

DOES HABITAT AFFECT CLONAL DEMOGRAPHY? AN EXPERIMENT WITH
POLYGONELLA MYRIOPHYLLA IN ROADSIDE AND FLORIDA SCRUB

by

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ABSTRACT

Polygonella myriophylla (Polygonaceae) is a clonal shrub listed as endangered and narrowly endemic to pyrogenic scrub ecosystems in central Florida. It is almost restricted to gaps within the matrix of shrubs in the scrub but also occurs along adjacent road-side habitats. I hypothesize that persistent disturbed microhabitats and more dynamic sand accretion in roadsides will increase rooting probabilities compared to more stable scrub habitats, affecting survival, growth and reproduction. In April 2004- March 2006, I compared plant (genet) and basal branch (ramet) performance between experimentally manipulated plants in native scrub and roadside habitats at two locations within the Lake Wales Ridge State Forest in Polk County: LC01 and Old School. We completed a total of 6 evaluations in each site (April, July and November 2004, May and November 2005, and March 2006). Fifteen plants per replicated habitat in LCO1 and Old School were selected based on presence of four unrooted branches. Each unrooted branch within a plant randomly received one of four possible treatments: forced branch burial, branch lifting, procedural control, and no manipulation (total N= 60 genets and 240 ramets). Forced burial was implemented to mimic sand burial and evaluate rooting probability and performance in both habitats. Branch lifting was applied to prevent sand burial and evaluate demography of unrooted branches in both habitats. The procedural control served to evaluate wire effects on ramet demography. The control provided vital and rooting rates of branches in natural conditions. Road populations exhibited larger crown area and higher monthly diameter (controlled by initial diameter) and higher monthly length growth rates compared to scrub populations. Rooting probability was

only affected by treatment one (buried wire) not habitat or site. Forced sand burial increased rooting (67 % after forced contact vs. 20-30 % for other treatments). Rooted branches did not exhibit variation in survival, growth, or fecundity compared to unrooted branches. Old School populations exhibited larger crown area, higher monthly diameter and monthly length growth rates compared to LC01 populations. Prescribed fires killed several plants explaining significantly higher branch survival at the unburned LC01 (66.1%) compared to recently burned Old School (36.2 %). LC01 populations exhibited higher fecundity and ramet survival compared to Old School populations. In February – December 2006, I describe the reproductive schedule at (LC01) in 10 road and 10 scrub plants. Monthly, I counted number of inflorescences and flowers per inflorescence (one inflorescence per plant) for each plant. Number of inflorescences per plant was highest between May and September and higher in road than in scrub. Our results indicate significant different demographic performance of *P. myriophylla* at plant and branch level between road and scrub habitats. A longer term study is needed to determine if the persistence of *P. myriophylla* is threatened by increasing roadside populations.

I would like to dedicate my thesis in memory of my friend and colleague, Boyd Lyon.

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CHAPTER ONE: INTRODUCTION

Clonal plants consist of a genet (product of single zygote) and potentially many initially connected vegetatively produced ramets. The fitness of clonal plants may be augmented through many pathways including continuous ramet production (De Steven 1989, Oborny and Kun 2002, Orive 1995), the ability to invade neighboring territories seeking more favorable resources (Peltzer 2002) by increasing number and distance among ramets (Jacqemyn et al 2006, Roiloa and Retuerto 2006), and the capacity to share acquired resources via connected ramets. A division of labor within ramets may develop, permitting specializations in storage, nutrient uptake, and sexual reproduction (Fischer and Kleunen 2002). Internal signaling between ramets may aid in plant defense against disease and herbivory (Fischer and Kleunen 2002). Alternatively, there are potential costs associated with vegetative reproduction. Ramets dispersed over a large area may experience individual environmental stresses such as resource allocation, disturbances, toxins, and pathogens (Price and Marshall 1999). Clonal growth may also incur metabolic costs including maintenance of the connections and energy required for resource allocation (Fischer and Kleunen 2002). Clonal and sexual reproduction incur direct costs (Bazzaz et al. 1987) and there is evidence of trade-offs at the individual level (Piquot et al 1998) in both resource rich and resource poor environments (Thompson and Eckert 2004).

Clonal species may diverge in their degree of ramet autonomy (Oborny and Kun 2002, Price and Marshall 1999). The life span of the connected spacers may be short-

lived or persist for many years (Bazzaz et al 1987) depending on the species (Piqueras and Klimes 1998). In some species, connected spacers are removed by either ramet death or decay via abscission tissues, leaving the ramet completely isolated (Oborny and Kun 2002) and capable of vegetative and sexual reproduction (Orive 1995). Clonally integrated ramets have the potential to become physiologically autonomous, developing individual root and reproductive systems and experiencing individual stresses and mortality rates (Oborny and Kun 2002).

It is common for perennial plants to reproduce both clonally through ramet production and sexually via seed production (Eckert 2002). A balance between these modes of reproduction may promote long-term persistence of a species occupying an unpredictable environment (Barsoum 2002, Jacquemyn et al 2006, Silvertown et al 1993). The advantages to reproduce sexually or vegetatively may be influenced by genetic and/or ecological factors such as spatial heterogeneity (Price and Marshall 1999, Eckert 2002). Clonal growth may be encouraged in habitats with limited seed production (Oborny and Kun 2002). Seed production and dispersal into novel habitats may be promoted as an escape from competition, high population density, and/or seed mortality next to the parent plant (Ericksson 1992). Plants occupying stable habitats are suggested to allocate more resources to vegetative propagation while plants occupying highly disturbed habitats allocate more resources to sexual reproduction (Ikegami 2004).

The Florida scrub is an endemic rich ecosystem characterized by xerophytic evergreen plants and dominated by dwarf oaks and palms and with or without a pine

(generally *Pinus clausa*) overstory (Menges and Hawkes 1998). Scrub soils are generally more than 90% sand with an acidic pH and limited nutrients (Weidenhamer and Romeo 2004). Habitat alteration and loss can potentially threaten the persistence of scrub species such as *Polygonella myriophylla*. Between 1945 and 1990, approximately 83% of the native scrub habitat was lost to agricultural, commercial, or residential development, and the remnant scrub fragmented and altered by fire suppression (Menges et al. 1993). *Polygonella myriophylla* is usually restricted to gaps within the matrix of oaks and Florida rosemary in native scrub but also occurs along adjacent road-side habitats.

The establishment of unimproved roads neighboring scrub ecosystems may affect the demography of plant species. Plants living in sandy road habitats are expected to endure the continuous effects of sand burial and sand erosion. Plants occupying roadsides appear larger in size compared to native scrub plants which may be expected since long-distance clonal spreading is commonly found in highly disturbed areas (Fahrig et al. 1994). Roadside populations of the herbaceous perennial, *Hypericum cumulicola*, exhibited more variable population dynamics, earlier reproduction, higher fecundity, and more erratic life spans than populations in native scrub (Quintana-Ascencio et al. 2007). Road verge populations of the rare shrub, *Grevillea barklyana*, an Australian endemic, exhibited higher reproductive potential and higher seed production than population in non-road habitats, likely resulting from an increase in water and mineral nutrients and less competition for resources (Hogbin et al. 1998).

My goal was to evaluate if demographic variation of *Polygonella myriophylla* at plant (genet) and branch (ramet) level exists between native scrub and roadside habitats. I hypothesized that persistent disturbed microhabitats and more dynamic sand accretion in roadside would increase rooting probabilities compared to more stable scrub habitats, affecting survival, growth and reproduction. I describe the variation in flowering through the year among plants in scrub and roadside. I implemented treatments to compare vital and rooting probability rates in experimentally covered and uncovered branches (rooting treatments) in scrub and road habitat. We carried out an experiment comparing genet level parameters such as flowering status and maximum crown diameter, and ramet level parameters like stem diameter, length, mortality, fecundity, and rooting probability between sites, habitats, and among rooting treatments.

CHAPTER TWO: MATERIALS AND METHODS

Study species

Polygonella myriophylla (Polygonaceae) is a clonal hermaphroditic, woody perennial (Chafin 2000, Weekley and Menges 2003) listed as endangered and narrowly endemic to pyrogenic scrub ecosystems of the Lake Wales Ridge in central Florida (Fig. 1). It is found in Orange, Polk, Highlands, and Osceola Counties (Christman and Judd 1990, Turner et al. 2006) in 119 scrub sites covering approximately 10,000 hectares and protected in less than 300 hectares (Christman and Judd 1990). Flowers are grouped close together in inflorescences at branch tips. It is commonly surrounded by bare zones likely associated with release of allelopathic chemicals (gallic acid and hydroquinone) which negatively affects neighboring plant and animal species (An et al. 1996, Weidenhamer and Romeo 2004). These natural fire breaks may serve to reduce the likelihood of shrub death by fire (Weidenhamer and Romeo 2004). Seedling recruitment is rare, and mostly associated with fire and/or disturbance. *Polygonella myriophylla* frequently produces adventitious roots at branch nodes in contact with sand, and individual branches may root multiple times (personal observation). Spacers between ramets are frequently broken resulting in physically independent ramets.

Study Sites

Our study was conducted at four sites within the Lake Wales Ridge State Forest (LWRSF) in Polk County, Florida. The Lake Wales Ridge is a 160 km long, 30 km wide sandy upland situated within Polk, Orange, Highlands and Osceola counties in south-

central Florida (USFWS 1993). The first two sites were near Old School road (27° 40' 47" N, 81° 26' 10" W). One plot was located within Sand-pine Scrub and the other in a nearby sandy road. The scrub site was burned by prescription in 2005. Sand-pine Scrub is characterized by a 15-100 year fire return interval (Meyers 1990) with well-drained soils and dominated by *Pinus clausa* (sand-pine) and several understory shrubs including *Quercus myrtifolia*, *Q. geminata*, *Q. chapmanii*, *Lyonia ferruginea*, *Serenoa repens*, and *Sabal etonia* (Menges et al. 1993). The remaining two sites were at LC01 (27° 11' N, 81° 21' W), a 21.4 acre burn unit on the Arbuckle Tract of the LWRSF. LC01 was burned by prescription in 1998 (Weekley and Menges 2003). One plot was situated within Scrubby Flatwoods (oak scrub) and the remaining plot was located on an adjacent road. Scrubby Flatwoods are characterized by a 10-20 year fire return interval (Menges 2007) with moderately well-drained soils and may be dominated by scattered or dense pine stands including *Pinus elliottii* var. *densa*, *P. clausa*, *P. palustris*, *S. repens*, *Aristida stricta*, *Quercus inopina*, *Q. myrtifolia*, *Q. geminata*, *Q. chapmanii*, *S. etonia*, *Ilex glabra*, *Panicum absissum*, and several species of *Lyonia* (Abrahamson and Abrahamson 1996, Menges et al. 1993). In the interval 2002-2006 average annual rainfall was 1239 mm, average minimum annual temperature 17.3 °C and average maximum annual temperature 28.6 °C (SECC 2007). Individual plants used in the roadside study were located within 1 meter of the unpaved road. The effects of established roads on adjacent vegetation are suggested to reach between three and ten meters beyond the road path (Godefroid and Koedam 2004).

Reproductive variation

On February 11, 2006 we tagged, measured (maximum length and its perpendicular) and counted inflorescences in 10 road and 10 scrub plants selected along parallel 20 m transects in the LC01 site. I selected the nearest plant to stratified random points at two m intervals along the transects. We revisited these plants once a month 10 additional times. Each time (except in December) we collected an inflorescence per plant. Inflorescences were counted clockwise and one was selected using a value from a table of random numbers. In the lab, we counted the number of flowers per inflorescence under a microscope. We measured final plant size (maximum length and its perpendicular) in each habitat on December 18, 2006. We compared median number of inflorescences, and flowers and the relative change in area (assuming an elliptic shape) between road and scrub habitat.

Experimental demography

Fifteen plants per habitat were selected at each experimental site. Plants were chosen based on presence of at least four unrooted branches. Plants separated by ≥ 30 centimeters were considered 'genets'. All plants were marked with flags and identified by aluminum tags. Each of four unrooted branches per genet received one of four possible treatments. The treatments were applied using random number series that were assigned to consecutively clockwise numbered branches. A total of 60 plants and 240 branches were used in this study. For every treatment, the branch was marked with a non-toxic waterproof marking stick 15 centimeters from the branch tip and an individually color coded twisted plastic wire. This position will be referred to as the reference point throughout this paper and represents the reference for our evaluations of change in branch

length and branch diameter. Our treatments were as follows: (1) Forced burial, a pliable wire was placed at the reference point forcing contact with the ground and covered with sand; (2) Elevation, a pliable wire was placed lifting the branch two centimeters from the ground and preventing contact with sand; (3) Wire control, a pliable wire was placed alongside the branch at the reference point; and (4) Control, no wire used (Fig. 2). We buried the branches in treatment one to mimic sand burial in road habitats and evaluated probability of rooting and performance of covered branches in both habitats. We lifted branches in treatment two to reduce chances of burial and evaluate demography of unrooted branches in both habitats. Treatment three was a procedural control of the effect of the wire. Treatment four provided vital and rooting rates of branches in natural conditions.

After the initial set-up in April 2004, we completed a total of 5 evaluations in each plot in July 2004, November 2004, May 2005, November 2005, and March 2006. At every visit, data were collected on genet survival and growth by measuring maximum crown diameter. Branch growth, mortality, fecundity, and rooting probability were recorded for all treated branches. Branch growth was measured as changes in branch length and diameter between evaluations. Distance between the reference point and branch tip was considered branch length with the initial length of 15 centimeters used as the baseline. Branch diameter variation was calculated at the reference point with calipers (0.01 cm precision). Fecundity was calculated by counting inflorescences present between reference point and branch tip. Roots newly present within 5 cm of reference point were recorded as adventitious rooting.

Although all experimental branches were initially marked with two different labels, we lost 37 (13%) out of 240 treated branches over the course of the study due to missed and fading labels. In this analysis we excluded all missing branches (5-13 lost branches across treatments; 26 branches in Old School and 11 in LC01).

Data analysis

The categorical data from the experimental study (rooting probabilities, survival, and reproduction of treated branches) were analyzed by habitat, site and treatment with logistic regression models. Monthly changes in branch diameter and branch length were calculated as the geometric mean of the ratios between evaluations corrected for interval length. Analysis of covariance was used to evaluate monthly changes in branch diameter and diameter growth rates were compared among habitats, sites, and treatments. Analysis of variance was used to evaluate monthly changes in branch length and length growth rates were compared among habitats, sites, and treatments. At LC01 (reproductive schedule study), I used repeated measurements to assess median number of inflorescences per genet and flowers per inflorescence between habitats. A paired t test was used to evaluate size change among plants between habitats. All data were analyzed using SPSS 11.5.

CHAPTER THREE: RESULTS

Reproductive study (LC01)

Overall, *Polygonella myriophylla* occupying road habitat did not exhibit a higher number of inflorescences compared to plants occupying scrub habitat (median =62 and 26.5, respectively, Mann-Whitney $U=41.5$, $P=0.520$) but in some months the number of inflorescences displayed was higher in road vs. scrub habitat ($F= 4.79$, $P=0.042$ for the polynomial order 4 of within subject contrasts for the interaction between month and habitat). The proportion of flowering road and scrub plants increased during the spring and rapidly decreased at the beginning of winter (Fig. 3), and the number of inflorescences per plant was larger between May and September than in other months (Fig. 4A; $F= 7.867$, $P=0.012$) for the quadratic polynomial of within subject contrasts for month).

The proportion of plants flowering was similar among habitats (Fig. 3). Of 10 visits per plant, 49 of 100 possible times there were no inflorescences on plants in the road, and 52 of 100 there were no inflorescences in the scrub. We found one plant in each habitat that never flowered during 2006 and one plant in each habitat that flowered only once. There was only one plant that flowered every month throughout the study. It was located in scrub habitat and produced the highest number of inflorescences in one evaluation of any plant (in October; 581 inflorescences).

The number of flowers per inflorescence was not significantly different between road and the scrub habitat (Fig. 4B). Number of flowers per inflorescence was highest in

July and August (12-15 flowers), and lower and more variable in other months (Fig. 4B, $F= 10.480$, $P<0.0001$ for the quadratic polynomial of within subject contrasts for month).

Despite an uneven distribution of plants of different sizes among habitats (70 % of scrub plants were $<.20 \text{ m}^2$ vs. 10 % of road plants were $< 0.20 \text{ m}^2$, Fig. 5) our data did not show significant differences in initial size (mean initial area= $1.25 \pm 2.19 \text{ m}^2$ and $1.45 \pm 1.48 \text{ m}^2$ in scrub and road respectively, $t=0.506$, 18 d.f, $P=0.248$, data log transformed) or growth (mean area difference = $-0.24 \pm 0.50 \text{ m}^2$, and $0.58 \pm 1.44 \text{ m}^2$ scrub and road respectively, $t=0.950$, 17 d.f. $P=0.355$) between *Polygonella. myriophylla* plants in road and scrub in the LC01 transects.

Experimental demography

Initial plant crown area of experimental genets varied between sites and habitats. At the beginning of the experiment, genet basal cover was larger in Old School (mean = 1.49 m^2 , $sd = 1.10$) than LC01 (0.85 m^2 , $sd = 1.17$). In both locations, road plants were larger than scrub plants (Fig. 6; Table 1). A prescribed fire in fall 2005 killed seven plants at the Old School scrub site. Five plants at the roadside habitat in Old School and one plant at the scrub habitat in LC01 died of unknown causes.

Rooting was affected by treatments but not by habitat or site. Overall, the proportion of rooted branches by the end of the study was 34.1%. Forcing contact of branches to sand increased rooting probability (67.5% after forced contact vs. 19.6%-29.8% for other treatments; (Fig. 7; $G_3= 26.04$, $P<0.0001$). The likelihood of rooting was not significantly different between the lifted wire and the controls ($G_2= 1.349$, $P=0.510$).

There were no significant differences in rooting probability between sites or habitats ($G_1=0.528$, $P=0.467$ & $G_1=0.047$, $P=.828$, respectively).

Branch survival throughout the study was affected by site but not by habitat or rooting treatments. LC01 had significantly higher survival (66.1%) than those at Old School (34.7%; $G_1=20.65$, $P<0.001$) which was burned. Survival was not significant between habitats or treatments ($G_1=2.692$, $P=0.101$, $G_3=5.951$, $P=0.114$, respectively, Fig. 8). There were no differences in survival between habitats within sites ($P>0.177$). Treated branches that rooted during the study did not exhibit significantly higher survival compared to unrooted treated branches ($G_1=1.106$, $P=0.293$).

There was an effect of location and habitat, but no treatment on monthly diameter growth rate (Table 2, Fig. 9A and 9B respectively for location and habitat) and monthly branch length growth rate (Table 3, Fig. 10). Initial branch diameter was used as covariate in estimating monthly branch diameter to control for faster growth exhibited in small plants compared to larger plants. Initial plant size and initial diameter did not correlate to monthly length growth therefore no covariate was used for this analysis. Monthly diameter growth rate was significantly higher in Old School (marginal mean=1.040 mm/month, sd=0.004) than in LC01 (1.018 mm/month, sd=0.003) and higher in road habitat (1.035 mm/month, sd=0.004) than in scrub (1.024 mm/month, sd=0.003). Monthly length growth rate was also significantly higher in Old School (mean=1.08 cm/month, sd=0.07) than in LC01 (1.05 cm/month, sd=0.08) and higher in road habitat (1.07 cm/month, sd=0.07) than in scrub (1.05 cm/month, sd=0.08).

The proportion of flowering among branches during the experiments was significantly higher in summer months (April: 45-57%, May: 46-58 % and July: 62-68 %, Old School and LC01 respectively) than in spring and winter (March: 3-9 %, November 2004: 3-16 % and November 2005: 0-33 %, Old School and LC01 respectively). Flowering probability was higher in LC01 than Old School in November 2004 ($G=7.6$, 1 d.f., $P=0.006$, $N=168$ branches), and November 2005 ($G=21.2$, 1 d.f., $P<0.001$, 109 branches). Flowering probability was higher for the rooted experimental branches only in July 2004 compared to unrooted treated branches ($P=0.022$). The proportion of branches with flowers was higher in road habitat than scrub in April 2004 ($G=19.5$, 1 d.f., $P<0.0001$) and November 2005 ($G=6.5$, 1 d.f., $P=0.013$). There was no effect of treatment on flowering probability.

CHAPTER FOUR: DISCUSSION

Polygonella myriophylla occupying road and scrub habitats exhibited contrasting demography. Roadside plants had more inflorescences, were larger and grew faster than scrub plants. Increased moisture levels, (Hogbin et al 1998, Petru and Menges 2004), higher mineral nutrients, and lower abundance of competitors in road habitats (Hogbin et al 1998) compared to scrub may explain these demographic differences. Other clonal plants living in habitats with contrasting resource levels and disturbance also exhibit variable demographics. The clonal desert cactus, *Opuntia rastrera*, exhibited faster growth and higher vegetative reproduction in scrubland than in grasslands where reproduction was mainly via seedling recruitment (Mandujano et al 1998, Mandujano et al 2001). The invasive cordgrass, *Spartina densiflora*, living in low marsh habitats, exhibited greater tiller density, natality and mortality compared to plants residing in more stable high marsh habitats (Nieva et al. 2005). *Ranunculus repens* exhibited 'guerilla' clonal growth (long-distance spreading) with longer stolon internodes in woodland habitats and allocated more biomass to root systems in grassland habitats (Doust 1981). The clonal palm *Oenocarpus mapora* displayed higher seedling survivorship in wind disturbed areas and lower seedling survivorship in mature forest areas (De Steven 1989). Populations of the clonal plant *Mimulus primuloides* exhibit variable demographics at different altitudes (Douglas 1981). Low altitude populations suffered greatest inter-specific competition, middle altitude populations exhibited highest allocation to vegetative reproduction, and disturbed high-altitude populations displayed smallest plant size with an increased allocation to sexual reproduction. The mode of reproduction

exhibited in clonal plants occupying disturbed and stable habitats appears to be species-specific and likely influenced by level of competition and disturbance.

Flower production was influenced by location and habitat. In five out of six evaluations, the LC01 site displayed higher fecundity compared to Old School. The prescribed burns in 1998 at LC01 and in 2005 at Old School may explain these findings. By the beginning of this study the scrub at Old School had gone 50 + years without being burned (Park Biologist Anne Malatesta, personal communication). Fire suppression in pyrogenic ecosystems may reduce flowering responses in many species (Abrahamson et al. 1996). For example, a demographic study on the prairie perennial, *Silene regia*, found unburned populations suffered lower survival, lower fecundity, and low seedling recruitment (Menges and Dolan 1998). The lower fecundity found in Old School may partially reflect effects of past fire suppression. Furthermore, in year two of the study, a prescribed burn completely killed seven out of fifteen plants in Old School scrub. By the study end, the plants killed by fire failed to resprout. Increased sexual reproduction is expected in larger genets (De Steven 1989) and larger ramets (Hartnett 1990) but the larger road plants did not exhibit an overall higher fecundity than scrub plants in this study. Fire suppression, affecting flowering probability, and the prescribed burn affecting ramet survival, may explain why site was a better indicator of fecundity than habitat.

Clonal integration increases the overall survival among ramets (Pan and Price 2002). We expected roadside *P. myriophylla* to exhibit a larger number of connected ramets to buffer adverse effects of sand accretion and therefore display different survival

rates compared to scrub plants. However, in this study, branch and genet survival were affected by site not habitat. Perhaps the road sites used in this experiment are minimally disturbed thus clonal integration may not play an important role in established road plants. Higher survival of LC01 ramets was likely a result of the prescribed fire in 1998 and the prescribed burn in 2005 killing 7/15 plants in Old School scrub. Thirteen out of sixty “genets” (8-scrub, 5-road) died during this study from the prescribed burn and other unknown causes. An experimental study utilizing a higher number of road and scrub plants in two long-unburned and two recently burned sites might provide a better estimate of survival between habitats and sites. Furthermore, a longer term study may provide more accurate estimates of survival. For example, in a 38-year demographic study on the perennial bunchgrass *Bouteloua gracilis*, genets were replaced at approximately the same rate they were lost (Fair et al. 1999).

In a two year demographic study, comparing three road and three scrub populations, *P. myriophylla* exhibited a higher mean annual ramet mortality in roadside (32 – 37.6%) than scrub (21.3%) habitat (Horn and Quintana-Ascencio, unpublished data). In the Carter Creek site, the road population lost many ramets to full sand burial. This road population is adjacent to a high traffic area and subjected to constant sand accretion. Full sand burial has been suggested to decrease plant growth and increase mortality (Bach 2001). Sand burial and erosion likely explains the overall higher annual ramet mortality found in this demographic study.

The spatial structure of a clonal plant's habitat is suggested to promote the efficient use of available space by either promoting seed dispersal or clonal growth (Winkler and Fisher 2002). It is not clear how *P.myriophylla* populations entered into road habitats. It's probable that both seed dispersal and clonal invasion from scrub into road habitat is taking place. The mode of reproduction favored is likely dependent on the quality of the habitat. For example, scrub habitat with low resource availability and little competition may promote *P.myriophylla* plants to invade clonally since space is available for clonal spread but resources may be too low for seed production. It has been suggested that seed production requires more energy than vegetative reproduction (Douglas 1981) and vegetative propagules are suggested to exhibit higher survival than seeds (De Steven 1989, Winkler and Fisher 2002). Therefore, clonal growth may be selected for when colonizing disturbed road habitats. Alternatively, scrub habitat yielding moderate resources and higher levels of competition may not provide ample space for plants to clonally spread but offer adequate resources to promote seed dispersal. After *P.myriophylla* colonizes and establishes in road habitats, plants appear to exhibit 'guerilla' clonal growth commonly found in disturbed habitats (Fahrig et al 1994) and characterized by long-distance clonal spreading which facilitates spatial exploration and resource acquisition (Karlson et al 1996).

We did not observe any seedling recruitment around established road populations between April 2004 and March 2006 (this study) and only one seedling was observed in long-unburned scrub populations between March 2005 and July 2007 (companion study at Carter Creek Preserve). However in the same study at Carter Creek, we observed 82

seedlings in recently disturbed scrub (by fire and mechanical treatment). Disturbed road habitats exhibit more dynamic sand movement compared to native scrub gaps (Petru and Menges 2004). Sand burial beyond a species threshold depth is suggested to prevent seed germination and increase mortality (Petru and Menges 2004). This may likely explain the lack of seedlings observed in road habitats. I suggest vegetative reproduction is more successful than sexual reproduction in plants occupying road habitats but believe seed production among roadside plants is sufficient to influence seedling recruitment at scrub habitats.

Forced burial increased rooting but no significant differences in survival, growth and reproduction were found between forced rooted ramets in roadside and native habitat. Rooted ramets did not sever from the mother genet in this study so they did not exhibit independent survival, growth, or reproduction. Hence, rooted and unrooted ramets in this study displayed vital rates comparable to their mother genet. A true test on the demographic variation between rooted and unrooted ramets would compare severed and unrooted ramets of the same genet. In this study, covering ramets with sand promoted high adventitious root production. The higher sand movement found in road habitats will likely promote higher rooting in roadside plants compared to scrub plants. Sexual and vegetative reproduction are suggested to compete for resources (Thompson and Eckert 2004) thus road plants exhibiting high rooting will likely allocate more resources to clonal growth rather than sexual reproduction.

We found demographic variation in mortality, fecundity, and growth between road and scrub populations of *Polygonella myriophylla*. The long-term persistence of road populations is a concern since seedling recruitment may be rare in roadside habitats. Therefore, our main focus should be the conservation of *P. myriophylla* individuals currently residing in scrub habitat. Seedling recruitment in long-unburned scrub is also minimal, but enhanced by fire. The results of the companion study at Carter Creek Preserve suggest the application of prescribed fire will likely promote seedling recruitment from underground seed banks in scrub habitat. Furthermore, if road plants disperse seed into improved scrub habitat, seedling recruitment may be promoted which could benefit scrub populations.

APPENDIX A: TABLES

Table 1 Analysis of variance of initial plant crown area (cm²) by location and habitat.

Source	Sum of Squares	df	Mean Square	F	Sig.
Habitat	5.271	1	5.271	7.035	.009
Location	25.226	1	25.226	33.664	.000
Habitat* Location	.024	1	.024	.033	.857
Error	176.846	236	.749		
Total	536.654	240			

Table 2 Analysis of covariance of monthly diameter growth rate by treatment, habitat, and location, using initial diameter as covariable

Source	Sum of Squares	df	Mean Square	F	Sig.
Initial diameter (covariate)	.005	1	.005	4.518	.035
Habitat	.006	1	.006	5.127	.025
Treatment	.001	3	.000	.211	.889
Location	.024	1	.024	21.199	.000
Habitat * Treatment	.002	3	.001	.486	.693
Habitat * Location	.000	1	.000	.261	.610
Treatment * Location	.004	3	.001	1.205	.309
Habitat * Treatment * Location	.003	3	.001	.890	.447
Error	.199	178	.001		
Total	206.192	195			

Table 3 Analysis of variance of monthly length growth rate by treatment, habitat, and location and their interactions.

Source	Sum of Squares	df	Mean Square	F	Sig.
Initial area of the plant	0.015	1	0.015	2.927	0.089
Initial diameter of the branch	<0.0001	1	<0.0001	0.037	0.848
Treatment	.024	3	.008	1.519	.211
Habitat	.023	1	.023	4.351	.038
Location	.026	1	.026	4.968	.027
Treatment * Habitat	<0.0001	3	<0.0001	.009	0.999
Treatment * Location	.006	3	.002	.393	.758
Habitat * Location	.013	1	.013	2.413	.122
Treatment* Habitat * Location	.009	3	.003	.603	.614
Error	.95	181	.005		
Total	225.414	199			

APPENDIX B: FIGURES



Figure 1 The Lake Wales Ridge in Central Florida



Treatment 1



Treatment 2



Treatment 3



Treatment 4

Figure 2 Experimental treatments applied to *Polygonella myriophylla*: (1) forced branch burial, (2) branch lifting, (3) procedural control, and (4) no manipulation

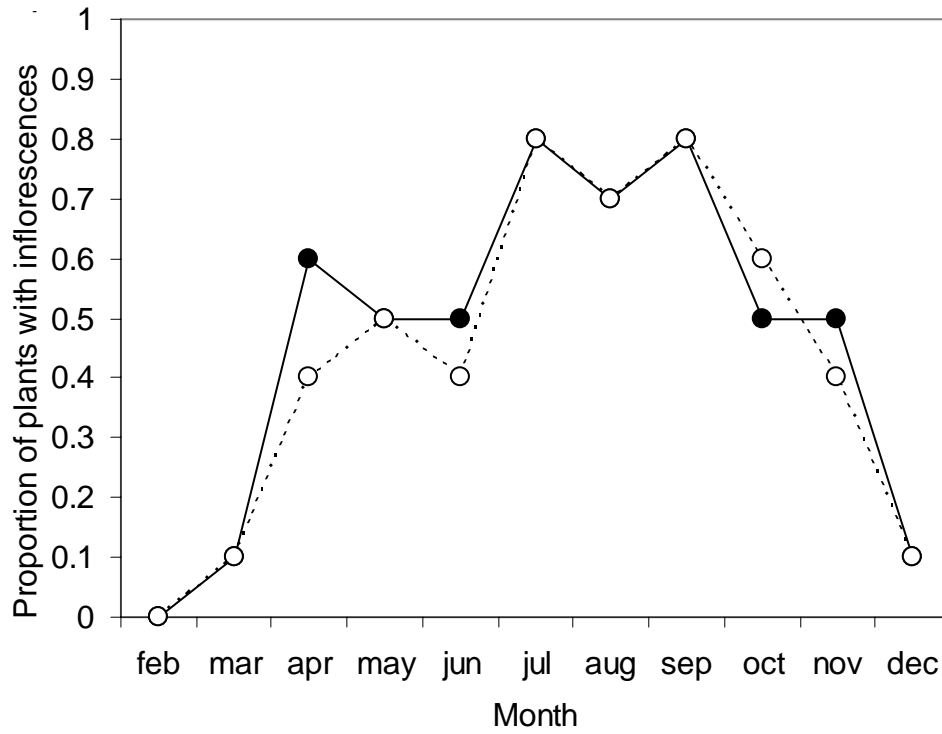


Figure 3 Proportion of plants with inflorescences at LC0I per month in road (filled circles) and scrub habitats (open circles).

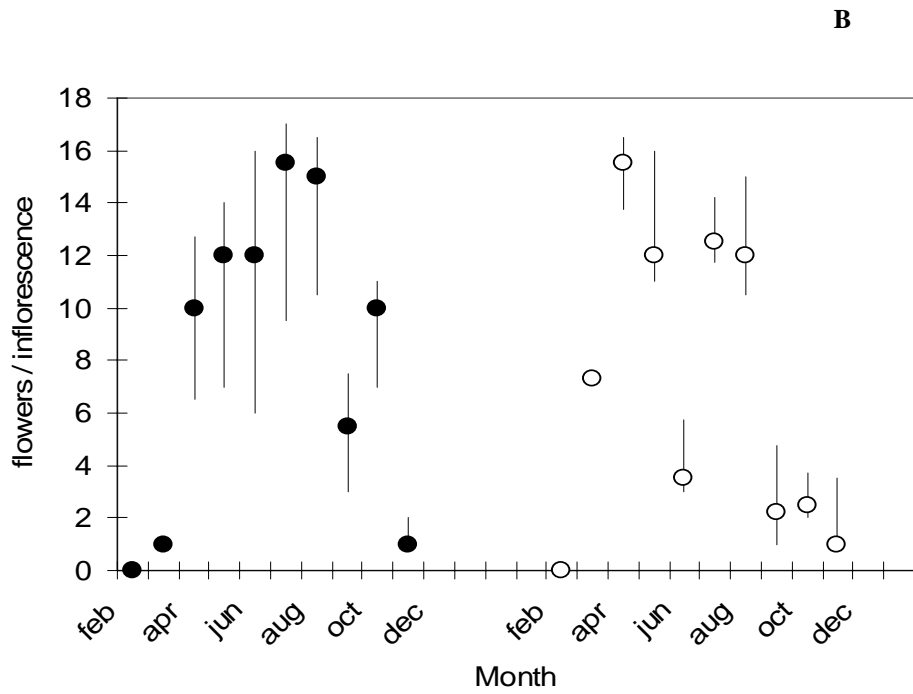
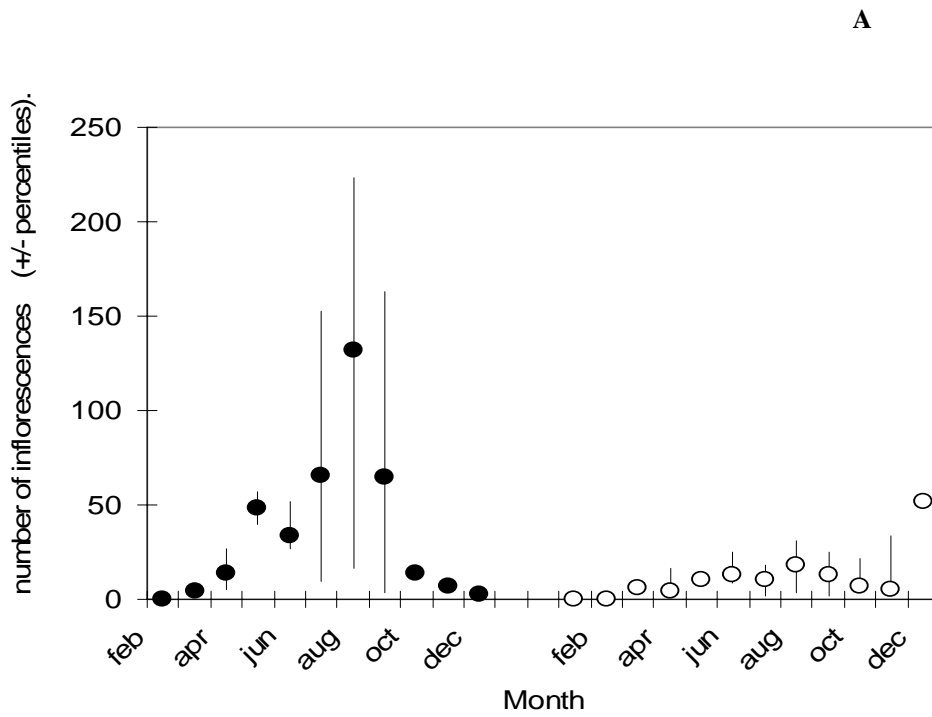


Figure 4 A. Median (25 lower and 75 upper percentiles) number of inflorescences of *Polygonella myriophylla* per month in road (filled circles) and scrub habitats (open circles). B. Median (25 lower and 75 upper percentiles) number of flowers/inflorescences of *Polygonella myriophylla* per month in road (filled circles) and scrub habitats (open circles).

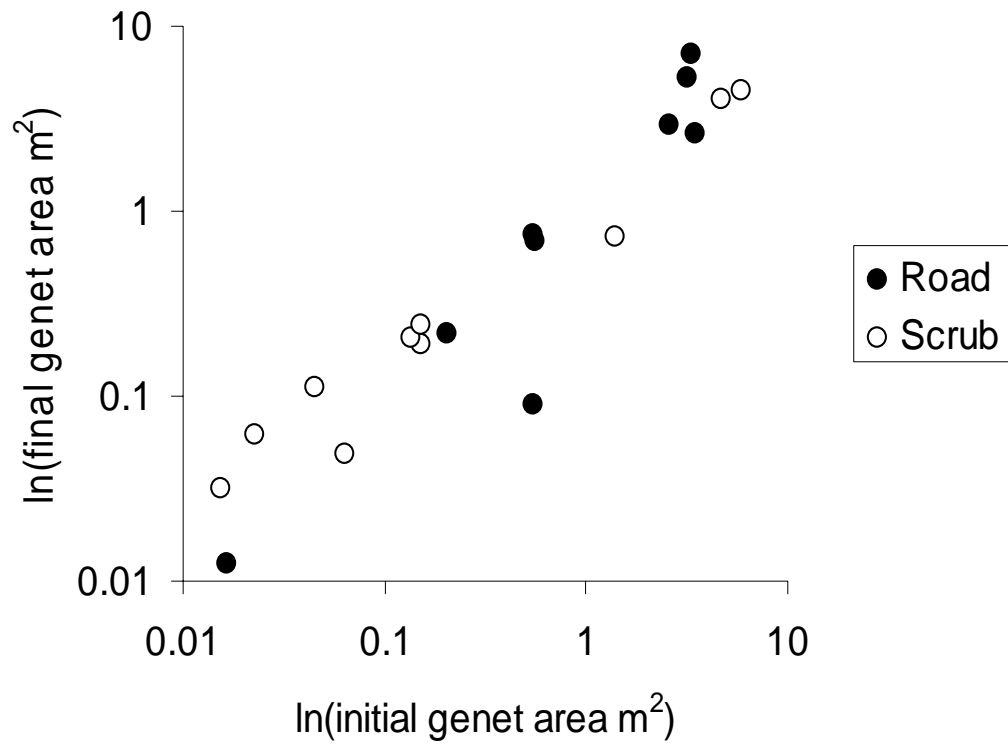


Figure 5 Plot of initial and final genet area (clusters of branches separated by >30 cm, crown area in m², February to December 2006) of *Polygonella myriophylla* in road and scrub habitats in LC01.

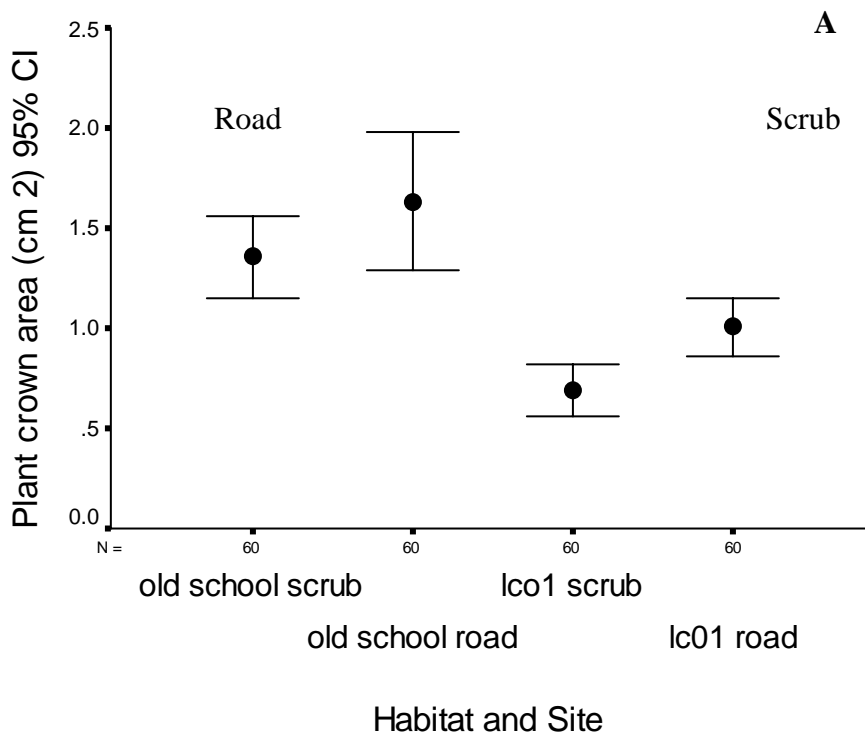


Figure 6 Plant crown area (m²) per site at beginning of the experiment in April 2004.

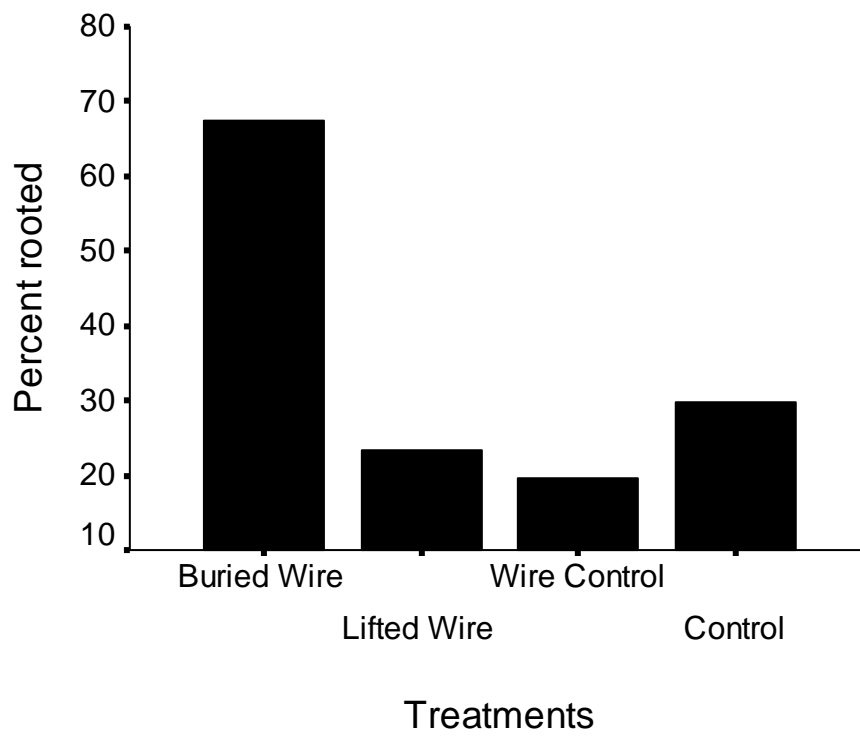


Figure 7 Percent rooted of treated branches

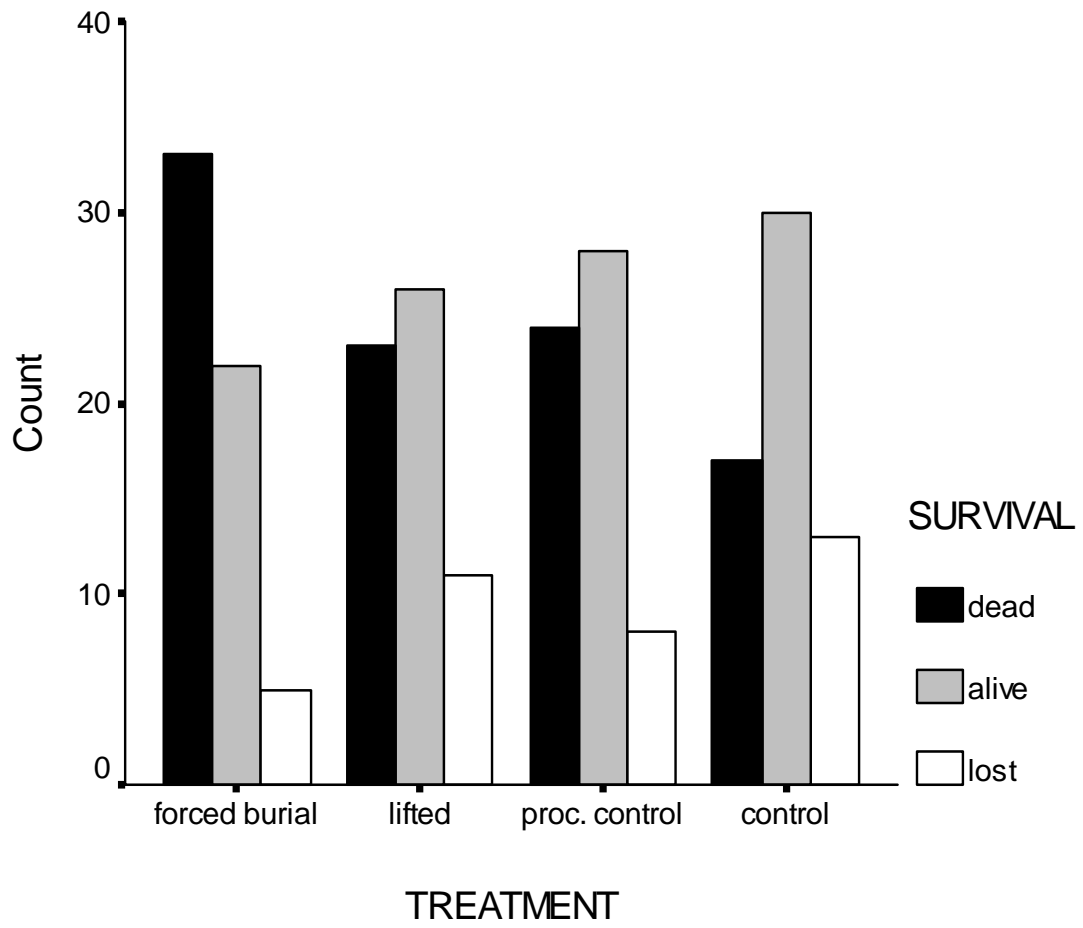


Figure 8 Number of branches surviving, dying and missing among treatments

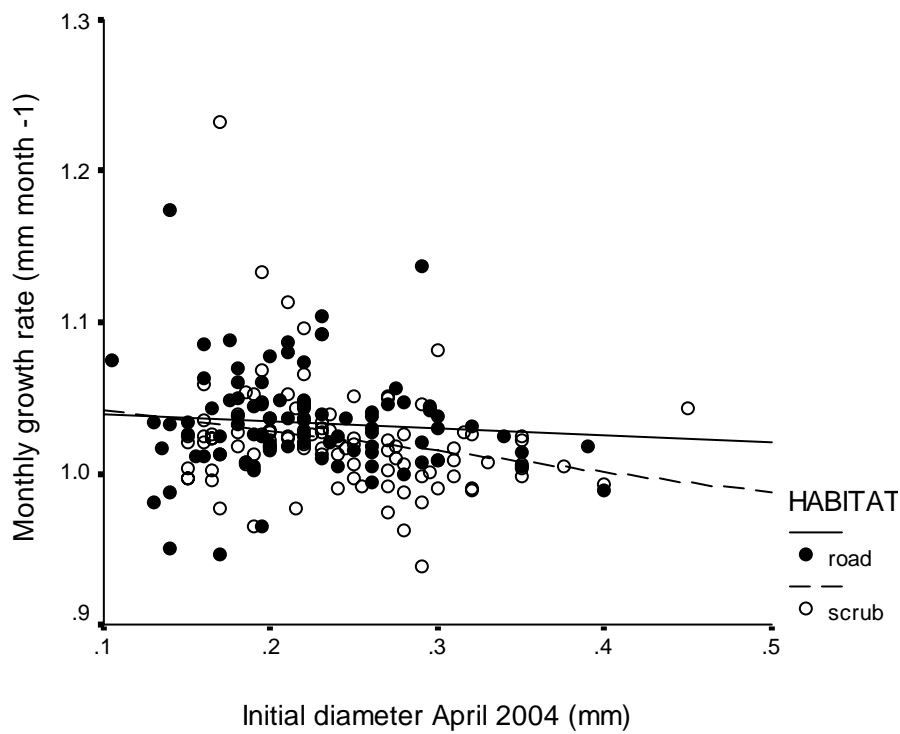
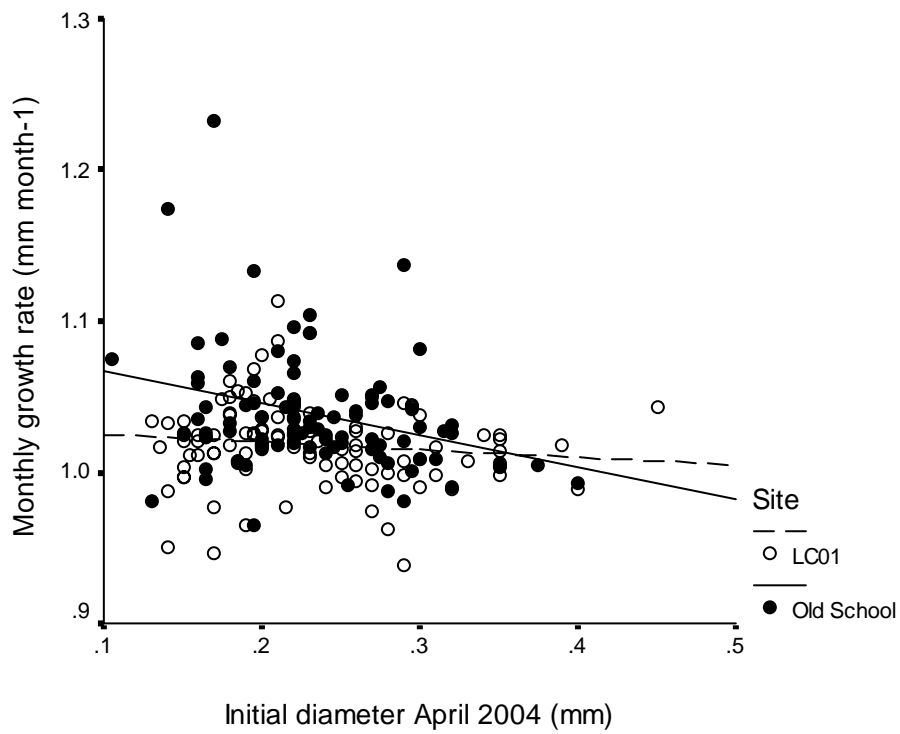


Figure 9 Plots of monthly branch diameter growth rate (mm) vs. initial diameter per site and habitat.

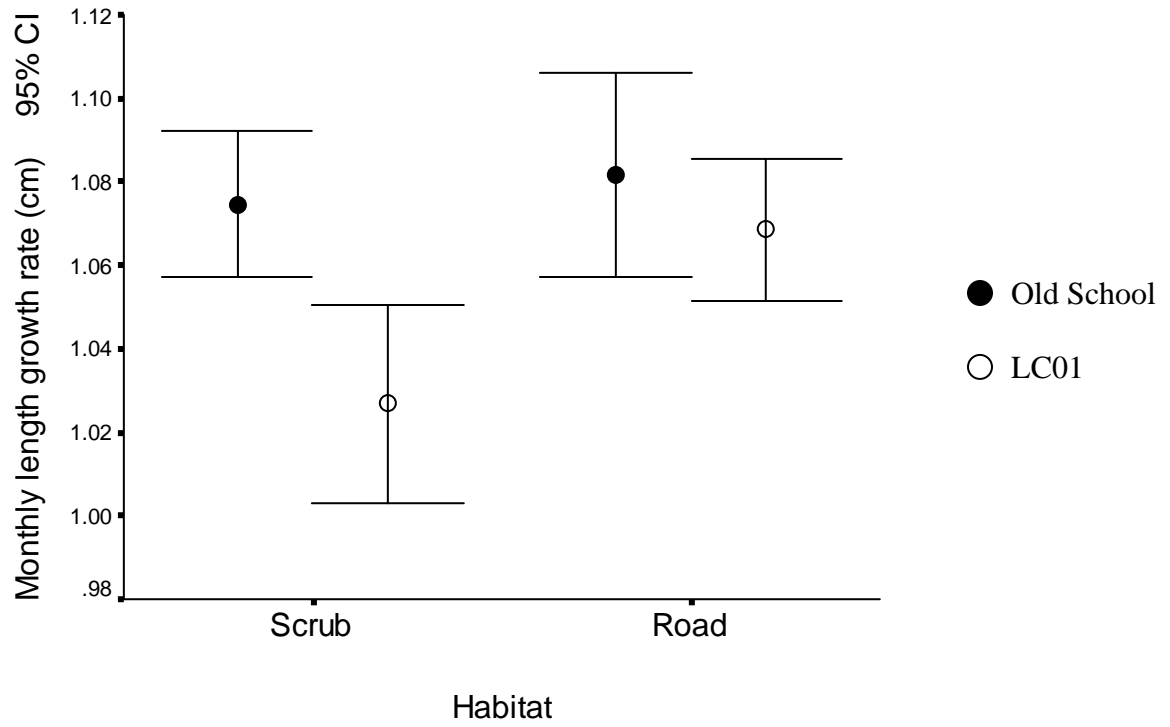


Figure 10 Monthly branch length growth rate per habitat and site (notice the y-axis starts with .98)

LIST OF REFERENCES

- Abrahamson, W.G., and C.R. Abrahamson. 1996. Effects of fire on long-unburned Florida uplands. *Journal of Vegetation Science* 7: 565-574
- An, M. Pratley, J.E. and T. Haig. 1996. Applications of GC/MS in alleopathy research: a case study. *Rapid Communications in Mass Spectrometry* 10: 104-105
- Bach, C.E. 2001. Long-term effects of insect herbivory and sand accretion on plant succession on sand dunes. *Ecology* 82(5): 1401-1416
- Barsoum, N. 2002. Relative contributions of sexual and asexual regeneration strategies of *Populus nigra* and *Salix alba* during the first years of establishment on a braided gravel river bed. *Evolutionary Ecology* 15:255-279
- Bazzaz, F.A., N.R. Chiarello, P.D. Coley, and L.F. Pitelka. 1987. Allocating resources to reproduction and defense. *Bioscience* 37(1): 58-67
- Chafin, L.C. 2000. Field guide to the rare plants of Florida. Florida Natural Areas Inventory, Tallahassee.
- Christman, S. P. and W. S. Judd. 1990. Notes on plants endemic to Florida scrub. *Florida Scientist* 53: 52-73.
- De Steven, D. 1989. Genet and ramet demography of *Oenocarpus mapora* ssp. *Mapora*, a clonal palm of Panamanian tropical moist forest. *Journal of Ecology* 77(2): 579-596
- Douglas, D.A. 1981. The balance between vegetative and sexual reproduction of *Mimulus primuloides* (Scrophulariaceae) at different altitudes in California. *Journal of Ecology* 69: 295-310
- Doust, L.L. 1981. Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*): I. The dynamics of ramets in contrasting habitats. *Journal of Ecology* 69(3): 743-755
- Eckert, C.G. 2002. The loss of sex in clonal plants. *Evolutionary Ecology* 15: 501-520
- Ericksson, O. 1992. Evolution of seed dispersal and recruitment in clonal plants. *OIKOS* 63: 439-448
- Fahrig, L. D.P. Coffin, W.K. Lauenroth, and H.H. Shugart. 1994. The advantage of long-distance clonal spreading in highly disturbed areas. *Evolutionary Ecology* 8: 172-187
- Fair, J., W.K. Lauenroth, and D.P. Coffin. 1999. Demography of *Bouteloua gracilis* in a mixed prairie: analysis of genets and individuals. *Journal of Ecology* 87: 233-243

- Fischer, M. and M.V. Kleunen. 2002. On the evolution of clonal plant life histories. *Evolutionary Ecology* 15: 565-582
- Godefroid, S. and N. Koedam. 2004. The impact of forest paths upon adjacent vegetation: effects of the path surfacing material on species composition and soil compaction. *Biological Conservation* 119: 405-419
- Hartnett, D.C. 1990. Size-dependent allocation to sexual and vegetative reproduction in four clonal composites. *Oecologia* 84: 254-259
- Hogbin, P.M., D.J. Ayre, and R.J. Whelan. 1998. Genetic variation and reproductive success of road verge populations of the rare shrub *Grevillea barklyana* (Proteaceae). *Heredity* 80: 180-186
- Ikegami, M. 2004. Functional specialization of ramets in a clonal plant network. PhD thesis Utrecht University, Utrecht, the Netherlands (<http://igitur-archive.library.uu.nl/dissertations/2004-0407-091227/inhoud.htm>)
- Jacquemyn, H., R. Brys, O. Honnay, M. Hermy, and I. Roldan-Ruiz. 2006. Sexual reproduction, clonal diversity and genetic differentiation in patchily distributed populations of the temperate forest herb *Paris quadrifolia* (Trilliaceae). *Oecologia* 147: 434-444
- Karlson R.H., T.P. Hughes, and S.R. Karlson. 1996. Density-dependent dynamics of soft coral aggregations: The significance of clonal growth and form. *Ecology* 77(5): 1592-1599
- Mandujano, M.del.C., C. Montana, M. Franco, J. Golubov, and A. Flores-Martinez. 2001. Integration of demographic annual variability in a clonal desert cactus. *Ecology* 82(2): 344-359
- Mandujano, M.del.C., C. Montana, I. Mendez, and J. Golubov. 1998. The relative contributions of sexual reproduction and clonal propagation in *Opuntia rastrera* from two habitats in the Chihuahuan desert. *Journal of Ecology* 86: 911-921
- Menges, E.S., W.G. Abrahamson, K.T. Givens, N.P. Gallo, and J.N. Layne. 1993. Twenty years of vegetation change in five long-unburned Florida plant communities. *Journal of vegetation science* 4(3): 375-386
- Menges, E.S. and C.V. Hawkes. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. *Ecological Applications* 8(4): 935-946
- Menges, E.S. and R.W. Dolan. 1998. Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, geographic location, population size, and isolation. *Journal of Ecology* 86: 63-78
- Menges, E.S. 2007. Integrating demography and fire management: an example from Florida scrub. *Australian Journal of Botany* 55(3): 261-272
- Meyers, R.L. 1990. Scrub and high pine. In: Myers, R.L. and Ewel, J.J. (eds.) *Ecosystems of Florida*, pp. 150-193. University of Central Florida Press, Orlando, FL.

- Nieva, F.J.J., E.M. Castellanos, J.M. Castillo, and M.E. Figueroa. 2005. Clonal growth and tiller demography of the invader cordgrass *Spartina Densiflora* Brogn. At two contrasting habitats in SW European salt marshes. *Wetlands* 25(1): 122-129
- Oborny, B. and A.Kun. 2002. Fragmentation of clones: how does it influence dispersal and competitive ability. *Evolutionary Ecology* 15: 319-346
- Orive, M.E. 1995. Senescence in organisms with clonal reproduction and complex life histories. *The American Naturalist* 145(1): 90-108
- Pan, J.J. and J.S. Price. 2002. Fitness and evolution in clonal plants: the impact of clonal growth. *Evolutionary Ecology* 15: 583-600
- Peltzer, D.A. 2002. Does clonal integration improve competitive ability? A test using Aspen (*Populus Tremuloides* [Salicaceae]) invasion into prairie. *American Journal of Botany* 89(3): 494-499
- Petru, M. and E.S. Menges. 2004. Shifting sands in Florida scrub gaps and roadsides: dynamic microsites for herbs. *American Midland Naturalist* 151:101-113
- Piqueras J. and L.Klimes. 1998. Demography and modeling of clonal fragments in the pseudoannual plant *Trientalis europaea* L. *Plant Ecology* 136: 213-227
- Piquot Y., D.Petit, M.Valero, J.Cuguen, P.de Laguerie, and P.Vernet. 1998. Variation in sexual and asexual reproduction among young and old populations of the perennial macrophyte *Sparangium erectum*. *Oikos* 82: 139-148
- Price, E.A.C. and C.Marshall. 1999. Clonal plants and environmental heterogeneity. *Plant Ecology* 141:3-7
- Quintana-Ascencio, P.F., Weekley, C.W. and E.S. Menges. 2007 Comparative demography of a rare species in Florida scrub and roadside habitats. *Biological Conservation* 137:263-270.
- Roiloa, S.R. and R.Retuerto. 2006. Small-scale heterogeneity in soil quality influences photosynthetic efficiency and habitat selection in a clonal plant. *Annals of Botany* 98: 1043-1052
- SECC. 2007. AgClimate [<http://AgClimate.org>]. Southeast Climate Consortium, Gainesville, FL 32611
- Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative plant demography-relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* 81: 465-476
- Thompson F.L., and C.G. Eckert. 2004. Trade-offs between sexual and clonal reproduction in an aquatic plant: experimental manipulations vs. phenotypic correlations. *Journal of Evolutionary Biology* 17: 581-592

Turner, W.R., D. S. Wilcove, and H. M. Swain. 2006. State of the Scrub. Conservation progress, management responsibilities, and land acquisition priorities for imperiled species of Florida's Lake Wales Ridge. Archbold Biological Station, Lake Placid, FL.

U.S. Fish and Wildlife Service. 1993. Endangered and threatened wildlife and plants: endangered of threatened status for seven central Florida plants. Federal register 58(79): 25746-25755

Weekley, C.W. and E.S. Menges. 2003. Species and vegetation responses to prescribed fire in a long-unburned, endemic-rich Lake Wales Ridge scrub. Journal of Torrey Botanical Society 130(4): 265-282

Weidenhamer, J. and J. Romeo. 2004. Allochemicals of *Polygonella myriophylla*: Chemistry and Soil Degradation. Journal of Chemical Ecology 30(5): 1067-1082

Winkler E. and M. Fischer. 2002. The role of vegetative spread and seed dispersal for optimal life histories of clonal plants: a simulation study. Evolutionary Ecology 15: 281-301