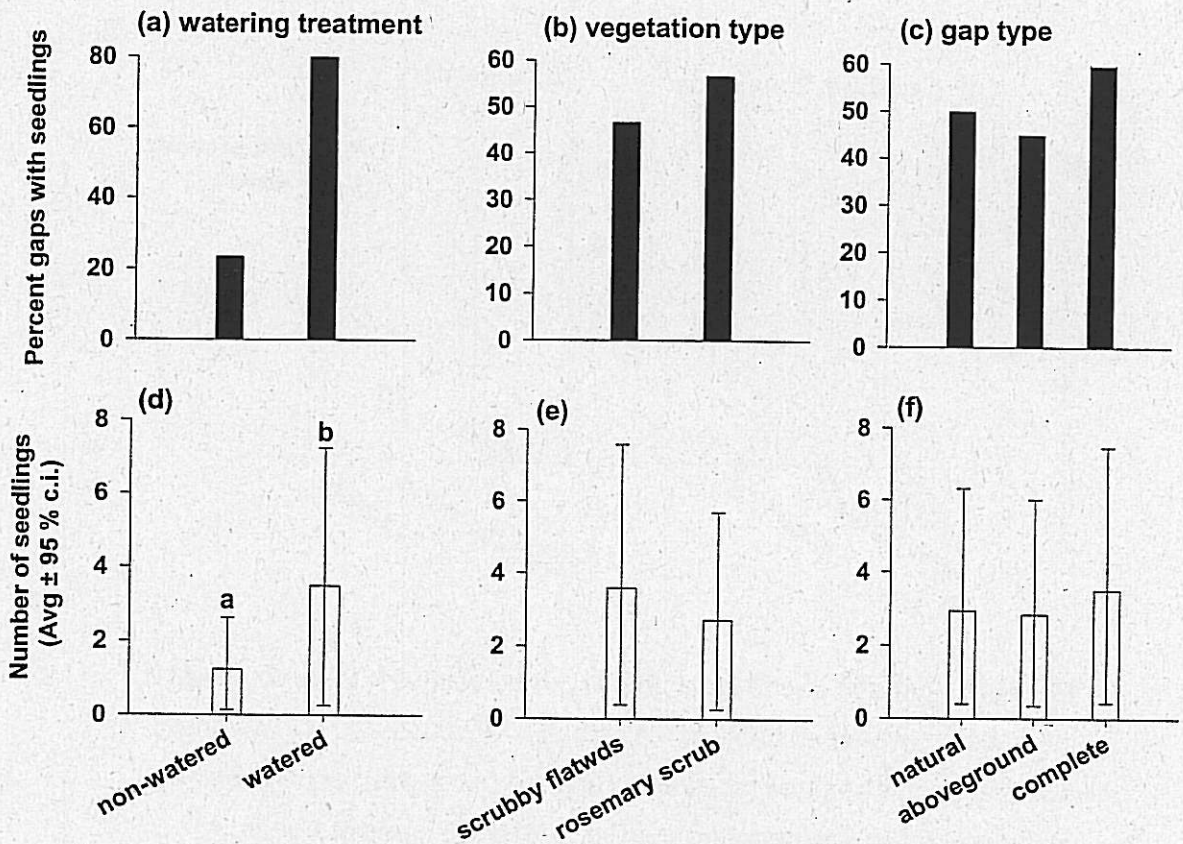


Figure 2. Proportion of gaps with seedlings and average seedling numbers (with asymmetric 95% confidence intervals) for all species recruiting in gaps: (a) and (d) non-watered vs. watered gaps ($n = 30$ for each treatment level); (b) and (e) scrubby flatwoods (= scrubby flatwds) vs. rosemary scrub gaps ($n = 30$ for each vegetation type); and (c) and (e) natural, experimental aboveground (= aboveground), and experimental complete gaps (= complete) with both aboveground and belowground biomass removed ($n = 20$ for each gap type). Different letters above error bars indicate significant differences in seedling numbers within graph. For 5 species, 3000 seeds were sown in the experiment, but for *Liatris* 900 and *Paronychia* 1800 seeds were sown. *Lechea deckertii* recruited spontaneously.

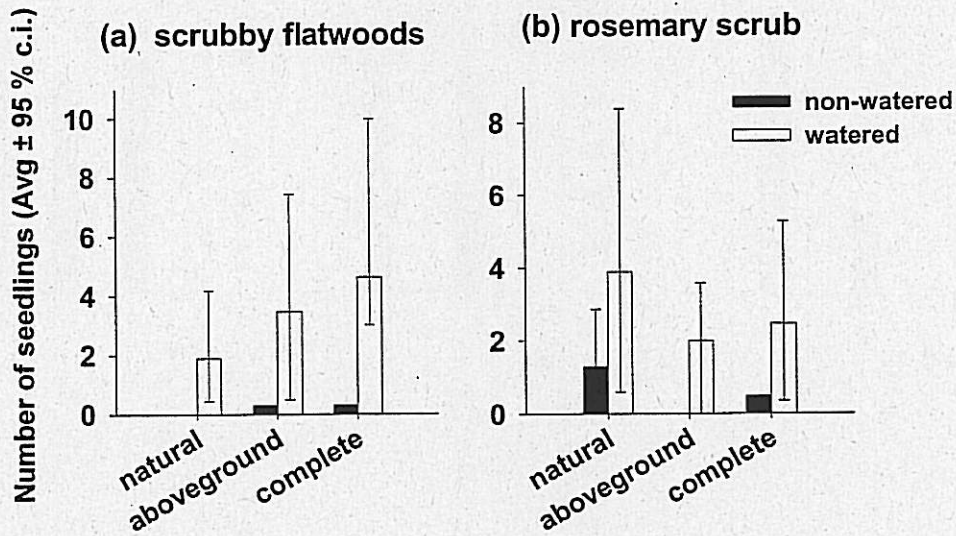


Figure 3. Average seedling numbers (with asymmetric 95% confidence intervals) in two scrub habitats (a) scrubby flatwoods and (b) rosemary scrub and in three gaps types: natural gaps (= natural), experimental aboveground (= aboveground) and experimental complete gaps (= complete). The effect of watering and the interaction watering*vegetation type*gap type were significant.

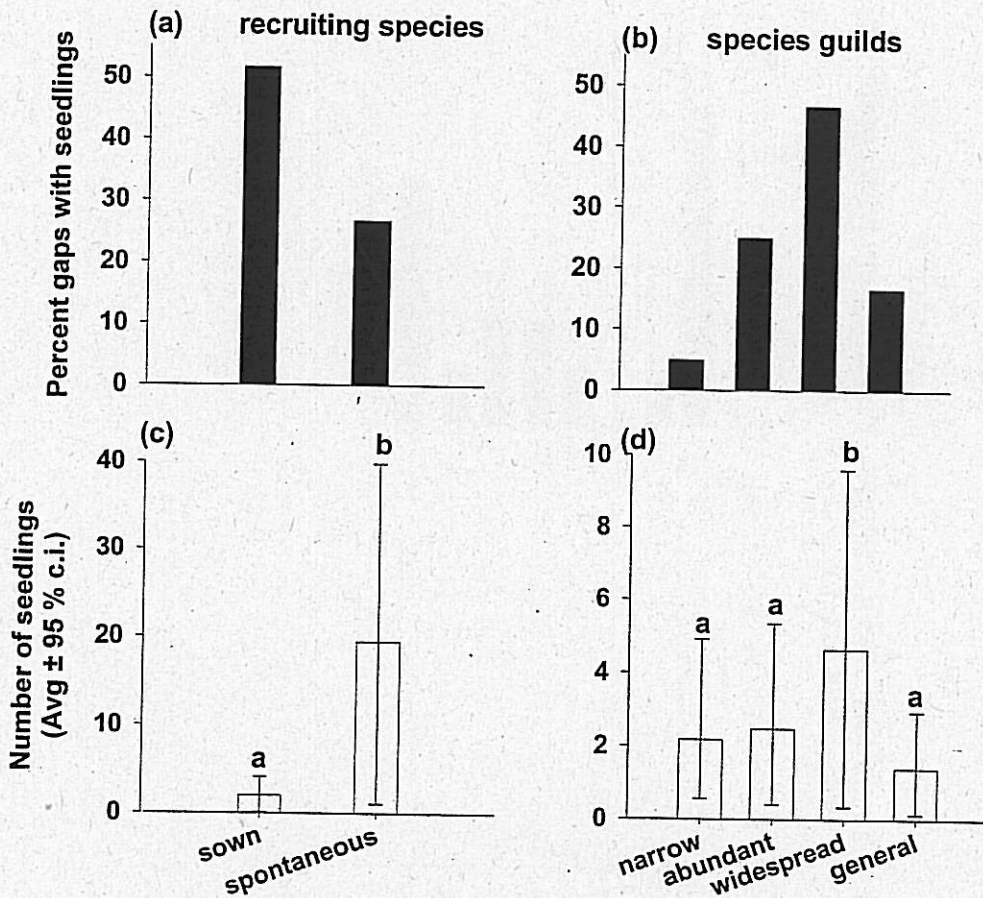


Figure 4. Proportion of gaps with seedlings of all gaps ($n = 60$) and average seedling numbers with asymmetric 95% confidence intervals, for (a) and (c) sown species and spontaneously recruited species (*Lechea*), (b) and (d) seedling numbers in species guilds: narrowly endemic gap specialists (= narrow), endemic gap specialists (= endemic), widespread gap specialists (= widespread) and gap generalists occurring in both gaps and scrub matrix (= general). Different letters indicate significant differences within graphs. Note different scales on y-axes.

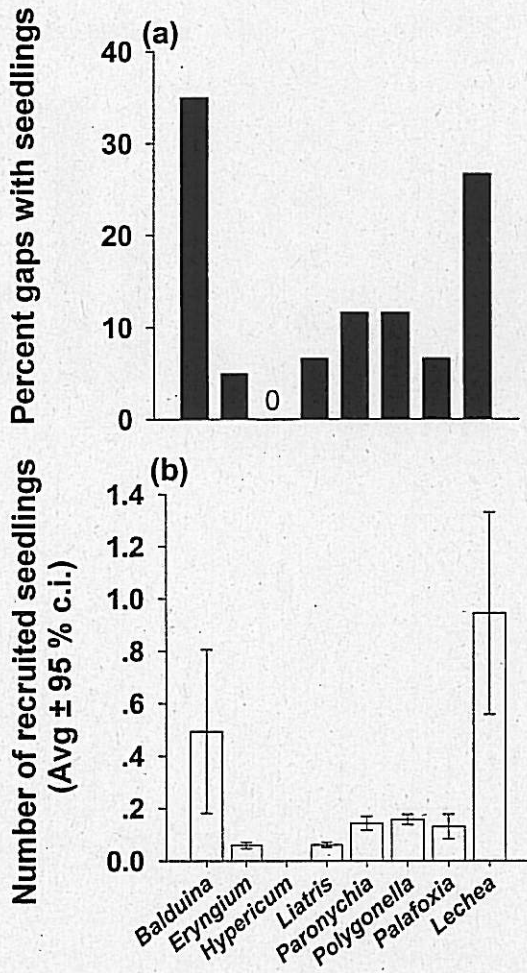


Figure 5. (a) Proportion of gaps with seedlings of all ($n = 60$) gaps and (b) average numbers of seedlings of sown species and spontaneously recruited *Lechea* in all gaps (with 95% confidence intervals). *Hypericum* had no seedling recruitment.

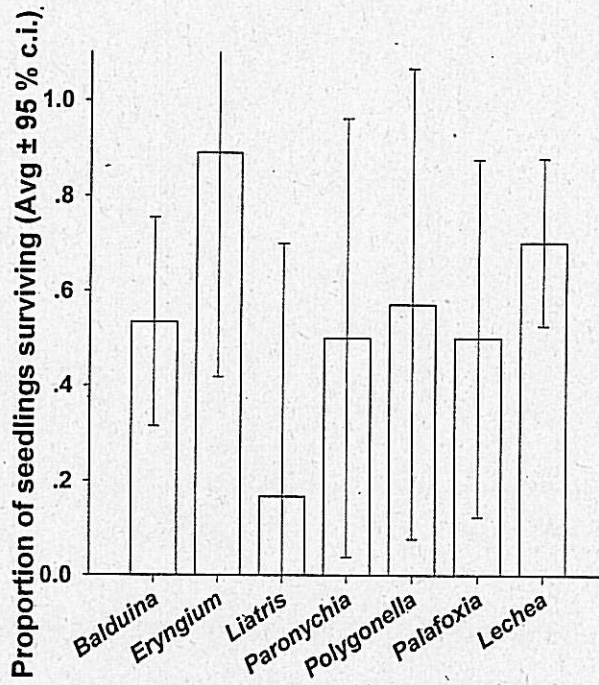


Figure 6. Average proportion of seedlings surviving in gaps (with 95% confidence intervals). *Hypericum* is not plotted due to zero germination.

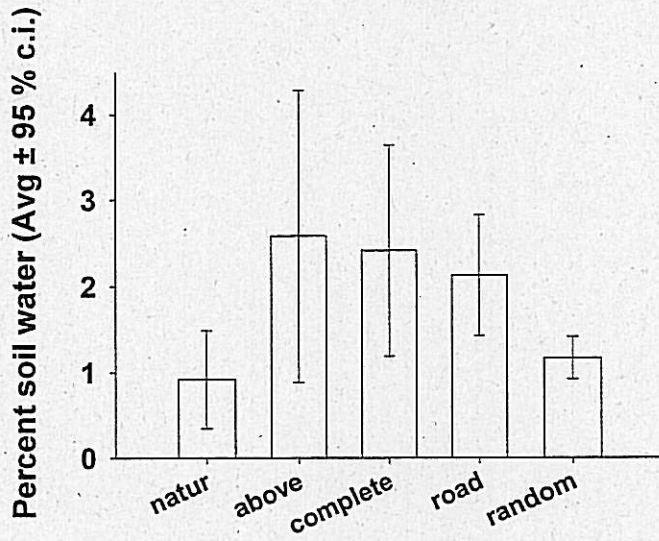


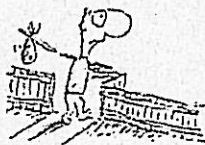
Figure 7. Differences in gravimetric soil moisture in natural gaps (= natur), experimental aboveground gaps (= above), experimental complete gaps (= complete), random points at roadsides (= road) and random points in the scrub matrix (= random) in July 2000 (n = 18). Bars are 95% confidence intervals.

How To GET THERE

Go to the end of the path until you get to the gate.



Go through the gate and head straight out towards the horizon.



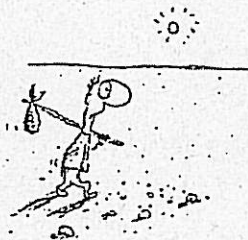
Keep going towards the horizon.



Sit down and have a rest every now and again.



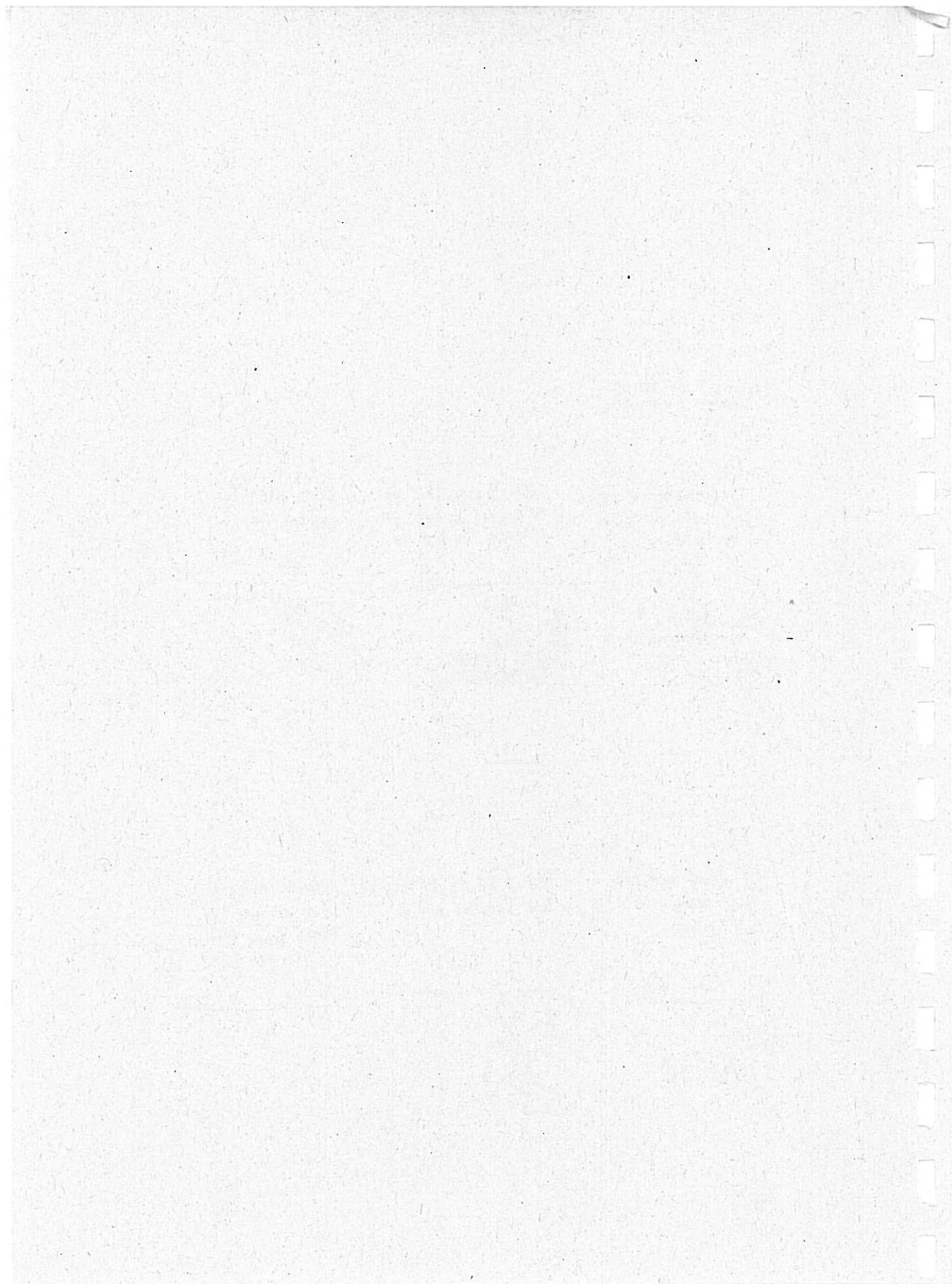
But keep on going. Just keep on with it.



Keep on going as far as you can. That's how you get there



Leung



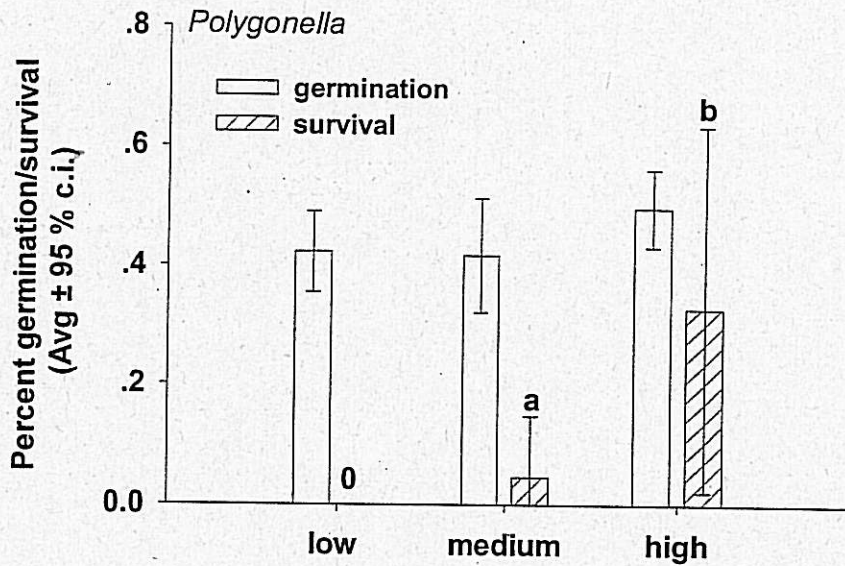


Figure 8. Germination and survival of *Polygonella* in a pot watering experiment in low, medium and high watering regimes. Average percent germination and survival with 95% confidence intervals. Different letters above error bars indicate significant differences in seedling survival within graph. Low watering treatment had no seedling germination.

Chapter 4

Mobile sand in the Florida scrub gaps and
sand roads: a dynamic microsite for herbs



Mobile sand in the Florida scrub gaps and sand roads: a dynamic microsite for herbs

Abstract

Florida scrub grows on relict beach ridges with xeric sands, which are constantly transported by winds. These sand movements likely affect microsites occupied by the Florida scrub herbs and species demography. I analyzed temporal variation in sand accretion and erosion in natural post-fire gaps within the shrub matrix and along sand roads at Archbold Biological Station in five time intervals: one and two weeks; and one, three, and six months. Also, in three experiments, I tested effects of sand movement on three herbaceous scrub species: *Balduina angustifolia*, *Paronychia chartacea* and *Polygonella basiramia*. In two pot experiments, I studied (1) seedling germination of seeds buried to 0, 5 and 20 mm sand depths, and (2) seedling survival with frequent but low (a) sand addition, keeping seedlings completely buried, (b) alternating sand addition and removal, and (c) infrequent high sand addition, versus (d) control. Finally, in a field experiment, I studied rosette growth with (a) sand addition, (b) sand removal, (c) alternating sand addition and removal, (d) controls protected from spontaneous sand movements, and (e) non-manipulated controls. Sand accretion and erosion fluctuated over time with sand erosion greater than accretion. With increasing time intervals, the range of oscillations increased. Over one-week intervals, sand depth changes ranged from a minimum of -17.3 mm to a maximum of 12.3 mm, in six-months interval the minimum-maximum range was -54.0 mm to 22.0 mm. Sand erosion was significantly greater and more variable along roads than in natural gaps. In pot experiments, significantly more seedlings

germinated from 0 and 5 mm sand depths compared to 20 mm depth. Seedling survival with experimental complete burial was lower than in other treatments. In the complete burial treatment, $22.3 \pm 5.39\%$ s.e. of seedlings survived in March, but no seedlings survived in April. Survival in other treatments was high ranging in March from $66 \pm 5.9\%$ to $75 \pm 8.9\%$, and in April from $17 \pm 5.8\%$ to $30 \pm 9.2\%$. Plants responded to sand removal by significant elongation of flowering stems. Effects of other treatments on growth did not differ significantly, but rosette mortality in the experiment ranged from 43% to 63%. The three study species responded to sand burial and erosion differentially. In the pot experiments, germination was highest in *Polygonella*, and seedling survival of *Polygonella* and *Balduina* in experimental treatments was higher compared to *Paronychia*. In the field experiment, *Paronychia* plants responded to sand removal treatment by increasing rosette diameter, and the other species elongated flowering stems. Results of this study indicate that mobile sand creates a constantly shifting array of microsites that can influence post-dispersal seed germination, survival, and growth. Roadside habitats have more dynamic patterns of sand movement than natural gaps, and could alter the demography of endemic Florida scrub plants.

Key words: endemic plant species, disturbance, gaps, sand accretion and erosion, seed burial, seedling germination and survival

Nomenclature: Wunderlin 1998

Introduction

Florida scrub is a xeric fire-prone ecosystem, dominated by shrub oaks, palmettos and ericaceous shrubs, with variable pine overstories and sparse, patchy herbaceous cover (Myers 1990; Menges & Hawkes 1998).

The scrub occurs on relict beach ridges and bars (Stout & Marion 1993) in several regions of Florida, originated several million years ago, when sand dunes and beaches were deposited along a shoreline (Watts & Hansen 1994). The depositions are nutrient poor, moderately to excessively drained acid quartzsammment soils (Entisols derived from quartz sands; Abrahamson et al. 1984; Kalisz & Stone 1984; Carter et al. 1999).

These sands are constantly transported by winds, accreting and eroding around plants, or forming shifting micro-dunes. The temporal variation and extent of these sand movements are not well known in the Florida scrub. Although presumably not as mobile as sands in deserts and semi-desert or coastal, lacustrine and inland dune systems (Brown 1997; Maun 1999; Maun & Perumal 1999; Okin et al. 2001), sand movements in Florida scrub could have important effects on the demography of plants, especially herbaceous plants and seedlings.

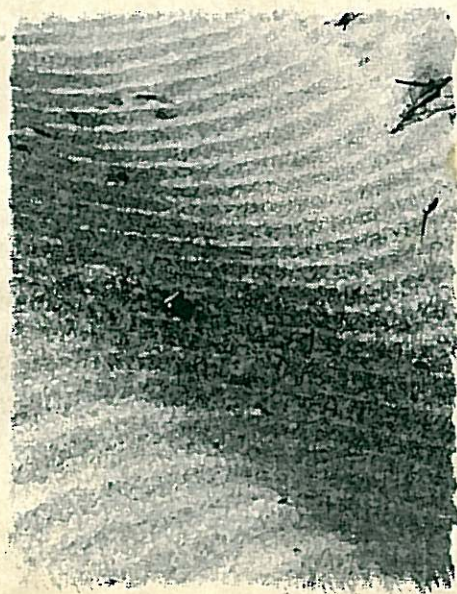
Mobile sands and dunes are disturbances that affect microsites of various plant species and consequently demographic parameters such as germination of buried seeds (Maun & Lapierre 1984; Maun 1994; Cheplick & Grandstaff 1997; Chen & Maun 1999; Rowland & Maun 2001; Hamzé & Jolls 2000; Quilichini & Debussche 2000), and survival and growth of seedlings (Maun 1994; Rowland & Maun 2001). Many studies have also explored the morphology and growth of dune species and their flowering and fecundity responses to sand accretion and erosion (Disraeli 1984; Zhang & Maun 1992; Marba & Duarte 1995; Brown 1997; Maun

1998; Bach 2001; Langlois et al. 2001). In the Florida scrub, effects of sand accretion on growth were studied for *Eryngium cuneifolium* (Menges & Kimmich 1996), but detailed experimental studies exploring burial effects on microsite and demography of scrub herbs are still needed.

Many Florida scrub herbs are obligate seeders, recruiting seedlings in areas of open bare sand in post-fire gaps within the matrix of dominant shrubs (Menges & Hawkes 1998; Young & Menges 1999; Quintana-Ascencio & Menges 1996; Chapter 3). Many of these herbs occur mainly in gaps within rosemary scrub (rosemary phase of sand pine scrub (Abrahamson et al. 1984) dominated by Florida rosemary (*Ceratiola ericoides*, Empetraceae), shrubby oaks (*Quercus spp.*) and occasional sand pines (*Pinus clausa*) growing on sandy Entisols of St. Lucie or Archbold series (Abrahamson et al. 1984; Myers 1990; Carter et al. 1999). Florida herbs plants frequently overlap from rosemary scrub to gaps in adjacent scrubby flatwoods on similar soils, dominated by the same oaks that occur in rosemary scrub, palmettos (*Sabal etonia*, *Serenoa repens*), and ericaceous shrubs (*Lyonia spp.*, *Vaccinium spp.*) (Abrahamson et al. 1984).

Sand roads dividing scrub units often may provide gap microhabitats, and many gap specialized Florida scrub herbs occur along sand roads, often in higher population densities than in scrub gaps (Hartnett & Richardson 1989; Myers 1990; Hawkes & Menges 1995; Lambert & Menges 1996). Little work has been done on demography and microsite characteristics of roadside populations of Florida scrub plants.

Microsites for scrub herbs in open gaps in Florida scrub and along roadsides may be affected by sand movements. Since many of the scrub species are endangered and endemic, exploring their microsite



Appendix

- Petrů, M.** 2001: Effects of small-scale disturbances on the recruitment of Florida scrub herbs. Conference Abstracts ABS Symposium, p. 17. (Chapter 3)
- Maliakal, K. S., **Petrů, M.**, Boyle, O. D. & Menges, E. S. 2001. Gapology in Florida scrub: integrating spatial and demographic approaches. Conference Abstracts ABS Symposium, p. 16. (Chapter 3)
- Petrů, M.** J. Lepš. (2000). Regeneration dynamics in populations of two hemiparasitic species in wet grasslands. In: White, P. S., Mucina, L., Lepš, J. (eds.) Vegetation science in retrospect and perspective. Proceedings of the 41th Symposium of IAVS. pp. 329-333. Opulus Press, Uppsala. (Chapter 1, part)

Other publications:

- Gough, L., Goldberg, E. D., Hershock, C., Pauliukonis, N. & **Petrů, M.** In press. Investigating the community consequences of competition among clonal plants. *Evolutionary Ecology* 15.
- Mill, R. R., Allard, D. J., Petrů, M. & Wang, H. A remarkable new arboreal epiphytic species of *Pedicularis* (Scrophulariaceae) from Nepal. Submitted to *Journal of Royal Edinburg Botanical Gardens*, April 2002.

Thesis related publications (incl. Conference Abstracts):

Petrú, M. Annual variation and experimental disturbance effects on demography of the strict biennial *Pedicularis sylvatica*. Submitted to *Journal of Vegetation Science* in March 2002.

(Chapter 2)

Petrú, M., Menges, E. S. Seedling establishment in natural and experimental Florida scrub gaps. Submitted to *Journal of Torrey Botanical Society* in January 2002.

(Chapter 3)

Petrú, M. 2001. Habitat disturbance affecting the population dynamics of a biennial *Pedicularis* spp. Conference Abstracts, Winter Annual Meeting of the British Ecological Society, p. 10.

(Chapter 2)

Petrú, M. 2001. Viability of populations in disturbed habitats; analysis for biennial plants. Conference Abstracts. 44th IAVS Symposium, p. 33.

(Chapter 2)

Petrú, M. 2001. Effect of small-scale disturbance on the recruitment of Florida scrub herbs. Proceedings of the Florida Scrub Symposium 2001, U.S. Fish and Wildlife Service, p. 33-35.

(Chapter 3)

Boyle, O. D., Maliakal, S. K., **Petrú, M.** and Menges, E. S. 2001.

Gapology in the Florida Scrub: Incorporating spatial and demographic approaches. Proceedings of the Florida Scrub Symposium 2001, U.S. Fish and Wildlife Service, p. 35-37.

(Chapter 3)

Posters

- (1) **Mobile sand in the Florida scrub gaps and sand roads: a dynamic microsite for herbs.** Will be presented at the Meeting of Ecological Society of America in Tucson, August 2002.
(Chapter 4)
- (2) **Annual oscillations in population structure of a strict biennial. The effects of experimental disturbances on *Pedicularis sylvatica*.** Will be presented at Population Biology Meeting in Prague, May 2002.
(Chapter 2)
- (1) **Seedling establishment in natural and experimental Florida scrub gaps.** Will be presented at Population Biology Meeting in Prague, May 2002 and displayed at Archbold Biological Station.
(Chapter 3)
- (2) **Effects of small-scale disturbances on the regeneration of Florida scrub plants.** 4th current research at Archbold Biological Station Symposium, Archbold Biological Station, Florida, January 2001.
(Chapter 3; Chapter 4)
- (3) **Gapology in Florida scrub: integrating spatial and demographic approaches** (co-author), 4th current research at Archbold Biological Station Symposium, Archbold Biological Station, Florida, January 2001.
(Chapter 3)

List of research presentations and publications:

Oral papers

- (1) Population dynamics of a biennial *Pedicularis sylvatica* and effects of disturbance. **Winter annual meeting British Ecological Society, Warwick, December 2001.**
(Chapter 2)
- (2) Disturbance in the Florida rare plants, seedling recruitment in gaps in the Florida scrub. **Invited seminar, University of Potsdam, Germany, October 2001.**
(Chapter 3)
- (3) Viability of populations in disturbed habitats; analysis for biennial plants. **44th IAVS Symposium, Friesing-Weihenstephan, Germany, July-August 2001.**
(Chapter 2)
- (4) Seedling recruitment in small-scale disturbances in the Florida scrub. **Final intern seminar at Archbold Biological Station, Florida, June 2001.**
(Chapter 3; Chapter 4)
- (5) Effects of small-scale gap disturbance on the recruitment of Florida scrub herbs. **Florida Scrub Symposium, Orlando, Florida, June 2001.**
(Chapter 3)

References

- sowing of *Pinus sylvestris* L. at different dates. Scand. Jour. For. Res. 16: 422-428.
- Wunderlin, R. P. 1998. Guide to the Vascular Plants of Florida. Univ. Press of Florida, Gainesville.
- Young, C. C. & Menges, E. S. 1999. Postfire gap-phase regeneration in scrubby flatwoods on the Lake Wales Ridge. Florida Scientist 62: 1-10.
- Zamfir, M. 2000. Effects of bryophytes and lichens on seedling emergence of alvar plants: evidence from greenhouse experiments. Oikos 88: 603-611.
- Zhang, J. & Maun, M. A. 1992. Effects of burial in sand on the growth and reproduction of *Cakile edentula*. Ecography 15: 269-302.
- Zobel, M., Otsus, M., Liira, J., Moora, M. & Mols, T. 2000. Is small-scale species richness limited by seed availability or microsite availability? Ecology 81: 3274-3282.

References

- Design and analysis of ecological experiments, pp. 134-157. Oxford Univ. Press, New York.
- Watts, W. A. & Hansen, B. C. S. 1994. Pre-Holocene and Holocene pollen records of vegetation history from the Florida peninsula and their climatic implications. *Palaeogeography, Palaeoclimatology, and Palaeoecology* 109: 163-176.
- Weller, S. G. 1989. The effect of disturbance scale on sand dune colonization by *Lithospermum caroliniense*. *Ecology* 70: 1244-1251.
- Wells, T. C. E. 1971. A comparison of the effects of sheep grazing and mechanical cutting on the structure and botanical composition of chalk grassland. In: Duffey, E. & Watt, A. S. (eds.) *The scientific management of animal and plant communities for conservation*, pp. 497-515. Blackwell Scientific, Oxford.
- Werner, P. A. 1975. Prediction of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia* 20: 197-201.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* 45: 229-299.
- Wilczynski, C. J. & Pickett, S. T. A. 1993. Fine root biomass within experimental canopy gaps: evidence for a below-ground gap. *J. Veg. Sci.* 4: 571-574.
- Williams, R. J. 1992. Gap dynamics in sub-alpine heathland and grassland vegetation in south-eastern Australia. *Jour. Ecol.* 80: 343-352.
- Winn, A. A. 1985. Effects of seed size and microsite on seedling emergence of *Prunella vulgaris* in four habitats. *Jour. Ecol.* 73: 831-840.
- Winsa, H. & Sahlen, K. 2001. Effects of seed invigoration and microsite preparation on seedling emergence and establishment after direct

References

- Tanrisever, N., Fronczek, F. R., Fischer, N. H. & Williamson, G. B. 1987. Ceratiolin and other flavonoides from *Ceratiola ericoides*. *Phytochemistry* 26: 175-179.
- Ter Borg, S. J. 1985. Population biology and habitat relations of some hemiparasitic Scrophulariaceae. In: White, J. (eds.) *The population structure of vegetation. Handbook of Vegetation Science Vol. 3*, pp. 463-487. Dr. W. Junk Publishers, Dodrecht.
- Ter Borg, S. J., Jansen, A. & Kwak, M. M. 1980. Life cycle variation in *Pedicularis palustris* L. (Scrophulariaceae). *Acta Bot. Neerl.* 29: 379-405.
- Thompson, K., Bakker, J. P. & Bekker, M. 1997. *Soil seed banks of North West Europe: Methodology, density and longevity*, pp. 276. Univ. Press, Cambridge.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton Univ. Press, Princeton.
- Van der Meijden, E., Klinkhamer, P. G. L., de Jong, T. J. & Van Wijk, C. A. M. 1992. Meta-population dynamics of biennial plants: how to exploit temporary habitats. *Acta Bot. Neerl.* 41: 249-270.
- Van Tooren, B. F. 1988. The fate of seeds after dispersal in chalk grassland: the role of the bryophyte layer. *Oikos* 53: 41-48.
- Verrecchia, E., Yair, A., Kidron, G. J. & Verrecchia, K. 1995. Physical properties of the psammophile cryptogamic crust and their consequences to the water regime of sandy soils, north-western Negev Desert, Israel. *J. Arid Environments* 29: 427-437.
- Viswanathan, D. 2000. Why biennials are so few: Habitat availability and the species pool. *Ecoscience* 7: 461-465.
- von Ende, C. N. 2001. Repeated measures analysis: Growth and other time-dependent measures. In: Scheiner, S. M. & Gurevitch, J. (eds.)

References

- Satterthwaite, W. S., Quintana-Ascencio, P. F. & Menges, E. S. In revision. Population viability of scrub buckwheat (*Eriogonum longifolium* var. *gnaphalifolium*) in relation to fire. *Ecol. Appl.*
- Schat, H., Ouborg, J. & de Wit, R. 1989. Life history and plant architecture: size-dependent reproductive allocation in annual and biennial *Centaureum*. *Acta Bot. Neerl.* 38: 183-201.
- Schmaltzer, P. 1992. Species composition and structure of oak-saw palmetto scrub vegetation. *Castanea* 57: 220-251.
- Sherman, R. E., Fahey, T. J. & Battles, J. J. 2000. Small-scale disturbance and regeneration dynamics in a neotropical mangrove forest. *Jour. Ecol.* 88: 165-178.
- Silvertown, J. 1983. Why are biennials sometimes not so few? *Am. Nat.* 121: 448-453.
- Silvertown, J. 1986. "Biennials": a reply to Kelly. *Am. Nat.* 127: 721-724..
- Sokal, R. R. & Rohlf, F. J. 2000. *Biometry*. Freeman. New York.
- Sousa, P. W. 1984. The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst.* 15: 353-391.
- Špačková, I., Kotorová, I. & Lepš, J. 1998. Sensitivity of seedling recruitment to moss, litter and dominant removal in an oligotrophic wet meadow. *Folia Geobot.* 33: 17-30.
- Stout, I. J. & Marion, W. R. 1993. Pine flatwoods and xeric pine forests of the southern (lower) coastal plain. In: Martin, W. H., Boyce, S. G. & Echternach, A. C. (eds.) *Biodiversity of the Southeastern United States. Lowland Terrestrial Communities*, pp. 373-446. John Wiley and Sons Publ., New York.
- Sykes, M. T. & Wilson, J. B. 1990. Dark tolerance in plants of dunes. *Funct. Ecol.* 4: 799-805.

References

- Quintana-Ascencio, P. F. 1997. Population viability analysis of a rare plant species in patchy habitats with sporadic fire. PhD thesis. State University of New York, Stony Brook.
- Quintana-Ascencio, P. F. & Menges, E. S. 2000. Competitive abilities of three narrowly endemic plant species in experimental neighborhoods along a fire gradient. *Am. J. Bot.* 87: 690-699.
- Quintana-Ascencio, P. F. & Menges, E. S. 1996. Inferring metapopulation dynamics from patch level incidence of Florida scrub plants. *Conserv. Biol.* 10: 1210-1219.
- Quintana-Ascencio, P. F. & Morales-Hernandez, M. 1997. Fire-mediated effects of shrubs, lichens, and herbs on the demography of *Hypericum cumulicola* in patchy Florida scrub. *Oecologia* 112: 263-271.
- Quintana-Ascencio, P. F., Menges, E. S. & Weekley, C. In press. A fire-explicit population viability analysis of *Hypericum cumulicola* in Florida rosemary scrub. *Conserv. Biol.*
- Quintana-Ascencio, P. F., Dolan, R. W. & Menges, E. S. 1998. *Hypericum cumulicola* demography in unoccupied and occupied Florida scrub patches with different time-since-fire. *Jour. Ecol.* 86: 640-651.
- Rabotnov, T. A. 1969. Plant regeneration from seed in meadows of the U.S.S.R. *Herbage Abstracts* 39: 269-277.
- Rothmaler, W. 1976. Exkursionsflora für die Gebiete der DDR und der BRD. Kritischer Band. Volk und Wissen, Berlin.
- Rowland, J. & Maun, M. A. 2001. Restoration ecology of an endangered plant species: Establishment of new populations of *Cirsium pitcheri*. *Restor. Ecol.* 9: 60-70.
- Růžička, V. 1999. Conditions required for germination of seeds in the genus *Pedicularis* [in Czech]. *Příroda* 15: 135-139.

References

- Parker, V. T. & Kelly, V. R. 1989. Seed banks in California chaparral and other Mediterranean climate shrublands. In: Leck, M. A., Parker V. T. & Simpson, R. L. (eds.) Ecology of soil seed banks, p. 231-255. Academic Press, San Diego.
- Pavlovic, N. B. 1994. Disturbance-dependent persistence of rare plants: anthropogenic impacts and restoration implications. In: Bowles, M. & Whelan, C. (eds.) Restoration of endangered plants, p. 159-193. Cambridge Univ. Press, Cambridge.
- Petraitis, P. S., Latham, R. E. & Niesenbaum, R. A. 1989. The maintenance of species diversity by disturbance. *The Quar. Rev. Biol.* 64: 393-418.
- Petrů, M. & Lepš, J. 2000. Regeneration dynamics in populations of two hemiparasitic *Pedicularis* species in wet grasslands. Proceedings IAVS Symposium, pp. 329-333. IAVS Opulus Press Uppsala, Sweden.
- Pickett, S. T. A. & White, P. S. 1985. Natural disturbance and patch dynamics: an introduction. In: Pickett, A. T. A. & White, P. S. (eds.) The ecology of natural disturbance and patch dynamics, p. 3-13. Academic Press, Orlando.
- Quilichini, A. & Debussche, M. 2000. Seed dispersal and germination patterns in a rare Mediterranean island endemic (*Anchusa crispa* Viv., Boraginaceae). *Acta Oecol.* 21: 303-313.
- Quintana-Ascencio, P. F. & Weekley, C. 2001. The population dynamics of *Hypericum cumulicola* in natural vs. human-modified habitats and with different fire return intervals. Report to Division of Forestry. Florida Department of Agriculture.

References

- Menges, E. S. & Quintana-Ascencio, P. F. In prep. Evaluating population viability with fire in *Eryngium cuneifolium*: deciphering a decade of demographic data. Ecol. Monogr.
- Menges, E. S. & Weekley, C. 1999. Final report on continued ecological monitoring and experimental research on four Florida scrub endemic plants. Report to Division of Forestry, Florida Department of Agriculture.
- Meusel, H. (eds.) 1978. Vergleichende Chorologie der zentraleuropäischen Flora 2, p. 407. Jena.
- Morgan, J. W. 1997. The effect of grassland gap size on establishment, growth and flowering of the endangered *Rutidosia leptorrhynchoides* (Asteraceae). Jour. App. Ecol. 34: 566-576.
- Myers, R. L. 1990. Scrub and high pine. In: Myers, R. L. & Ewel, J. J. (eds.) Ecosystems of Florida, pp. 150-193. Univ. of Central Florida Press, Orlando.
- Narukawa, Y. & Yamamoto, S. I. 2001. Gap formation, microsite variation and the conifer seedling occurrence in a subalpine old-growth forest, central Japan. Ecol. Research 16: 617-625.
- Oberdorfer, E. 1992. Süddeutsche Pflanzengesellschaften. Teil I., 3. Auflage, p. 314. Gustav Fischer Verlag, Jena.
- Oberdorfer, E. 1993. Süddeutsche Pflanzengesellschaften. Teil II.a, 3. Auflage, p. 355. Gustav Fischer Verlag, Jena.
- Okin, G. S., Murray, B. & Schlesinger, W. H. 2001. Degradation of sandy arid shrubland environments: observations, process modeling, and management implications. J. Arid Environments 47: 123-144.
- Ostertag, R. 1998. Belowground effects of canopy gaps in a tropical wet forest. Ecology 79: 1294-1304.

References

- seedlings on coastal dune systems. *Vegetatio* 111: 59-70.
- Maun, M. A. 1998. Adaptations of plants to burial in coastal sand dunes. *Can. J. Bot.* 76: 713-738.
- Maun, M. A. 1999. Effects of sand burial depth on seed germination and seedling emergence of *Cirsium pitcheri*. *Plant Ecol.* 140: 53-60.
- Mavraganis, K. & Eckert C. G. 2001. Effects of population size and isolation on reproductive output in *Aquilegia canadensis* (Ranunculaceae). *Oikos* 95: 300-310.
- McConnaughay, K. D. M. & Bazzaz, F. A. 1987. The relationship between gap size and performance of several colonizing annuals. *Ecology* 68: 411-416.
- McEvoy, P. B. & Rudd, N. T. 1993. Effects of vegetation disturbances on insect biological-control of tansy ragwort, *Senecio jacobaea*. *Ecol. Appl.* 3: 682-698.
- Menges, E. S. 1999. Ecology and Conservation of Florida Scrub. In: Anderson, R. C., Fralish, J. S. & Baskin, J. M. (eds.) *Savanna, barren, and rock outcrop plant communities of North America*, p. 7-22. Univ. Press, Cambridge.
- Menges, E. S., Weekley, C. W., Yahr, R., Brand, C. & Mundell, D. 2000. *Plants of Archbold Biological Station, Highlands County, Florida*. <http://www.archbold-station.org/abs/dta/lists/Plantlist>.
- Menges, E. S. & Hawkes, C. V. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. *Ecol. Appl.* 8: 935-946.
- Menges, E. S. & Kimmich, J. 1996. Microhabitat and time since fire: effect on demography of *Eryngium cuneifolium* (Apiaceae), a Florida scrub endemic plant. *Am. Jour. Bot.* 83: 185-191.
- Menges, E. S. & Kohfeldt, N. 1995. Life history strategies of Florida scrub plants in relation to fire. *Bull. Torrey Bot. Club* 122: 282-297.

References

- Kupferschmid, A. D., Stampfli, A. & Newbery, D. M. 2000. Dispersal and microsite limitation in an abandoned calcareous grassland of the southern prealps. *Folia Geobot.* 35: 125-141.
- Lambert, B. B. & Menges, E. S. 1996. The effects of light, soil disturbance and presence of organic litter on the field germination and survival of the Florida Goldenaster, *Chrysopsis floridana* Small. *Florida Scientist* 59: 121-137.
- Langlois, E., Bonis, A. & Bouzillé, J. B. 2001. The response of *Puccinellia maritima* to burial: A key to understanding its role in salt-marsh dynamics? *J. Veg. Sci.* 12: 289-297.
- Lennartson, T. & Svensson, R. 1996. Patterns in the decline of three species of *Gentianella* in Sweden illustrating the deterioration of semi-natural grasslands. *Symbolae Botanicae Upsaliensis* 31: 169-184.
- Lennartsson, T. & Oostermeijer, J. G. B. 2001. Demographic variation and population viability in *Gentianella campestris*: effects of grassland management and environmental stochasticity. *Jour. Ecol.* 89: 451-463.
- Löfgren, P., Eriksson, O. & Lehtilä, K. 2000. Population dynamics and the effect of disturbance in the monocarpic herb *Carlina vulgaris* (Asteraceae). *Ann. Bot. Fennici* 37: 183-192.
- Marba, N. & Duarte, C. M. 1995. Coupling of seagrass (*Cymodocea nodosa*) patch dynamics to subaqueous dune migration. *Jour. Ecol.* 83: 381-389.
- Maun, M. A. & Lapierre, J. 1984. The effects of burial by sand on *Ammophila breviligulata*. *Jour. Ecol.* 72: 827-839.
- Maun, M. A. & Perumal, J. 1999. Zonation of vegetation on lacustrine coastal dunes: effects of burial by sand. *Ecology Letters* 2: 14-18.
- Maun, M. A. 1994. Adaptations enhancing survival and establishment of

- Keizer, P. J., Van Tooren, B. F. & During, H. J. 1985. Effects of bryophytes on seedling emergence and establishment of short-lived forbs in chalk grassland. *Jour. Ecol.* 73: 493-504.
- Kelly, D. 1985a. Why are biennials so maligned? *Am. Nat.* 125: 473-479.
- Kelly, D. 1985b. On strict and facultative biennials. *Oecologia* 67: 292-294.
- Kelly, D. 1989a. Demography of short-lived plants in chalk grassland. I. Life cycle variation in annuals and strict biennials. *Jour. Ecol.* 77: 747-769.
- Kelly, D. 1989b. Demography of short-lived plants in chalk grassland. II. Control of mortality and fecundity. *Jour. Ecol.* 77: 770-784.
- Kelly, D. 1989c. Demography of short-lived plants in chalk grassland. III. Population stability. *Jour. Ecol.* 77: 785-798.
- Kiviniemi, K. 2001. Evolution of recruitment features in plants: a comparative study of species in the Rosaceae. *Oikos* 94: 250-262.
- Klinkhamer, P. G. L., de Jong, T. J. & Heiden J. L. H. 1996. An eight-year study of population dynamics and life-history variation of the 'biennial' *Carlina vulgaris*. *Oikos* 75: 259-268.
- Klinkhamer, P. G. L., de Jong, T. J. & Meelis, E. 1987. Delay of flowering in the 'biennial' *Cirsium vulgare*: size effects and devernialization. *Oikos* 49: 303-308.
- Kotorová, I. & Lepš, J. 1999. Comparative ecology of seedling recruitment in an oligotrophic wet meadow. *J. Veg. Sci.* 10: 175-186.
- Křenová, Z. & Lepš, J. 1996. Regeneration of a *Gentiana pneumonanthe* population in an oligotrophic wet meadow. *J. Veg. Sci.* 7: 107-112.

References

- grandiflora* (Convolvulaceae): effects of fire on plant and seed bank dynamics. *Am. J. Bot.* 76: 361-369.
- Hawkes, C. V. 2000. Biological soil crusts and their interactions with vascular plants in a xeric Florida shrubland. PhD thesis. University of Pennsylvania, Philadelphia.
- Hawkes, C. V. & Menges, E. S. 1995. Density and seed production of a Florida endemic, *Polygonella basiramia*, in relation to time since fire and open sand. *Amer. Mid. Nat.* 133: 138-148.
- Hawkes, C. V. & Menges, E. S. 1996: The relationship between open space and fire for species in xeric Florida shrubland. *Bull. Torrey Bot. Club* 123: 81-92.
- Hendrych, R. & Hendrychová, H. 1989. Die Pedicularis-Arten der Tschechoslowakei, früher und jetzt. *Acta Univ. Carol.-Biol.* 32: 403-456.
- Herndon, A. 1999. Life history of *Liatris ohlingerae* (Asteraceae), an endangered plant endemic to the Lake Wales Ridge, Florida. Fla. Fish and Wildl. Conserv. Comm. Final Rep. Tallahassee.
- Hobbs, R. J. & Huenneke, L. F. 1992. Disturbance, diversity, and invasion: Implications for conservation. *Conserv. Biol.* 6: 324-37.
- Holeksa, J. & Cybulski, M. 2001. Canopy gaps in a Carpathian subalpine spruce forest. *Forstwissenschaftliches Centralblatt* 120: 331-348.
- Hunter, M. & Menges, E. S. In press. Allelopathic effects and root distribution of *Ceratiola ericoides* on seven rosemary scrub species. *Am. Jour. Bot.*
- Johansen, J. R. 1993. Cryptogamic crusts of semiarid and arid lands of North America. *Jour. Phycol.* 29: 140-147.
- Kalisz, P. J. & Stone, E. L. 1984. The longleaf pine islands of the Ocala National Forest, Florida: a soil study. *Ecology* 65: 1743-1754.

- Geisselbrecht-Taferner, L., Geisselbrecht, J. & Mucina, L. 1997. Fine-scale spatial population patterns and mobility of winter-annual herbs in a dry grassland. *J. Veg. Sci.* 8: 209-216.
- Goldberg, D. E. & Werner, P. A. 1983. The effects of size of opening in vegetation and litter cover on seedling recruitment of goldenrods (*Solidago* spp.) *Oecologia* 60: 149-155.
- Greenberg, C. H., Neary, D. G. & Harris, L. D. 1994. Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. *Conserv. Biol.* 8: 1047-1057.
- Gross, K. L. 1981. Predictions of fate from rosette size in four biennial species: *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota* and *Tragopogon dubius*. *Oecologia* 48: 209-213.
- Grubb, P. J. 1984. Some growth points in investigative ecology. In: Cooley, J. H. & Gooley, F. B. (eds.) *Research Opportunities in Ecology*, pp. 51-74. Plenum Press, New York.
- Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of regeneration niche. *Biol. Rev.* 52: 107-145.
- Gutterman, Y. 1993. *Seed germination in desert plants*. Springer-Verlag, Berlin.
- Hamzé, I. S., Jolls, C. L. 2000. Germination ecology of a federally threatened endemic thistle, *Cirsium pitcheri*, of the Great Lakes. *Amer. Midl. Natur.* 143: 141-153
- Hart, R. 1997. Why are biennials so few? *Am. Nat.* 111: 792-799.
- Hartl, D. 1975. Scrophulariaceae. In: Hegi, G. *Illustrierte Flora von Mitteleuropa VI* (1), pp. 1-469.
- Hartnett, D. C. & Richardson, D. R. 1989. Population biology of *Bonamia*

References

- Ehrenfeld, J. G., Zhu, W. & Parsons, W. F. J. 1995. Above- and below-ground characteristics of persistent forest openings in the New Jersey pinelands. *Bull. Torrey Bot. Club* 122: 298-305.
- Eisto, A. K., Kuitunen, M., Lammi, A., Saari, V., Suhonen, J., Syrjasuo, S. & Tikka, P. M. 2000. Population persistence and offspring fitness in the rare bellflower *Campanula cervicaria* in relation to population size and habitat quality. *Cons. Biol.* 14: 1413-1421.
- Eriksson, O. 1996. Population ecology and conservation – some theoretical considerations with examples from the Nordic flora. *Symxbolae Botanicae Upsaliensis* 31: 159-167.
- Fischer, N. H., Williamson, G. B., Weidenhamer, J. D. & Richardson, D. R. 1994. In search of allelopathy in the Florida scrub: The role of terpenoids. *Journal of Chemical Ecology* 20: 1355-1379.
- Fisher, M. & Matthies, D. 1998a. Experimental demography of the rare *Gentianella germanica*: seed bank formation and microsite effects on seedling establishment. *Ecography* 21: 269-278.
- Fisher, M. & Matthies, D. 1998b. Effects of population size on performance in the rare plant *Gentianella germanica*. *Jour. Ecol.* 86: 195-204.
- Forst, C. C. 1998. Presettlement fir frequency regimes of the United States: a first approximation. Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Fire Ecology Conference Proceedings, Tall Timbers 20: 70-81.
- Gagnon, D., Menges, E. S., Weekley, C. & Quintana-Ascencio, P. F. In prep. Soil moisture patterns in relation to vegetation, gaps, time since fire, and occurrence of Florida scrub endemic plants.
- Garcia, A. 1992. Conserving the species-rich meadows of Europe. *Agricultural Ecosystems and Environments* 40: 219-232.

References

- Collins, B. S. & Battaglia, L. L. 2002. Microenvironmental heterogeneity and *Quercus michauxii* regeneration in experimental gaps. *Forest Ecol. Manag.* 155: 279-290.
- Connell, J. H., Lowman, M. D. & Noble, I. R. 1997. Subcanopy gaps in temperate and tropical forests. *Austral. Jour. Ecol.* 22: 163-168.
- Coulson, S. J., Bullock, J. M., Stevenson, M. J. & Pywell, R. F. 2001. Colonization of grassland by sown species: dispersal versus microsite limitation in responses to management. *Jour. App. Ecol.* 38: 204-216.
- de Jong, T. J. & Klinkhamer, P. G. L. 1988a. Population ecology of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a coastal sand-dune area. *Jour. Ecol.* 76: 366-382.
- de Jong, T. J. & Klinkhamer, P. G. L. 1988b. Seedling establishment of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a sand-dune area: the importance of water for differential survival and growth. *Jour. Ecol.* 76: 383-402.
- de Jong, T. J., Klinkhamer, P. G. L. & Metz, J. A. J. 1987. Selection for biennial life histories in plants. *Vegetatio* 70: 149-156.
- Denslow, J. S. 1984. Disturbance-mediated coexistence of species. In: Pickett, S. T. A. & White, P. S. (eds.) *Natural disturbance: The patch dynamics perspective*. Academic Press, New York.
- Disraeli, D. J. 1984. The effect of sand deposits on the growth and morphology of *Ammophila breviligulata*. *Jour. Ecol.* 72: 145-154.
- During, H. J. & Van Tooren, B. F. 1990. Bryophyte interactions with other plants. *Bot. Jour. Linn. Soc.* 104: 79-98.
- Edwards, G. R. & Crawley, M. J. 1999. Effects of disturbance and rabbit grazing on seedling recruitment of six mesic grassland species. *Seed Sci. Res.* 9: 145-156.

References

- Bullock, J. M., Hill, B. C., Silvertown, J. & Sutton, M. 1995. Gap colonization as a source of grassland community change – effects of gap size and grazing on the rate and mode of colonization by different species. *Oikos* 72: 273-282.
- Campbell, S. E., Seeler, J. S. & Glolubic, S. 1989. Desert crust formation and soil stabilization. *Arid Soil Research and Rehabilitation* 3: 317-328.
- Cantor, L. F. & Whitham, T. G. 1989. Importance of belowground herbivory: pocket gophers may limit aspen to rock outcrop refugia. *Ecology* 70: 962-970.
- Carrington, M. E. 1996. Post-fire recruitment in Florida sand pine scrub in comparison with California chaparral. PhD thesis. University of Florida, Gainesville.
- Carter, L. J., Lewis, D., Crockett, L. & Vega, J. 1999. Soil Survey of Highlands County, Florida. US Dept. of Agriculture and Soil Conservation Service.
- Chen, H. & Maun, M. A. 1999. Effects of sand burial depth on seed germination and seedling emergence of *Cirsium pitcheri*. *Plant Ecol.* 140: 53-60.
- Cheplick, G. P. & Grandstaff, K. 1997. Effects of sand burial on purple sandgrass (*Triplasis purpurea*) – the significance of seed heteromorphism. *Plant Ecol.* 133: 79-89.
- Coates, K. D. 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. *Forest Ecology and Management* 155: 387-398.
- Coile, N. C. 2000. Notes on Florida's Endangered and Threatened Plants. Florida Department of Agriculture and Consumer Services, Division of Plant Industry. Gainesville, Florida.

References

- Abrahamson, W. G., Johnson, A. F., Layne, J. N. & Peroni, P. A. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. *Florida Scientist* 47: 209-250.
- Bach, C. E. 2001. Long-term effects of insect herbivory and sand accretion on plant succession on sand dunes. *Ecology* 82: 1410-1416.
- Bakker, J. P., Dekker, M. & de Vries, Y. 1980. The effect of different management practices on a grassland community and the resulting fate of seedlings. *Acta Bot. Neerl.* 29: 469-482.
- Bazzaz, F. A. 1983. Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. In: Mooney, H. A. & Godron, M. Disturbances and ecosystems. Components of response, pp: 259-275. Springer-Verlag. New York, USA.
- Berg, R. Y. 1954. Development and dispersal of the seeds of *Pedicularis sylvatica*. *Nytt. Mag. Bot.* 2: 1-60.
- Bertin, R. I. 2001. Life cycle, demography and reproductive biology of herb Robert (*Geranium robertianum*). *Rhodora* 103: 96-116.
- Bowles, M. L., DeMauro, M. M., Pavlovic, N. B. & Hiebert, R. D. 1990. Effects of anthropogenic disturbances on endangered and threatened plants at the Indiana Dunes National Lakeshore. *Nat. Areas J.* 10: 187-200.
- Breining, D. R. & Schmalzer, P. A. 1990. Effects of fire and disturbance on plants and birds in a Florida oak/palmetto scrub community. *Amer. Midl. Nat.* 123: 64-74.
- Brown, J. F. 1997. Effects of experimental burial on survival, growth, and resource allocation of three species of dune plants. *Jour. Ecol.* 85: 151-158.

Concluding Remarks

might help to find clearer patterns. The same is true about Chapter 2, where significant results did not appear in the short time period of the experiment. In Chapter 4, stochasticity and high heterogeneity of the mobile sand dynamics require longer-term monitoring and larger sample size. Also data analyses can be extended, which I plan to do in future manuscript drafts. Species selection for Chapter 4 largely depended on germination rates, however extension to other species of the Florida scrub would be a useful contribution to a long-term demographical monitoring of these species.

Despite the limitations, the case studies in this thesis provide some insights and may contribute to generate common pattern in disturbance effects on plant populations, which, I believe, is an interesting and important topic in plant ecology.

Concluding Remarks

Results of these presented studies show positive responses of seedling recruitment and some demographical parameters to microsite conditions created by disturbances, and this pattern has been demonstrated by others elsewhere. However, my studies also bring some novel insights.

For the strict biennial *Pedicularis sylvatica*, not much has been known about the demography and population dynamics attributed to the life history. Similarly, complete gaps and the effects of mobile sand have not been well explored in the Florida scrub and seemingly has some significance for Florida scrub herbs.

Each study suggested several questions and future research ideas. These include, for example, density-dependent survival of *Pedicularis* seedling and consequences for the strictly biennial population dynamics (currently a BSc. project). Oscillating population trajectories in *Pedicularis sylvatica* (Chapter 2) need further monitoring to confirm this interesting ecological phenomenon. The effects of artificial gaps in the Florida scrub (including roadside microsites) on plant populations needs to be explored for more species, for longer time, and within an explicit management context.

Despite significant effort, the studies could not avoid some limitations. Variation in environmental conditions and time constraints typical of ecological field studies affected some of the results. The Florida scrub is a xeric ecosystem, with occasional periods of droughts. One of the experiments (Chapter 3) was affected by two consecutive drought years, and this environmental factor limited the conclusions that can be drawn from the experiment. Another study (Chapter 1) shows highly variable results. Greater number of observation units and longer monitoring time

gapů pro úspěšné vzcházení semenáčků bylinných druhů v různých ekosystémech a přinášejí důležité poznatky pro ochranu druhů a management jejich stanovišť. V křovinném ekosystému Floridy, antropogenní gapy mohou krátkodobě nahradit požárový režim v maloplošných ochranných projektech (třetí kapitola - Chapter 3). Ve vlhkých loukách v České republice, kombinace kosení a režimu pastvy může podpořit úspěšné uchycení semenáčků *Pedicularis sylvatica* (první kapitola - Chapter 1).

Vliv experimentálních disturbančních režimů na demografii, populační strukturu a dynamiku *Pedicularis sylvatica* nebyl výrazný. Populační dynamika výrazně oscilovala mezi lety a pravděpodobně byla kontrolována spíše vnitropopulačními mechanismy než disturbačními procesy. Nicméně, dlouhodobé opuštění managementu na vlhkých loukách může negativně ovlivnit populace tohoto druhu (druhá kapitola - Chapter 2).

Demografii bylinných druhů v křovinném ekosystému Floridy mohou ovlivnit mikrostanovištní podmínky a pohyblivý písečný substrát. Čtvrtá kapitola (Chapter 4) dokumentuje vliv písečných přesypů na klíčení, přežívání semenáčků a růst bylinných druhů v gapech a podél cest v tomto ekosystému. Okraje cest vykazovaly variabilnější mikrostanoviště, které mohou ovlivňovat variabilitu demografických parametrů rostlinných populací podél cest.

Mnohé ze studovaných druhů jsou druhy ohrožené nebo endemické, tudíž objasnění vlivu disturbancí na jejich mikrostanoviště a demografii je kritické pro ochranu druhů a management jejich stanovišť.

Tato diplomová práce spojuje několik příkladů experimentálních studií v kontextu disturbancí ovlivněné populační ekologie rostlinných druhů.

Microsites created by mobile sand in Florida scrub can influence the demography of scrub plants. Chapter 4 documents that dynamic sand microsites affect germination, seedling survival and growth of herbaceous species in the scrub gaps and along sand roads. Roadsides in this study had more dynamic pattern of sand movements, and this mobile sand can therefore alter the demography of roadside populations.

Many of the studied plants are endangered or endemic species and understanding how disturbances affect their microsites and demography is critical for species conservation and management of their habitats.

This thesis links several experimental research projects within the context of disturbance-mediated plant population ecology.

Souhrn

Studie prezentované v této diplomové práci dokumentují význam disturbancí pro vznik mikrostanovišť a pro demografii rostlinných druhů v xerickém křovinném ekosystému Floridy (Florida scrub) a v ekosystému vlhkých luk v České republice.

Experimentální disturbance, simulující režimy obhospodařování, poskytovaly vhodné mikrostanovištní podmínky pro regeneraci rostlinných druhů. Tato mikrostanoviště zahrnovala umělé nadzemní a podzemní gapy v křovinné vegetaci Floridy (třetí kapitola - Chapter 3), které zvýšily počet vzešlých semenáčků některých bylenných druhů podrostu. V českých vlhkých loukách, maloplošné gapy obnažené půdy simulovaly sešlapávání porostu při pastvě, a tento experimentální zásah spolu s experimentálním kosením poskytovaly příznivá mikrostanoviště pro vzcházení semenáčků ohroženého druhu vlhkých luk, *Pedicularis sylvatica* (první kapitola - Chapter 1). Tyto výsledky podtrhují důležitost

Summary

These presented studies document the significance of disturbance events for microsites and demography of plants in xeric Florida shrublands and wet grasslands in the Czech Republic.

Experimental disturbances (mimicking management regimes) often provided favorable microsites for plants. Those included artificial complete gaps in the shrub matrix of Florida scrub (Chapter 3), which had elevated seedling numbers of gap specialized scrub herbs. In the Czech wet meadows, small-sized gaps simulated trampling during grazing, and this treatment together with experimental mowing provided microsites for seedling recruitment of an endangered species *Pedicularis sylvatica* (Chapter 1). These results demonstrate the importance of gaps for successful seedling recruitment of herbaceous understory plants, and have some implications for species conservation and habitat management. In Florida scrub, artificial gaps may provide a short-term substitute for prescribed burning in small-scale conservation projects (Chapter 3). In wet meadows, the combination of mowing and grazing regimes may allow successful establishment of *Pedicularis sylvatica* seedlings (Chapter 1).

Effects of experimental disturbances on the demography of *Pedicularis sylvatica*, population structure and dynamics were not strong, and highly oscillating population dynamics seems to be driven endogenously rather than by disturbance events. However, long-term management abandonment in wet meadows will likely negatively affect populations of this species (Chapter 2). Therefore traditional mowing and grazing regimes are recommended.

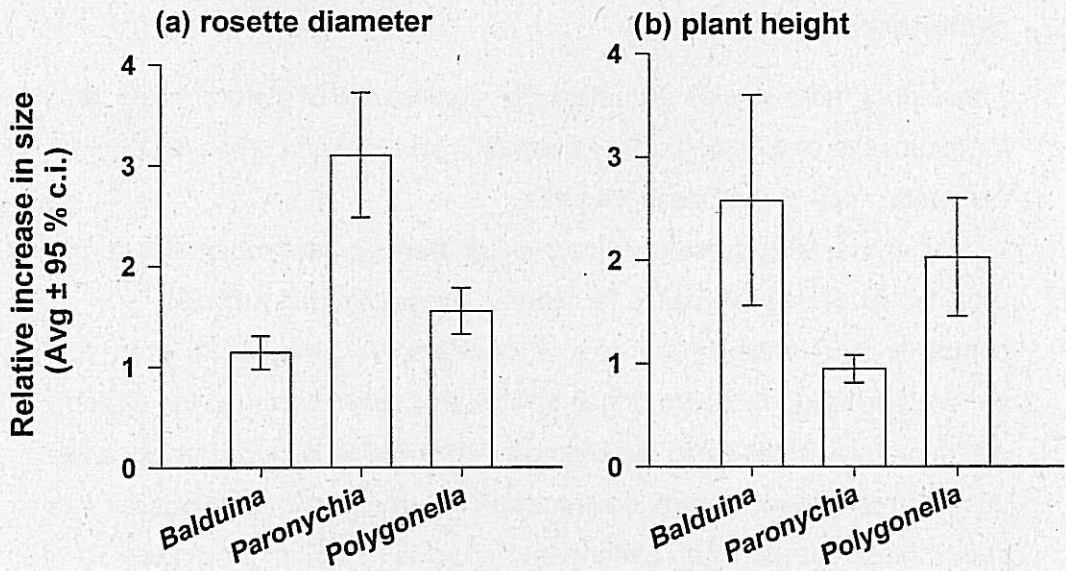


Figure 6. Relative increase in (a) rosette diameter and (b) plant height against initial measurements (averages with 95% confidence intervals) for *Balduina*, *Paronychia* and *Polygonella* in field sand addition and removal experiment. Different letters above error bars within graphs indicate significant differences among species.

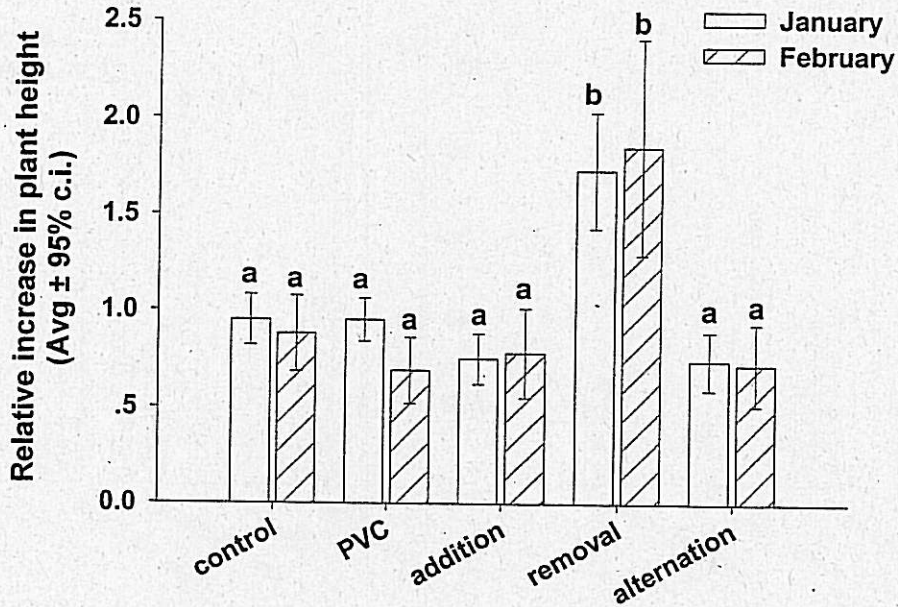


Figure 5. Relative increase in plant height against initial measurements (averages with 95% confidence intervals) in field sand addition and removal experiment plotted in January and February 2001, and five treatments (non-manipulated control (= control), plots protected from spontaneous sand movement with PVC collars (= PVC), sand addition (= addition), sand removal (= removal) and treatment alternating sand addition and removal (= alternation). Different letters above error bars within plots for each month indicate significant differences among treatments.

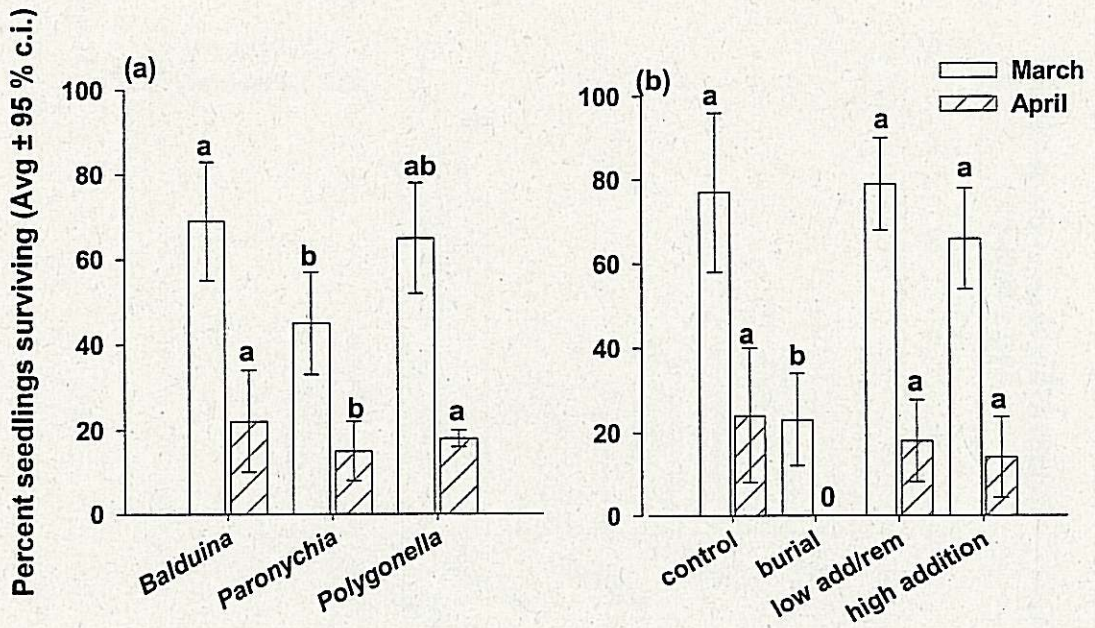


Figure 4. Average proportion of seedlings (with 95% confidence intervals) surviving in sand addition and removal experiment in March and April 2001 for (a) three species and (b) experimental treatments (control, complete burial (= burial), low alternating sand addition and removal (= low add/rem), and high sand addition (= high addition). Different letters above error bars within plots for each month indicate significant differences.

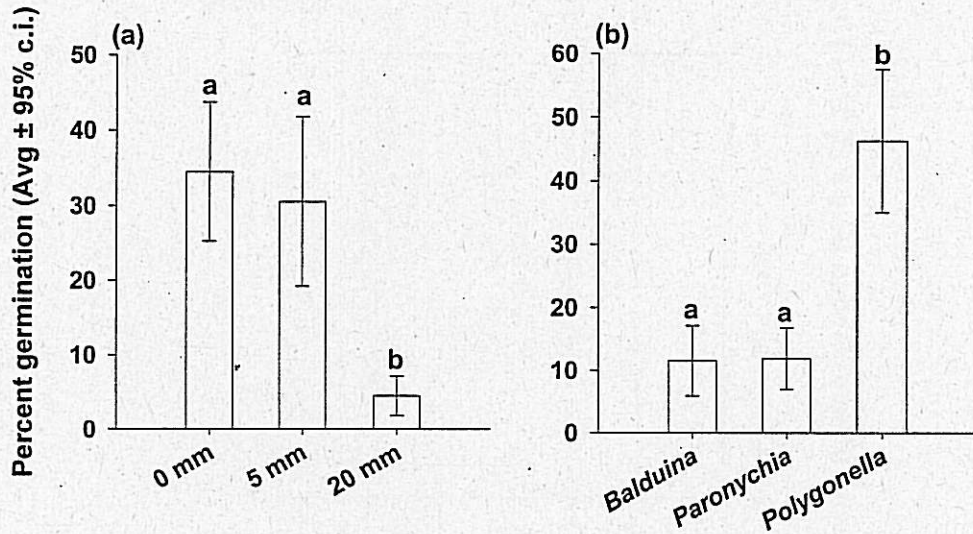


Figure 3. Percent germination from (a) burial levels 0, 5 and 20 mm for (b) three species: *Balduina*, *Paronychia* and *Polygonella*. Means with 95% confidence intervals. Different letters above error bars indicate significant differences in germination within graphs.

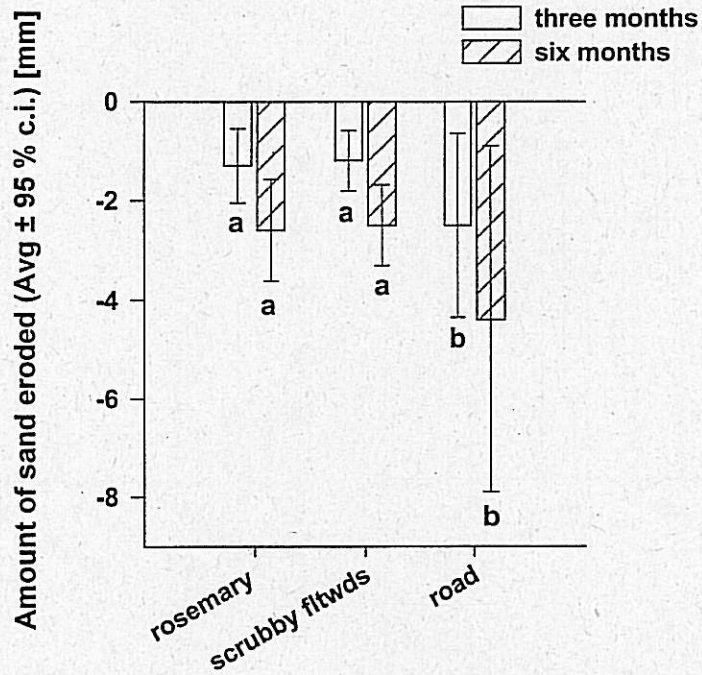


Figure 2. Sand erosion in gaps in rosemary scrub (= rosemary), gaps in scrubby flatwoods (= scrubby fitwds), and in along roadsides (= road), in the three- and six-months intervals. Averages from observations in each time interval with 95 % confidence intervals. Different letters above error bars within each time interval plot indicate significant differences between gaps and the road points.

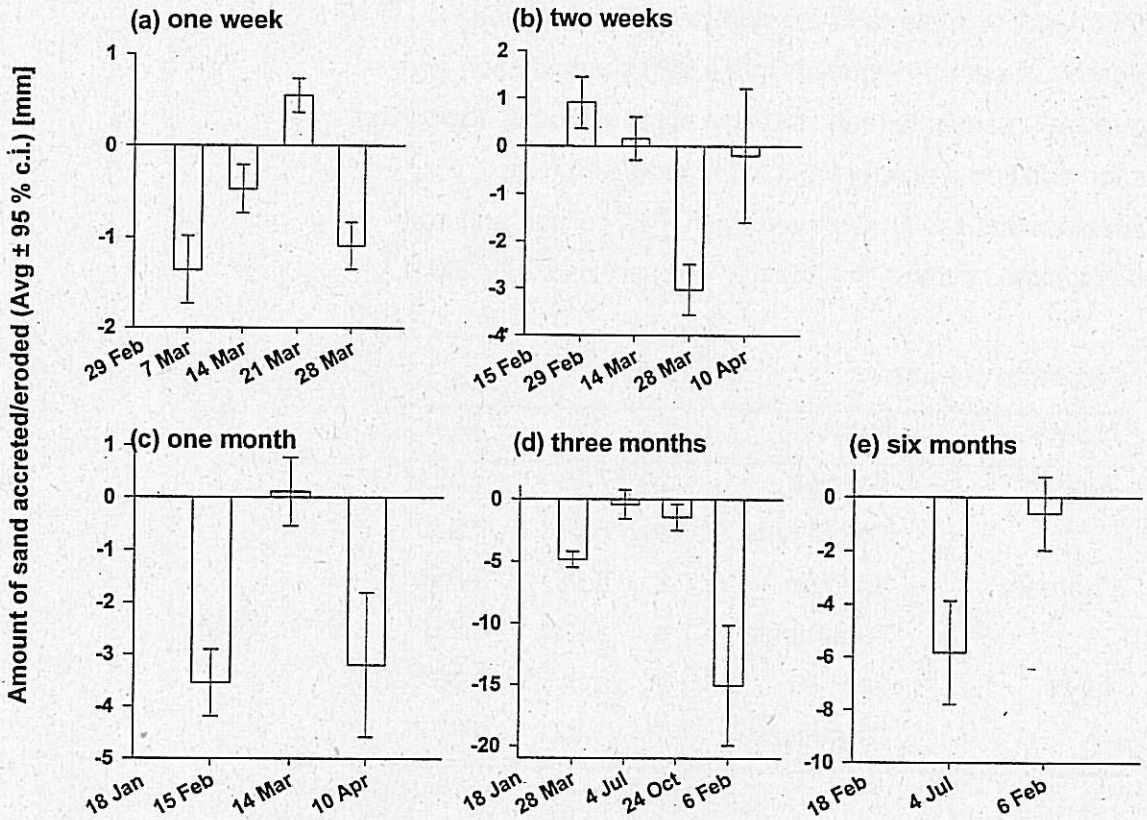


Figure 1. Sand accretion and erosion at Archbold Biological Station over time intervals of (a) one week, (b) two weeks, (c) one month, (d) three months, (e) six months, averaged across all gaps in rosemary scrub patches 28, 46 and 91, and gaps in adjacent scrubby flatwoods and road points. Error bars are 95 % confidence intervals. Note different scales on y-axes.

Table 4. Results of Kruskal-Wallis tests for size increase of (a) rosette diameter and (b) plant height of *Balduina*, *Paronychia* and *Polygonella* in the field sand addition and removal treatments (sand addition, sand removal, alternating sand addition and removal, control protected from spontaneous sand movements with PVC collars, and non-manipulated control) in January, February and July 2001.

(a) rosette diameter

Month	Factor	df	H	p
January	Species	2	27.83	<0.001
	Treatments	4	5.49	0.240
February	Species	2	6.95	0.031
	Treatments	4	1.98	0.738
July	Species	2	28.86	<0.001
	Treatments	4	1.83	0.767

(b) plant height

Month	Factor	df	H	p
January	Species	2	0.17	0.919
	Treatments	4	31.30	<0.001
February	Species	2	9.14	0.010
	Treatments	4	18.39	<0.001
July	Species	2	26.86	<0.001
	Treatments	4	2.64	0.621

Table 3. Oscillations in sand erosion (minimum - negative values) and accretion (maximum - positive values) and median values from observations for each time interval (one and two weeks, one, three and six months).

Time interval	Min-max oscillations [mm]	Median oscillations [mm]
One week	-17.3 to 12.3	-10
Two weeks	-29.2 to 19.0	0
One month	-33.2 to 13.0	-20
Three months	-48.3 to 18.0	-10
Six months	-54.1 to 22.0	-23

Table 2. Results of repeated measures ANOVA for sand movement in time intervals of one and two weeks, one, three and six months as a function of site (vicinity of rosemary patches 28, 46 and 91) in Archbold, and position (gap in rosemary scrub, gap in scrubby flatwoods and road point). MS Error terms for between and within subjects are reported for each time interval under the respective column headings separated by semi-column.

Source	One week (0.04; 0.06)			Two weeks (0.09; 0.17)			One month (0.10; 0.49)			Three months (0.10; 0.26)			Six months (0.20; 0.73)		
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Site	2	1.31	0.276	2	1.67	0.196	2	4.79	0.011	2	0.87	0.442	2	1.11	0.336
Position	2	0.22	0.807	2	2.03	0.139	2	1.38	0.259	2	4.30	0.017	2	3.61	0.032
Site*Position	4	1.66	0.168	4	1.45	0.228	4	1.11	0.359	4	1.67	0.160	4	2.67	0.038
Error	78			71			68			73			81		
Within Subjects															
Time	3	32.80	<0.001	3	10.09	<0.001	2	11.34	<0.001	3	19.99	<0.001	1	16.76	<0.001
Time*Site	6	1.64	0.137	6	1.15	0.333	4	1.36	0.252	6	9.73	0.004	2	8.75	<0.001
Time*Position	6	1.55	0.162	6	0.98	0.442	4	1.56	0.189	6	1.66	0.675	2	0.99	0.375
Time*Site*Position	12	1.32	0.207	12	1.45	0.145	8	1.07	0.390	12	6.47	<0.001	4	7.88	<0.001
Error (Time)	234			213			136			219			81		

Table 1. Summary of sand movement measurements in 5 time intervals: one and two weeks; and one, three, and six months. N = number of measurement intervals used for analyses (differences between two consecutive measurements).

Time interval	N	Measurement dates
One week	4	(29 Feb-7 Mar); (7 Mar-14 Mar); (14 Mar-21 Mar); (21 Mar-28 Mar)
Two weeks	4	(15 Feb-29 Feb); (29 Feb-14 Mar); (14 Mar-28 Mar); (28 Mar-10 Apr)
One month	3	(18 Jan-15 Feb); (15 Feb-14 Mar); (14 Mar-10 Apr)
Three months	4	(18 Jan-28 Mar); (28 Mar-4 Jul); (4 Jul-24 Oct); (24 Oct-6 Feb)
Six months	2	(18 Jan 2000-4 Jul 2000); (4 Jul 2000-6 Feb 2001)

sand removal) indicate that mobile sands can significantly affect post-dispersal seed distribution and germination, seedling survival and growth parameters of Florida scrub plants. Because sand movements are variable over time and space, and differ between scrub and roadside microhabitats, they may be important in demographic variation of Florida scrub plants.

populations under identical conditions in the growth chamber (Quintana-Ascencio, unpubl.). Roadside habitats seem to create more cases of sand removal, and thus more variable microsite conditions. This environmental variability may increase variability in population parameters. Roadside populations of *Hypericum cumulicola* have more variable plant densities than scrub populations (Quintana-Ascencio & Weekley 2001). In my experiment, sand erosion increased elongation of flowering stems of plants along roads. Since sand movements may affect other demographical parameters in these roadside populations, demographic responses of Florida scrub herbs to sand movements need further investigation.

Sand burial and erosion affected the three studied species differentially. Seed burial to greater depths reduced germination of all species. *Polygonella basiramia* germinated at the highest rates, consistent with high germination rates in several field and experimental germination studies (Hawkes 2000; Quintana-Ascencio & Menges 2000; Maliakal, unpubl.; Chapter 3). Seedling survival of all species was low with complete burial, especially so for *Paronychia chartacea*. In the field experiment, increase of rosette diameter did not differ among sand addition and removal treatments but differed significantly among the three species. Rosette diameter increased the most in *Paronychia chartacea*, which is prostrate and produces flowers on rosette branches. *Paronychia* responded to experimental treatments with lateral increases in rosette diameter, but plants did not change in height. On the other hand, *Balduina* and *Polygonella* responded to experimental sand removal by elongation of flowering stems.

The species responses (elevated germination from lower burial levels, high mortality of seedlings with complete burial, and plant growth stimulated by

transpiration. However, seedling survival decreased in my experiment when seedlings were completely buried. Also Maun (1994), Cheplick & Grandstaff (1997) and Langlois et al. (2001) show that seedlings of many dune species cannot survive complete burial. The field observations in this study found constant sand depositions rare. Sand accretion usually alternated with sand erosion, and this experimental treatment did not affect seedling survival. Florida scrub species may be adapted to such fluctuating sand movements.

Many plants show positive growth and reproduction responses to sand accretion (Disraeli 1984; Maun & Lapierre 1984; Zhang & Maun 1992; Maun 1994; Menges & Kimmich 1996; Brown 1997; Cheplick & Grandstaff 1997; Langlois et al. 2001). However, in my field experiment, only sand removal enhanced lengths of flowering stems. This may have been a stress-mediated response leading to earlier reproduction. Elongation of flowering stem responded significantly to experimental treatments only in January and February. In July, treatment effects on growth did not differ significantly among treatments. This may have been a consequence of high rosette mortality, reducing sample sizes.

Gaps are favorable microsites for many Florida scrub herbs (Menges & Hawkes 1998). The extent of sand movements was significantly lower in gaps than at roads, since the gap area and sand-stabilizing shrubs at the gap boundary may have limited sand movement events. Sand roads showed variable and more dynamic patterns of sand movements. Field observations found sand erosion greater than deposition. This sand erosion may uncover seeds from greater depths and allow germination in the surface sand layers, as I confirmed in the pot burial experiment. In a different experiment, roadside populations of the Florida scrub plant *Hypericum cumulicola* had higher germination rates than some gap

surface and be alternately buried and uncovered. In shorter time intervals (one and two weeks) sand deposition and erosion can affect seed distribution and subsequently germination rates. Over short-time intervals, the amount of sand accreted and eroded in the field could affect seedlings as they germinate over several weeks or months. The burial experiment shows that seed germination of scrub herbs significantly decreased with burial under more than 0.5 centimeters of sand.

The magnitude of burial effects on seeds and seedlings varies depending on the dune system. Many studies document negative effects of seed burial on germination (e.g. Maun & Lapierre 1984; Cheplick & Grandstaff 1997; Chen & Maun 1999; Hamzé & Jolls 2000; Quilichini & Debussche 2000). However, some plants in coastal sand dunes, such as *Ammophila breviligulata*, from coastal dunes in northeastern United States (Disraeli 1984), or *Cirsium pitcheri* on Great Lakes shores (Chen & Maun 1999; Hamzé & Jolls 2000), are largely adapted to burial in several centimeters of sand, and show positive survival and growth responses to burial up to a threshold depth. Increasing burial levels beyond this threshold reduced germination and increased mortality (Maun 1998). For germination in the studied Florida scrub plants, this threshold (if it exists) must be very small, since germination was suppressed by more than 0.5 cm of sand burial

To survive sand burial, plants must to grow upward through sand while surviving a period of darkness (Sykes & Wilson 1990). In the Florida scrub, light can penetrate thin surface sand layers. Seedlings of two scrub herbs, *Eryngium cuneifolium* and *Hypericum cumulicola* can remain green while covered by thin layer of sand for several months (pers. obs.). The translucent sand allows photosynthesis and may facilitate seedling survival by protecting seedlings against overheating and rapid

Effects of sand addition and removal on rosette growth

Sand addition and removal treatments did not differ in their effects on changes in rosette diameter (Table 4) but differed significantly in their effects on changes in plant heights in January and February 2001 (Table 4). Stem elongation was greatest in the sand removal treatment (Figure 5). Rosette diameter and growth of flowering stems differed significantly among species (Table 4). Rosette diameter increased most in *Paronychia* (Figure 6a) whereas heights of flowering stems increased more in *Balduina* and *Polygonella* (Figure 6b). The relative increase in rosette diameter and heights of flowering stems in response to experimental treatments did not differ between January and February but both were significantly greater in July (for increase in diameter Kruskal-Wallis: $H = 24.5$, $df = 2$, $p < 0.001$, for increase in height Kruskal-Wallis: $H = 42.6$, $df = 2$, $p < 0.001$, Figure 5). Rosette mortality across treatments was high and ranged from 43% to 63% at the end of the experiment.

Discussion

This study is the first to quantify the extent and variation in sand movements for several time intervals in Florida scrub. It also documents the significance of these mobile sands for Florida scrub herb demography. Oscillations in sand accretion and erosion reached several centimeters, and increased with longer time intervals, while erosion exceeded accretion. Given the variability and stochasticity of the dynamic wind-sand system in Florida scrub, longer-term observations would be useful.

The studied species and many other rare scrub herbs have very small seeds easily dispersed by wind. These seeds may also roll on the sand

Sand erosion was significantly greater and more variable along roads than in natural gaps (Figure 2, note large confidence intervals). Also the interaction of site and site*position (gaps or road)*time were significant (Table 2).

Effects of seed burial on germination and survival

Significantly more seedlings germinated from 0 and 5 mm sand depths compared to 20 mm (Kruskal-Wallis: $H = 34.0$, $df = 2$, $p < 0.001$, Figure 3a). Seedlings of *Polygonella* were the most frequent and their proportions were significantly greater than proportions of the other species (Kruskal-Wallis: $H = 27.4$, $df = 2$, $p < 0.001$, Figure 3b). Seedling survival did not differ among burial levels (Kruskal-Wallis: $H = 5.7$, $df = 2$, $p = 0.059$), and did not differ significantly among species (Kruskal-Wallis: $H = 0.2$, $df = 2$, $p = 0.159$). The speed of germination (number of days from the beginning of experiment until the first seedling appeared; 13.8 ± 1.28 s.e. days) did not significantly differ among burial levels (Kruskal-Wallis: $H = 4.9$, $df = 2$, $p = 0.084$) nor among species (Kruskal-Wallis: $H = 2.9$, $df = 2$, $p = 0.237$).

Effects of sand addition and removal on seedling survival

Seedling survival differed significantly among species in the sand removal/addition experiment (in March Kruskal-Wallis: $H = 7.9$, $df = 2$, $p = 0.019$, in April $H = 11.4$, $df = 2$, $p = 0.003$). *Paronychia* had the lowest survival (Figure 4a) Survival also differed among treatments (in March Kruskal-Wallis: $H = 33.7$, $df = 3$, $p = 0.002$, in April $H = 14.65$, $df = 3$, $p = 0.002$), with the overall lowest survival for the burial treatment (Figure 4a,b). Survival was relatively high in March, but significantly declined from March to April (Mann-Whitney: $Z = -7.1$, $p < 0.001$, Figure 4).

measurements of the longest horizontal axis of each rosette (rosette diameter) and plant height (including flowering stems in *Balduina* and *Polygonella*), and I further measured plants at the end of January, February and June 2001. I calculated the relative growth increase by January, February and June 2001 as ratios of the rosette diameter and plant heights in these months, against the initial measurements in December 2000.

Experimental data did not usually meet assumptions for parametric tests even after various transformations. Therefore, I used non-parametric Kruskal-Wallis tests comparing differences among species and treatment levels. Non-parametric Mann-Whitney U tests compared pair-wise significant differences with Bonferoni adjusted significance levels (Sokal & Rohlf 2000). For species pair-wise comparisons in all experiments, the significance level was 0.017. Treatments in the burial experiment were compared pair-wise on significance level 0.017. In seedling survival experiment the significance level was 0.008, and in the field experiment it was 0.005. Mann-Whitney U test and Kruskal-Wallis tests compared temporal differences among and between measurements.

Results

Sand movement

Sand accretion and erosion fluctuated widely across all time intervals (significant effects of time, Table 2, Figure 1). Over shorter time intervals, episodes of erosion and accretion were evident, with much variation among points (Figure 1). At longer time intervals, sand erosion was greater than accretion (Figure 1). With increasing time intervals, the range of sand oscillations increased (Table 3) and differed significantly among gaps in rosemary scrub and scrubby flatwoods, and road points (Table 2).

added to and removed from the pot area with a tablespoon was equivalent to 2 mm of sand regularly spread over the pot area), (c) high sand addition treatment (adding three tablespoons of sand to pots every two weeks, an amount equivalent to 6 mm of sand per pot area), and (d) control. The experimental design (4 treatments \times 3 species) had 10 replicates resulting in a total of 120 pots. I scored seedling survival at the beginning of March and April 2001.

I placed pots of both pot experiments outdoors in indirect light beneath an overhanging roof, and watered them to saturation. I randomized the initial pot position, and switched the position of the pot groups four times during the course of the experiments.

Field sand addition/removal experiment on rosettes

In a field experiment, I tested effects of sand addition and removal on rosette growth in extant roadside plants of each of the three focal species. I randomly selected 10 rosettes for each of the following treatments: (a) sand addition, (b) sand removal, (c) alternating sand addition and removal, (d) controls protected from spontaneous sand movements, and (e) non-manipulated controls. In (a) – (d) treatments, I surrounded each rosette with a PVC collar 15 cm in diameter and 5 cm tall, stabilized by burial to about half its height. In (a) sand addition treatment, I regularly spread 1 tablespoon of sand around the rosette. In (b) sand removal treatment I removed the same amount of sand from the rosette vicinity. I repeated treatments each month from December 2000 to March 2001. For (c), I alternated sand removal and addition monthly. The experimental design (5 treatments \times 3 species) had 10 replicates resulting in a total of 150 rosettes. At the end of December 2000, I took initial pre-treatment

within-subject factor 'time' and between-subject factors 'site' for differences between scrub patches, and 'position' for differences between gaps and road points. Some measurements on flags were lost to occasional animal disturbance creating an unbalanced design.

Seed burial experiment

I tested the effects of seed burial in sand on seedling germination and survival, in an experiment on potted seeds. For each species, I planted 20 seeds in three burial depths: 0, 5 and 20 mm into individual pots (8 by 8 cm by 9 cm deep). Seeds of all species were collected locally as they matured shortly before the experimental set up. The experimental design (3 depths × 3 species) had 10 replicates resulting in a total of 90 pots. I evaluated seedling recruitment every three days from the end of December 2000 until the beginning of February 2001, when no additional seedlings germinated and seedling mortality exceeded germination. At the end of February 2001, I evaluated seedling survival.

Sand addition/removal experiment on potted seedlings

To test effects of sand addition and removal of different frequency and intensity on seedling survival in the same three species, I conducted an experiment on potted seedlings. At the end of December, I planted 50 seeds into individual pots of the same size as in burial experiment and let seedlings germinate until the beginning of February. In pots with high seedling densities, I thinned to 5 seedlings per pot, resulting in seedling counts 0-5 per pots depending on initial recruitment. I applied four treatments: (a) frequent sand addition, keeping seedlings completely buried by continuous sand addition to seedlings as they grew, (b) weekly alternating sand addition and removal (the amount of dry sand regularly

Mitigation 40) and along the western side of a road adjacent to rosemary patch 46.

Study species

I studied sand movement effects of three herbaceous species of the Florida scrub with diverse life history traits (a Federally endangered perennial herb *Polygonella basiramia* (Polygonaceae), a Threatened annual *Paronychia chartacea* ssp. *chartacea* (Caryophyllaceae) (Coile 2000), and a widespread biennial *Balduina angustifolia* (Asteraceae). For simplicity I refer to each species by its generic name. The species are gap specialists, *Paronychia* and *Polygonella* are central Florida Ridges endemics, and *Balduina* is a widespread gap specialist.

Sand movement monitoring

I monitored sand movement at points in the center of 10 natural gaps (median diameter of 5 m), randomly selected along two perpendicular belt transects 50 m long, 4 m wide in three rosemary scrub patches and in adjacent scrubby flatwoods. Along sand roads adjacent to study scrub patches, I randomly selected 10 points along a 50 m transect. At all points, I placed an aluminum flag with a metal tag and set the flag height to 15 cm height. I placed flags on 15 January 2000 and measured the distance from the sand surface to the flag top to the nearest mm at intervals of one and two weeks; and one, three, and six months (Table 1). I calculated amount of accreted and eroded sand as an absolute difference between two nearest measurements (positive value for sand accretion and negative value for erosion).

I analyzed temporal variation in sand movement for each time interval in a repeated measures ANOVA model in SPSS version 10:0 Inc., with

requirements and effects of mobile sands may be important for effective species management and conservation.

In this study, I analyze temporal variation of sand accretion and erosion in natural gaps within the matrix of the Florida scrub and along sand roads. I also explore the effects of sand movements on seedling ecology of two endemic and one common herbaceous Florida scrub species. I experimentally test germination and survival of seedlings from seeds buried to 0, 5 and 20 mm depths, and seedling survival and growth of rosettes in experimental sand addition and removal treatments.

Methods

Study site

I conducted the studies at Archbold Biological Station (ABS), at the southern end of Florida's Lake Wales Ridge (27° 11' N, 81° 21' W, Highlands Co., 13 km south of Lake Placid), comprising approximately 2000 ha of Florida scrub and other native plant communities. The climate, history, vegetation, and soils were described by Abrahamson et al. (1984). I monitored sand movement in natural gaps in three patches of rosemary scrub in the northern, central and southern part of ABS (rosemary patches 28, 46 and 91), in adjacent scrubby flatwoods, and along adjacent sand roads. At the time of this study, these parts of Archbold had not been burned for about 6, 8 and 14 years, since 1994, 1992 and 1986 respectively.

I located a field experiment exploring effects of sand addition and removal treatments on rosette growth of herbaceous species in roadside populations along wide sand roads, in northern part of Archbold, adjacent to rosemary patch 1, in the northwestern part of Archbold (section