

LARGE HERBIVORE IMPACTS ON DEMOGRAPHIC CHARACTERISTICS AND  
POPULATION DYNAMICS OF AN ENDANGERED ORCHID (*SPIRANTHES*  
*PARKSII* CORRELL)

A Thesis

by

CARISSA LYN WONKKA

Submitted to the Office of Graduate Studies of  
Texas A&M University  
in partial fulfillment of the requirements for the degree of  
MASTER OF SCIENCE

December 2010

Major Subject: Rangeland Ecology and Management

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Approved by:

Chair of Committee,	William E. Rogers
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## ABSTRACT

Large Herbivore Impacts on Demographic Characteristics and Population Dynamics of  
an Endangered Orchid (*Spiranthes parksii* Correll). (December 2010)

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Chair of Advisory Committee: Dr. William E. Rogers

*Spiranthes Parksii* Correll is an endangered orchid of Texas. Populations of *S. parksii* are threatened by habitat loss and degradation resulting from human population growth and attendant development and resource extraction. Conservation easements have been established for the protection of the species, but little is known about the population dynamics of *S. parksii* and the biotic and abiotic factors which drive them. A baseline of ecological information is necessary to the creation of effective management plans for the conservation of this species.

The work presented here is an experimental investigation of the affects of large herbivores on *S. parksii* population dynamics. We explored direct impacts of herbivore browsing as well as indirect impacts resulting from removal of neighboring vegetation on *S. parksii* population fluctuations and the demographic parameters underlying them.

To determine direct herbivore affects on demographic characteristics and their implications for *S. parksii* population dynamics, we established 32, 1.5mx1.5m plots in areas of high *S. parksii* abundance. Each of the plots was randomly assigned one of two treatments: herbivore exclusion and control. Demographic parameters were recorded for

each individual located within the plots. The data suggest that large and small herbivore browsing affects different lifecycle transitions through removal of photosynthetic and reproductive tissue. These transition alterations have the potential to affect *S. parksii* population growth.

To investigate the indirect impacts of herbivory on *S. parksii* population dynamics, we established 32 5mx5m plots. Each plot was randomly assigned one of four fertilizer treatments: control, nitrogen addition, phosphorus addition, and nitrogen and phosphorus additions. One half of each plot was randomly assigned one of two biomass removal treatments: unaltered control and biomass removal during orchid dormancy. Demographic data was collected for individuals within the plots. Plots with phosphorus and nitrogen+phosphorus additions generally differed regarding orchid demographic variables from nitrogen addition plots and unfertilized controls. Also, available light tended to be greater during orchid flowering in plots with biomass removed than in unclipped controls.

A complete understanding of both direct and indirect herbivore impacts on *S. parksii* population dynamics is necessary for effective conservation of this endangered orchid.

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## CHAPTER I

### INTRODUCTION

Herbivores have the potential to substantially alter both plant population dynamics and competitive interactions between species (Hulme 1996, Augustine and McNaughton 1998). Removal of plant tissues by herbivores may reduce plant fitness, altering the subsequent population structure. However, plants have evolved under herbivore pressure and may have compensatory adaptations for dealing with the stress of herbivory (Rosenthal and Kotanen 1994). Selectivity of herbivores plays a role in community structuring by herbivory. Those plants selected frequently by herbivores decrease under heavy herbivory, giving unselected plants a competitive advantage (Marquis 1992). The extent and direction of changes in population dynamics and community competitive interactions, however, is particular to the species and environment in which it is located (Olf and Ritchie 1998).

Given the complexity of plant responses to herbivores, and the importance of these responses to population dynamics and competitive interaction, understanding plant-herbivore interactions is vital to developing a body of knowledge useful for conservation of an endangered species (Bevill et al. 1999). Experimental manipulation of herbivory can help to determine the impacts of herbivores on plant abundance, distribution, dynamics, and interactions, and should be the basis for management strategies aimed at conservation of rare plants.

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This thesis follows the style of Ecology

CHAPTER II  
BIOLOGY, ECOLOGY, AND CONSERVATION OF NAVASOTA LADIES'  
TRESSES (*SPIRANTHES PARKSII* CORRELL), AN ENDANGERED TERRESTRIAL  
ORCHID OF TEXAS

**Introduction**

Navasota Ladies' Tresses (*Spiranthes parksii* Correll) is a federally listed endangered species which is endemic to east-central Texas (USFWS 2006). It occurs in thirteen Texas counties (Figure 1) with ninety-three percent of known population sites in Brazos and Grimes counties, two counties in the Brazos River Valley of east-central Texas (TMPA 1991)(Figure 1). This percentage is considered to be inflated due to the high concentration of survey efforts in this area. Oil, natural gas, lignite, and other developments, as well as urban expansion and exurban development pose significant threats to *S. parksii* populations(USFWS 2006).

Our goal is to provide an outline for future scientific study and subsequent management aimed at developing a more complete baseline of ecological data, including environmental factors responsible for regulating *S. parksii* population dynamics and distribution.

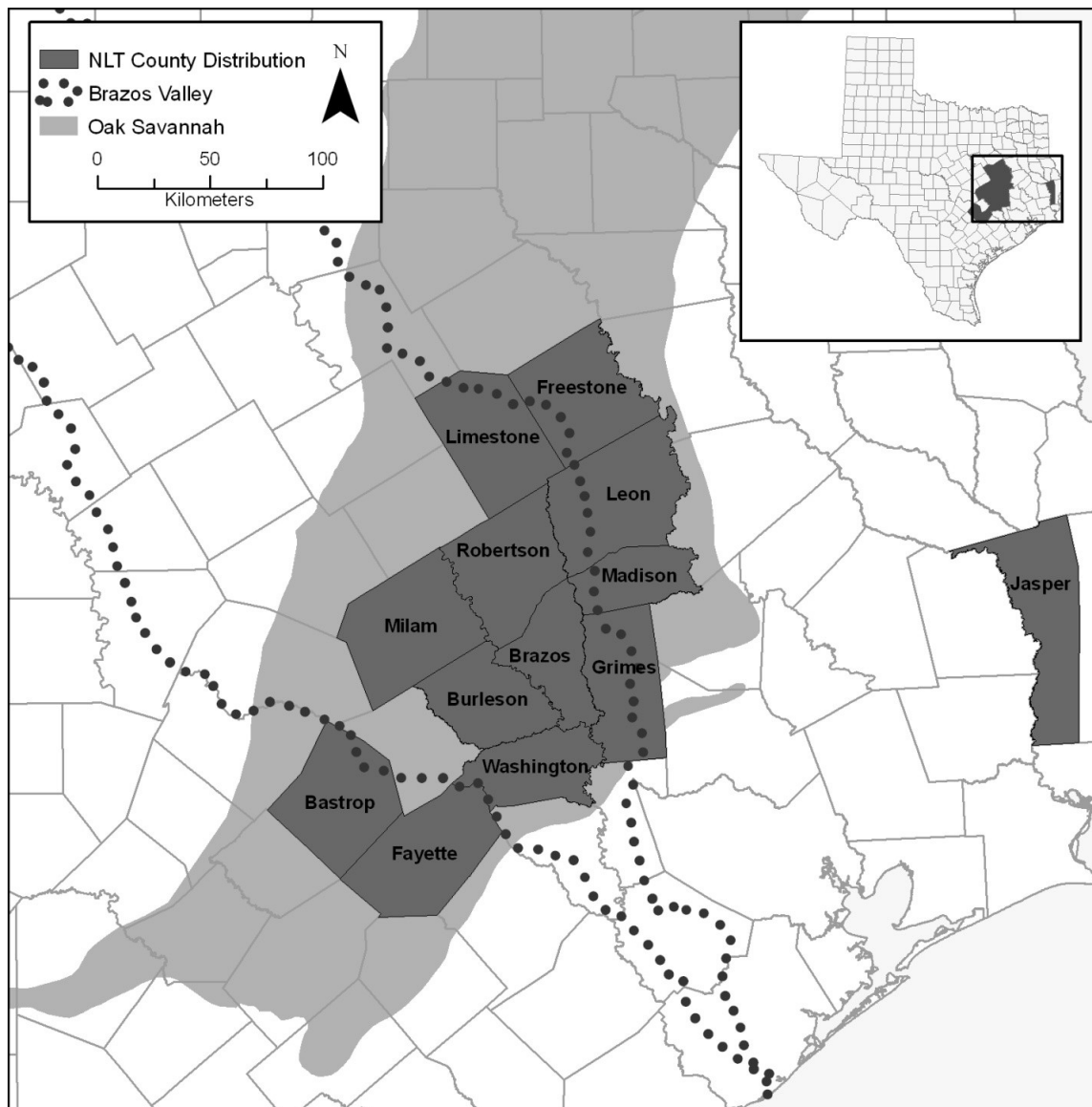


Fig. 1. Distribution of *Spiranthes parksii* populations.

### ***S. parksii* Biology**

#### *Description*

*Spiranthes parksii* has a leafless flowering stem 15 to 30 cm in height terminated by a 3 to 7 cm flowering spike composed of up to four ranked coils of flowers spiraling

counterclockwise around the stalk (Figure 2). Bracts with whitish tips subtend the flowers which have obovate petals and dentate lip margins (Luer 1975, Poole et al. 2007). The flowers extend horizontally from the rachis and the dorsal sepal extends beyond the petals and curls upward at the apex. The lateral sepals hug the corolla and extend slightly beyond the dorsal sepal, curved up at the ends like horns (Sheviak 1991, Pelchat 2000). *S. parksii* may have a green stripe on the inner petals between the dorsal and lateral sepals, and a creamy color. The basal rosette has 1-5 lance-like to elliptical leaves and does not usually occur simultaneously with a flowering spike, but may emerge as the flower senesces (Figure 3).



Fig. 2. *Spiranthes parksii* flowering stalk.

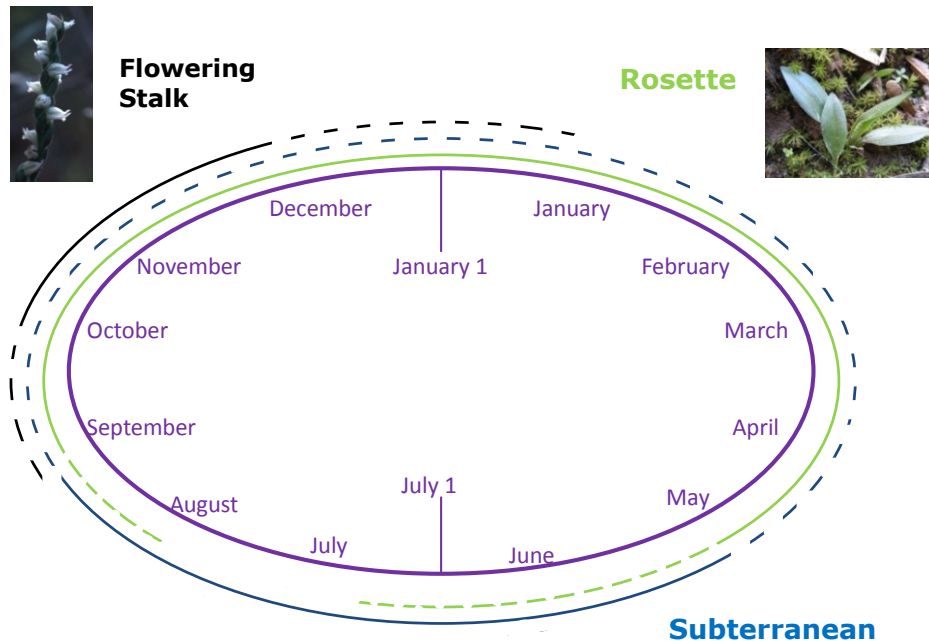


Fig. 3. Timing of *Spiranthes parksii* life cycle (Solid lines depict the average timing. Dashed lines depict the range of timing possible.)

*Spiranthes parksii* is sympatric with *Spiranthes cernua*, *Spiranthes lacera* var. *gracilis*, *Spiranthes sylvatica*, *Spiranthes vernalis*, and *Spiranthes praecox* throughout its range. These species are distinct from *S. parksii* with the exception of *S. cernua* which has undulate lip margins, white petal color, dorsal sepals similar in length to the petals, flowers that often droop from the rachis, and bracts often lacking white tips. Vegetatively, *S. parksii* and *S. cernua* appear identical, which poses difficulties for distinguishing the endangered orchid from its more abundant congener when only rosettes are present.

### *Life History*

*Spiranthes parksii* is perennial. It produces basal rosettes between September and May with peak leaf size generally occurring from late February to early March. Rosettes usually disappear by mid-May, but in wet, cool years, they may persist well into the summer months. *S. parksii* flowers may emerge as early as September, but generally emergence peaks in October, with anthesis and fruiting in October or November and seed dispersal generally occurring in December (USFWS 1984, Hammons 2008) (Figure 3). The plants survive underground from about April or May until September as fleshy tuberous roots with no aboveground leaves, stems, or flowers (Figure 4). *S. parksii* leaf production and flowering are variable. Hammons et al. (2010) found 20% of permanently marked unknown *Spiranthes* rosettes (both *cernua* and *parksii*) flowered in 2007, only 5% in 2008, and even fewer in 2009. Similarly 63% of the same marked individuals produced basal rosettes in 2008 and only 35% in 2009.

Current observations and data suggest radical population fluctuations (USFWS 1984, TMPA 1991). However, this may reflect the variability of leaf and flower production of individuals and not actual fluctuations in numbers of *S. parksii* present, since below ground structures of individual plants can persist for several years without producing flowering stems or rosettes.

### *Reproduction*

*Spiranthes parksii* can reproduce both sexually and asexually (Catling and McIntosh 1979, Sheviak 1982). Glucose-rich secretions near the lip of the flower may





Fig. 4. *Spiranthes parksii* tuberous root.

attract pollinators (Catling and McIntosh 1979), and observations of visits to *S. parksii* flowers by honey bees and bumble bees, suggests that pollen dissemination by insects occurs; however, detailed examinations of potential pollinators have not yet been conducted. Long-tongued bumble bees are important pollinators of other *Spiranthes* species (Larson and Larson 1990), and *S. parksii* shares a similar morphology with these bee-pollinated species, such as protandrous flowers and easily detachable pollinia, which adhere to viscid stigmata (Catling 1982b). The widely-spaced, patchy distribution of *S. parksii* likely limits cross pollination among isolated populations.

A high percentage of polyembryonic seeds (80-90%) in *Spiranthes parksii* suggests that 7rotocor (asexual seed production) may be the primary mode of reproduction (Sheviak 1976, Catling and McIntosh 1979, Catling 1982a). *S. cernua*, the

potentially close relative of *S. parksii*, exhibits high levels of apomixes (Sheviak 1982). Both species may reproduce primarily through adventitious embryony in which a sporophyte is proliferated from the parent ovular tissue (Sipes and Tepedino 1995). High levels of 8rotocor have been found to correspond to low occurrence of pollinators (Manning 1981, Lloyd 1988). *Spiranthes* generally have fewer pollinators than other orchids (Tremblay 1992), and Schmidt and Antlfinger (1992) found pollinator limitation to occur for *S. cernua* at the edges of its range. The high level of 8rotocor in *S. parksii* may also be an adaptation to low abundance of pollinators throughout its limited range.

#### Seed Dispersal and Recruitment

Orchid seeds are primarily dispersed by wind, water, and animal contact (Arditti 1967b). They are small with thin seed coats and impermeable testae that contain air bubbles. These features make air and water dispersal particularly effective (Arditti 2000). Little is known about *Spiranthes parksii* dispersal, but their patchy distribution suggests a limited dispersal shadow. The tiny size of *S. parksii* seeds suggests dispersal by wind and water, and given the proximity of many populations to game trails, dispersal through epizoochory is possible. Endozoochory is not a likely mode of dispersal for *S. parksii*. While herbivory of *S. parksii* flowering stalks by deer, rabbit, feral hog, and livestock appears to be significant, much of the observed herbivory occurs before anthesis suggesting that substantial dispersal by herbivores is not likely. Understanding dispersal in *S. parksii* is crucial to its conservation since the survival of local populations in extremely fragmented landscapes may depend on long-distance dispersal of seeds (Ozinga et al. 2004).

Seeds of *Spiranthes parksii* have no endosperm. Therefore, 9rotocorm development can only occur after penetration of the seed by mycorrhizae (Wells 1981b). This symbiotic relationship between the plant and the mychorrizal fungus continues throughout its life. *Spiranthes* generally have multiple symbionts but all are saprophytic. There is some seasonal variation in the amount of infection as the fungi move in sequestration of resources. While *S. cernua* within the range of *S. parksii* have been discovered to have associations with three anamorphic genera of fungi, *Ceratorhiza*, *Monilopsis* and *Epulorhiza*, *S. parksii* appear to associate with only one, *Epulorhiza* (Ariza 2010). The degree of specificity between *S. parksii* and mychorrizal fungi warrants further investigation as fungal distribution is likely an important factor determining its distribution and recruitment (Rasmussen and Rasmussen 2007).

Flowering *Spiranthes parksii* show high fungal infection in the middle of the root and decreasing infection along the periphery (Ariza 2010). Isolation and identification of mycorrhizae associated with *S. parksii* throughout its life cycle as well as determination of seasonal variation could aid in understanding *S. parksii* distribution. Dynamics of litter decomposition potentially drive the distribution of *S. parksii* because of their impact on the fungal substrate which might drive the distribution of the symbiont required for *S. parksii* seedling development and resource acquisition (Batty et al. 2002).

While germination has been observed *in situ* after eight weeks (Hammons 2010), the amount of time the *Spiranthes parksii* seedling remains underground as a mycorrhizome is unknown. This stage has been determined to last two to four years on average for orchids in general and about two years for the closely related *S. cernua*

(Rasmussen 1995). The length of time before first rosette formation is variable among orchids and related to the amount of carbon storage in root tubers. The number of root tubers on an individual *S. parksii* which has produced a rosette, generally varies between two and eight (Hammons et al. 2010) (Figure 4). Hammons et al. (2010) also found a positive, correlation between total leaf length and total root tuber length for *Spiranthes* (both *parksii* and *cernua*) rosettes, suggesting a strong relationship between below-ground carbon stores and the production of above-ground structures.

### **Ecology**

The climate throughout the range of *Spiranthes parksii* is mild with a mean annual temperature of 19-20 °C with mean annual precipitation between 914 and 1016 mm (Bomar 1983). Summers are hot and humid and winters are cool with infrequent freezing temperatures. Elevations range from 60 – 110 m with flat to gently sloping terrain and deep acidic, sandy, or loam soils from parent material of recent alluvial deposits or Tertiary sandstone (SCS 1979).

*Spiranthes parksii* flowering appears linked to rainfall. Parker (2001) found rainfall 8-10 weeks before flowering in August and September to increase numbers of *S. parksii* which flower during a given year. Wilson (2002) also found that increased spring and fall rainfall led to greater numbers of flowering *S. parksii*. Hammons (2008) found August rainfall to positively correlate with number of flowering *S. parksii*.

*Spiranthes parksii* is found in upland post oak woodlands and savannas with grassland patches, often along the stream banks of upland tributaries of the Navasota and Brazos River drainages (USFWS 2006). They are most often found in lightly forested

post oak savanna at the edge of upland drainages or along drip lines at the interface between wooded and adjacent grassland patches, although individuals may be found in more open, grassland areas. When found in large grass patches, the plant may have established prior to clearing of woody vegetation and persisted for long periods. Although previously thought to be rare in frequently disturbed areas, *S. parksii* seems to be abundant along game and cattle trails, and is found along fence rows and power line rights-of-way (Wilson 2002), which suggests the importance of either periodic disturbance or relatively high levels of light. Hammons (2008) found that *S. parksii* is likely to occur with some leaf litter, but is more often found in thin rather than thick litter cover. *S. parksii* generally occurs in areas with moderate to high (41-100%) shade. However, it is possible that their establishment in areas of high shade occurred prior to canopy closure and subsequent reductions in light levels.

Bai and Smeins (2007) categorized 800 soil mapped and GPS located plants from the USFW/TPWD files by geologic formation and soil series. They found *Spiranthes parksii* occurring on 15 geologic formations, (primarily Manning and Wellborn), and 29 soil series, (primarily Burlewash, Elimina, Singleton, Shiro, Arol, and Burlewash-gullied). However, these data may be biased by search efforts concentrated in the areas of documented occurrence. Also, neither plant locations nor soil/geology locations were field-checked. Nonetheless, when surveying in the vicinity of mapped Manning or Wellborn geologic formations on Burlewash, Elimina, Singleton, Shiro, Arol, and Burlewash-gullied soils there is increased likelihood of *S. parksii* occurrence.

### *Genetics*

The species status of *Spiranthes parksii* has recently been questioned. Both Walters (2005) and Dueck and Cameron (2007) found little genetic difference between *S. cernua* and *S. parksii* upon examination of DNA sequencing and AFLP microsatellite marker data. *S. cernua* is a compilospecies which exhibits considerable morphological variability. However, Manhart and Pepper (2007) state that a lack of genetic variation between *S. parksii* and *S. cernua* AFLP markers is not proof that *S. parksii* is not a unique species. They view clear morphological and ecological differentiation to be evidence of genetic differences which they failed to detect due to the limited sample of loci explored. Recent reevaluation by the U.S. Fish and Wildlife Service of *S. parksii* status and recovery has declared that *S. parksii* will continue to retain species status until conclusive evidence establishes synonymy of *S. parksii* and *S. cernua* (USFWS 2009).

### *Conservation*

Formal consultation under Section 7 of the Endangered Species Act has resulted in the creation of 24 protected reserves for *Spiranthes parksii*. However, five of these areas are not yet permanently protected, and all are relatively small isolated tracts of land (USFWS 2009). The potential impact of fragmentation on *S. parksii* is unknown. Given the potential for fragmentation to modify environmental conditions (Saunders et al. 1991, Murcia 1995) and the likelihood that species occurring within limited ranges are more likely to be extirpated by extensive habitat destruction (Rabinowitz 1981), it is important to evaluate the effectiveness of this system of small reserves in maintaining adequate populations of *S. parksii*.

Formal consultation has occurred in conjunction with all state or municipal development projects. In addition to preserve creation, Section 7 requires scientific study, as well as the monitoring of populations in the preserves (USFWS 2009) and has also resulted in a requirement of land management in most permanent preserves. However, proper land management activities must first be determined through scientific study. Also, the development of a system for protection of *Spiranthes parksii* on private lands would aid in the conservation of the species, as The Endangered Species Act confers little protection to endangered species on private land and much of the land in east-central Texas is privately owned.

Development of successful transplant methods by Hammons et al. (2010) may reduce losses of *Spiranthes parksii* populations to continued development. They have shown post-transplant production using a soil intact relocation method to be comparable to production of undisturbed plants. They suggest the possibility of improving production in transplanted individuals by relocation of individuals from degraded habitats where they exist as remnant populations to protected areas where the environmental conditions are more favorable. The improvement of greenhouse propagation methods could also decrease losses to development. These techniques could prove invaluable as conservation tools as development continues in *S. parksii* habitat, especially as the constituents of favorable habitat become more fully identified.

Continued exploration of the environmental factors important to *Spiranthes parksii* persistence is crucial in order to develop management strategies, especially in preserves. The post oak savannas of east Texas have become increasingly thickened by

understory brush encroachment. Oak savannas were historically maintained through a combination of factors, including drought, animal browsing, and understory fires (Scholes and Archer 1997). The thickening is hypothesized to be caused by an interaction of climate change, fire suppression, and altered grazing regimes (Archer et al. 1988, Abrams 1992). This is important to *S. parksii* conservation because the increases in woody plant abundance may influence important ecosystem processes (Van Auken 2000, Breshears 2006), alter the composition and structure of the understory (Bowles and McBride 1998), and change the dynamics of understory competition for resources (Nielsen et al. 2003). An understanding of *S. parksii* response to encroachment is necessary to implement effective management. Woody brush removal and maintenance with fire and grazing may be necessary to restore an understory competition dynamic more favorable to *S. parksii*. However, the response of *S. parksii* to fire and grazing is currently poorly understood. Timing of fires may be crucial as burning during flowering or rosette production may reduce *S. parksii* viability. Additionally, given the alteration of the structural components of the ecosystem due to woody encroachment, a reestablishment of the historical fire return interval of one to six years may be ineffective due to substantially reduced understory fuel and the resulting altered fire behavior (VanAuken 2000).

Feral pig disturbance might also have an impact on *Spiranthes parksii* abundance and distribution. Feral pigs are abundant in east-central Texas, and they have the potential to directly alter disturbance regimes and the resulting dynamics of the plant community (Mack and D'Antonio 1998, Siemann et al. 2009). They have been reported



to cause plant death (Kotanen 1995) and root destruction (Singer et al. 1984). Mack and D'Antonio (1998) also report an alteration in arthropod numbers resulting from pig disturbance, which could substantially modify nutrient fluxes within the disturbed community. Siemann et al. (2009) reported increased nitrogen availability in areas disturbed by feral pigs. However, little is known regarding *S. parksii* nutrient requirements and response to soil disturbance. Soil disturbance might facilitate recruitment by offering safe areas of low competition for *S. parksii* establishment. However, this positive disturbance effect might be offset by tuber loss to pig consumption. Understanding *S. parksii* population dynamics in relation to disturbance is necessary to effectively manage *S. parksii* habitat.

## **Conclusions**

*Spiranthes parksii* habitat loss is proceeding rapidly. An understanding of the ecology of the species with an emphasis on factors important to establishment, recruitment, and maintenance is essential for the conservation of *S. parksii*. Limiting resources and responses to disturbance have been increasingly seen as crucial to species conservation (Soule and Kohm 1989, Nielsen et al. 2003).

Unfortunately this species has been viewed as the opponent of progress given the overlap of its range with one of Texas' fastest growing areas of urban and industrial development. The population growth rate was 16% for Brazos county, and 8.7% for Grimes county between 2000 and 2009 (TSDC accessed 2010). Also, construction and extraction in the Brazos Valley is anticipated to increase by 23.4% by 2012 (BVCOG 2010). A more complete understanding of *Spiranthes parksii* population dynamics

informed by continued study of the ecology and biology of *S. parksii* will foster effective conservation which is compatible with human population growth and continued development. This complete understanding must include knowledge of *S. parksii* genetic properties, insight regarding the biotic and abiotic factors regulating *S. parksii* distribution and abundance, the relationship of those factors to disturbance, and the impact of habitat fragmentation on those relationships.

CHAPTER III  
HERBIVORY DISRUPTS THE LIFECYCLE OF AN ENDANGERED ORCHID  
(*SPIRANTHES PARKSII* CORRELL)

**Introduction**

Plant-herbivore interactions can have major influences on the distribution, abundance, and dynamics of plant populations (Crawley 1983). Herbivores consume 18 percent of total yearly terrestrial biomass on average (Cyr and Pace 1993). Consumption of plant reproductive structures and photosynthetic tissues can have long lasting impacts on overall plant fitness (Krupnick et al. 1999). This loss of individual fitness has the potential to translate into reduced population growth rates. This is especially pertinent for rare and endangered species, as small alterations in population dynamics can have disproportionate effects on growth rates for populations with lower numbers of reproducing individuals (Dennis et al. 1991). Any reduction in growth rate has the potential to greatly reduce population viability for endangered species (Brigham and Schwartz 1997).

The adverse impacts of herbivores on individuals, resulting from direct consumption of photosynthetic and reproductive tissues include: decreased growth rates and survivorship (Morrow and LaMarche 1978, Rausher and Feeny 1980, Strauss 1991), lowered fecundity through reduced seed production and decreased lifetime flowering (Doak 1992), and lower recruitment because of seedling mortality (Hulme 1994).

Fecundity is lowered either directly through flower removal, or indirectly through leaf removal. Loss of photosynthetic tissues above a certain threshold will not allow for adequate carbon assimilation for flowering in subsequent years. Individual growth rates and survival can be reduced directly through biomass loss (Ritchie and Tilman 1995, Hulme 1996) or indirectly because of diminished competitive ability (Crawley 1989).

Reduction of growth, fecundity, survival, and recruitment of individuals has the potential to influence plant population dynamics. In a review of herbivore impacts on plant populations, Maron and Crone (2006) found herbivory to decrease population growth rates by 0.06 individuals per unit time on average. While many studies suggest that floral damage has a more pronounced impact on plant population dynamics than leaf removal (Crawley 1989, Krupnick et al. 1999, Strauss et al. 2004), there is much evidence that leaf herbivory can also greatly reduce fitness, resulting in lower population growth rates (Crawley and Ross 1990, Brzosko et al. 2002, Maron and Crone 2006).

The reduced fitness of populations resulting from herbivore consumption is detrimental to many endangered species. Herbivore pressure plays an important role in reducing population viability for many endangered species (Warner and Cushman 2002, Côté et al. 2004, Mesipuu et al. 2009). Consumption lowers population recruitment and growth directly and can also lower a population's resistance to stochastic perturbation. Understanding herbivore impacts on population dynamics of endangered species is invaluable to effective conservation.

The work presented here aims to experimentally determine the impacts of herbivore consumption on an endangered orchid, *Spiranthes parksii* Correll. We

investigated the effects of herbivory on *S. parksii* demographic characteristics and developed deterministic stage structures models to explore the impact of these effects on the *S. parksii* lifecycle and population growth rates.

## **Methods**

### *The Species*

*Spiranthes parksii* Correll is an endangered terrestrial orchid, endemic to Texas. Its current known distribution includes thirteen counties in east-central Texas (USFWS 2009). The main threat to *S. parksii* persistence is habitat loss and degradation associated with urban and exurban development and resource extraction, as it occurs in areas of human population growth.

*S. parksii*, like many terrestrial orchids, experiences a complex lifecycle (Rassmusen 1995). Minute wind or water-dispersed seeds require a mycorrhizal symbiont for protocorm development (Wells 1981a). The orchid persists underground as a mycorrhizome for an undetermined amount of time developing carbon stores adequate for leaf production before producing its first rosette. Once sufficient carbon stores are accumulated, a basal rosette of one to five leaves can emerge anytime from September through May. Some years, an individual will produce a flowering stalk in the fall (USFWS 2009). These are usually leafless, although a basal rosette may develop as the flowering stalk senesces. The flowering stalk matures producing a spike with five to twenty flowers (Poole et al. 2007). A capsule will develop in each flower and will dehisce releasing seeds in November or December. Herbivores consume both flowering stalk and basal rosette tissue. Prominent herbivores of aboveground vegetation

occurring in the range of *S. parksii* include cattle, deer, hogs, rabbits, rodents, insects, and mollusks. The extent of belowground herbivory on *S. parksii* is currently unknown.

### *Study Area*

This research was conducted on a 246ha landfill construction site determined to have a large population of *S. parksii* by the United States Fish and Wildlife Service through an ecological assessment. The site is located in west-central Grimes county (96°8'51.66"W 30°35'47.25"N). As mitigation for the destruction of orchids in the landfill footprint, 56ha of land within the site has been set aside in permanent conservation easements (USFWS 2009). The study plots are located across the site in the footprint and within the deed restricted areas.

The area receives approximately 100 cm of annual precipitation mainly in spring and fall. The summers are generally dry. The average minimum temperature is 4.32 °C and the average maximum temperature is 35.67 °C (SRCC 1971-2000). The site consists of upland areas of post oak savanna with bottomlands of closed canopy oak thickets. The soils are predominantly well drained loamy fine sands and fine sandy loams of the Burlewash series (NCSS 2009). The area was used primarily for moderate grazing and game hunting during the past several decades. Currently there are no cattle on the site, and no hunting has occurred for the past two years. Deer, hogs, rabbits, rodents, and herbivorous insects are found across the study site.

### *Field Methods*

We established 32, 1.5x1.5m plots in areas of high *S. parksii* abundance. Each of the plots was randomly assigned one of two treatments: herbivore exclusion and

control. Herbivore exclusion was implemented by construction of large herbivore exclosures around plots (fencing was used which effectively excluded vertebrate herbivores rabbit-sized or larger). Individual orchids within plots were permanently marked. Demographic parameters such as flowering stalk density, flowering stalk height, number of flowers, rosette density, rosette leaf area, and number of leaves were recorded for each individual located within the plots. Herbivore damage was also recorded for each individual. We employed a ten-day sampling interval during one growing season (from September 27, 2009 to May 9, 2010) in order to carefully track individual life-stage transitions and herbivore damage.

Leaf area was calculated as a function of the length of the longest leaf axis (L) and maximum leaf diameter (d). The equation  $0.7854Ld$  for the area of an ellipse was used given the roughly elliptical shape of *Spiranthes spp.* rosettes. Rosette area was obtained for each individual by adding the leaf area of each leaf present for a given sampling period. The data are reported as plot averages of maximum rosette area obtained per individual. Percent herbivore damage was recorded for each leaf at each time interval by estimating the percent of the leaf removed by consumption. Maximum percent damage was averaged for each plot.

We also explored how herbivory impacts the timing of the *Spiranthes spp.* lifecycle. We recorded the number of days each individual expressed aboveground structures (rosette, flowering stalk, flowers). Total time above ground was also recorded and averaged for all individuals in each plot.

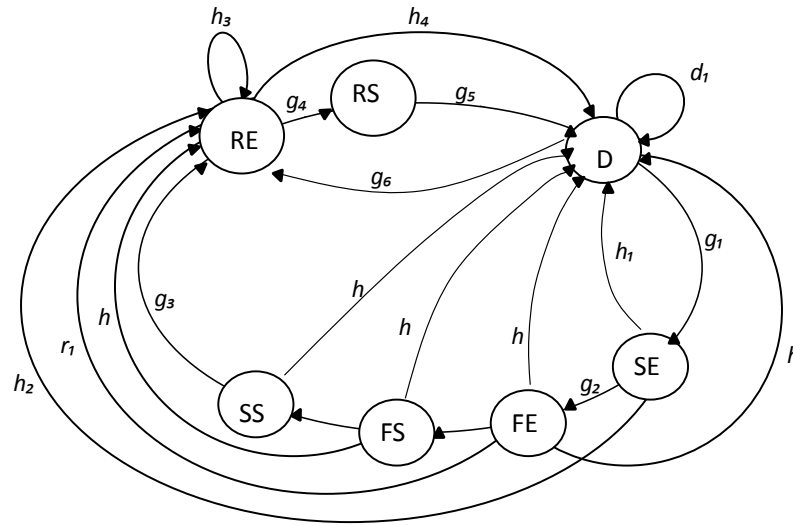
### *Statistical Analysis*

We analyzed these data, log transformed in some cases to attain a normal distribution, with t-tests, and fisher's exact tests (for contingency tables) to determine direct herbivore impacts on demographic characteristics. We used life stage transition proportions to parameterize deterministic life-stage matrix models in order to explore herbivore impacts of *S. parksii* population dynamics. *S. parksii* occurs on this site with its congener *Spiranthes cernua*. These two species are vegetatively indistinguishable. We report the data as it pertains to *Spiranthes spp.* because most individuals did not flower during the duration of the study, rendering it impossible to definitively identify individuals to species (of the 272 individuals included in the study, there are 57 *S. parksii*, 3 *S. cernua*, and 212 unknown *Spiranthes*). However, *S. parksii* and *S. cernua* exhibit similar life cycles, and any impacts documented for the two species combined are likely conservative compared to the impacts for *S. parksii* alone.

### *Models*

We used transition probabilities and demographic data to present the *Spiranthes spp.* lifecycle in a stable-stage matrix model (figure 5). This matrix was used to model population dynamics and project population growth rates ( $\lambda$ ) and determine the contributions of the matrix elements to  $\lambda$ . Population growth rates are expressed as the dominant eigenvalue of the matrix (Caswell 2001). Elasticities can be calculated based on the dominant eigenvalue to determine the importance of each transition to that eigenvalue (de Kroon et al. 1986).





	D	SE	FE	RE	RS
D	$d_1$	$h_1$	$0$	$h_4$	$g_5$
SE	$g_1$	$0$	$0$	$0$	$0$
FE	$0$	$g_2$	$0$	$0$	$0$
RE	$g_6$	$h_2$	$r_1$	$h_3$	$0$
RS	$0$	$0$	$0$	$g_4$	$0$

Fig. 5. Stage-transition graph and matrix for *Spiranthes sp.* The stages are dormant (D), flowering stalk emergence (SE), flower emergence (FE), rosette emergence (RE), and rosette senescence (RS). Arrows in the graph refer to possible transitions from one stage to the next, and their labels represent the proportion of individuals moving or contributing to the stage the arrow points to. The mechanisms of the transitions are growth ( $g$ ), herbivory ( $h$ ), dormancy ( $d$ ), and reproduction ( $r$ ).

Growth (*g*) herbivory (*h*) and dormant (*d*) transitions were parameterized using the proportions of plants moving from one stage to the next or remaining in the same stage for each sampling interval. Reproductive I transitions included proportions of individuals moving between stages, but also included the potential contribution of one stage to the next in the form of new individuals. Given the limited duration of sampling to date in this study, we have limited data related to *Spiranthes spp.* fecundity. Data regarding germination rates, recruitment, and duration of dormancy between germination and rosette formation are required to accurately project  $\lambda$  from matrix models, especially for a species with a complicated life history like *Spiranthes sp* (Caswell 1982). Similarly, multiple years of data should be employed in the construction of matrices to explore the impacts of environmental fluctuation on  $\lambda$  using stochastic models (Caswell 2001, Kaye and Pyke 2003). Our goal with these data is not to accurately project  $\lambda$  or determine population viability. We seek only to look at relative impacts of herbivory on growth rates and population viability.

## Results

### *Demographic characteristics*

Average rosette area increased in the protected plots compared with the unprotected plots (Figure 6). The greater maximum leaf area of protected plots is likely the result of decreased herbivory in the exclosures (Figure 7). While leaf area was decreased by herbivory in the unprotected plots, percent-change in rosette density was not different for the two treatments (Figure 8). Herbivores were not frequently removing entire rosettes, but rather, removing substantial proportions of the rosette. In most cases

the rosettes continued to grow following partial removal, but they never attained the maximum leaf area of their uneaten neighbors.

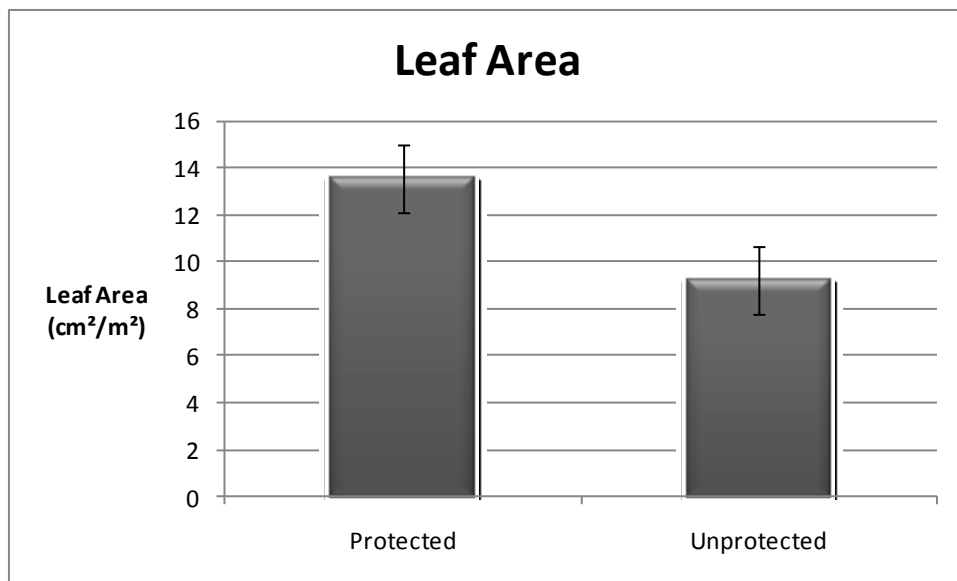


Fig.6. Average maximum leaf area obtained per plot in cm<sup>2</sup> leaf area per m<sup>2</sup>. t-ratio=2.15 p=0.04

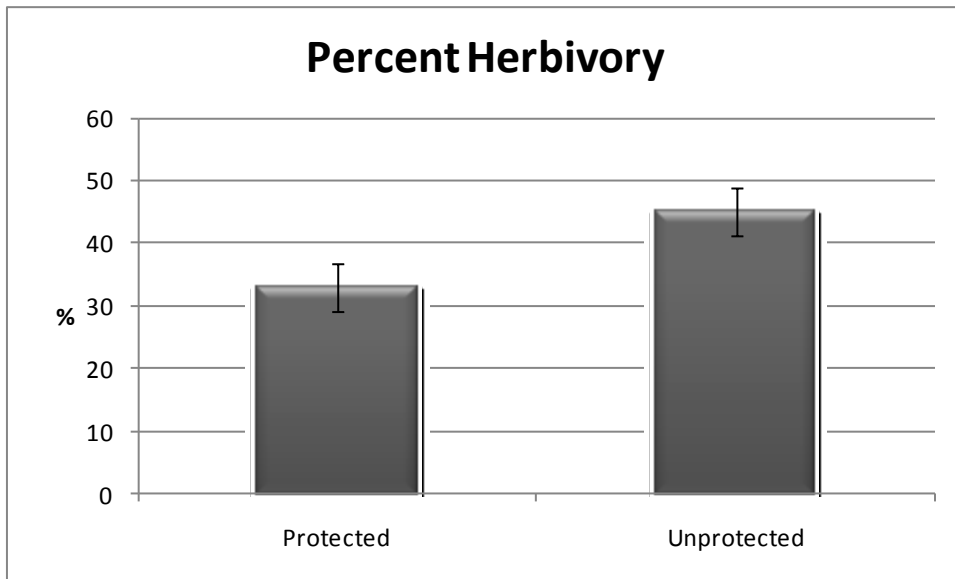


Fig. 7. Maximum percent herbivory damage of rosettes.  $t$ -ratio=-2.27  $p$ =0.04

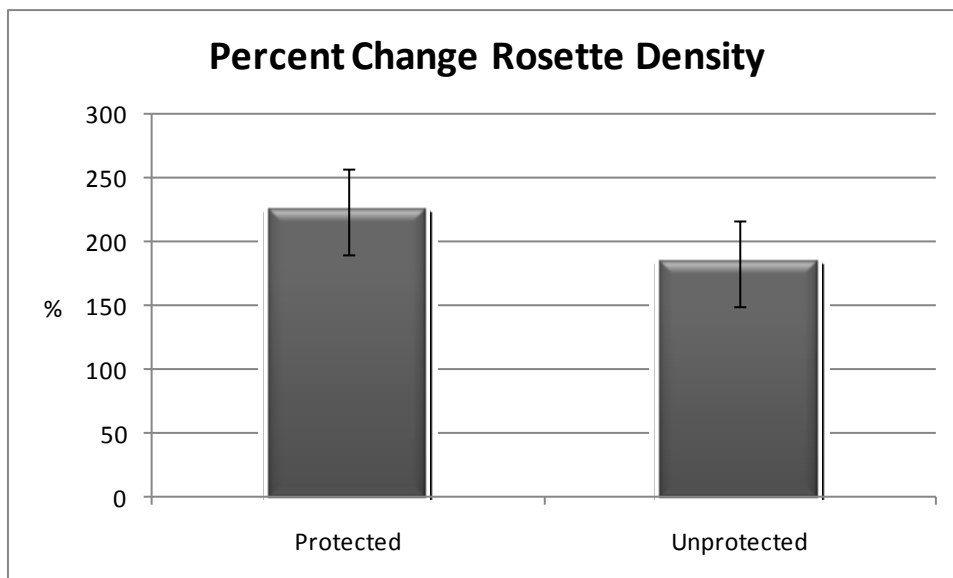


Fig. 8. Percent change in rosette density. Calculated as number of  $((\text{rosettes per m}^2 \text{ at time interval 21}) - (\text{rosettes per m}^2 \text{ at time interval 1})) / (\text{rosettes per m}^2 \text{ at time interval 1})$ . Interval 21 was the interval at which maximum average density was greatest.  $t$ -ratio=0.86  $p$ =0.40

Proportion of flowering stalks producing flowers was significantly decreased in unprotected plots (Figure 9) due to stalk herbivory prior to flower production. Overall, individuals in protected plots expressed above-ground structures longer than those in unprotected plots (Figure 10). Statistical parameters for demographic characteristics are listed in table 1.

Table 1. Statistical parameters for *Spiranthes spp.* demographics

	DF	MSq	MSE	t	p
Leaf Area	30	148.7	32.2	2.15	0.04
Percent Herbivory	30	1157.7	225.6	2.27	0.03
Percent Change Rosette Density	30	13162.5	17981.8	-0.93	0.36
Production of Above-Ground Structures	30	717.0	118.9	2.46	0.02
Number of Flowers	20	123.6	27.7	4.45	0.05

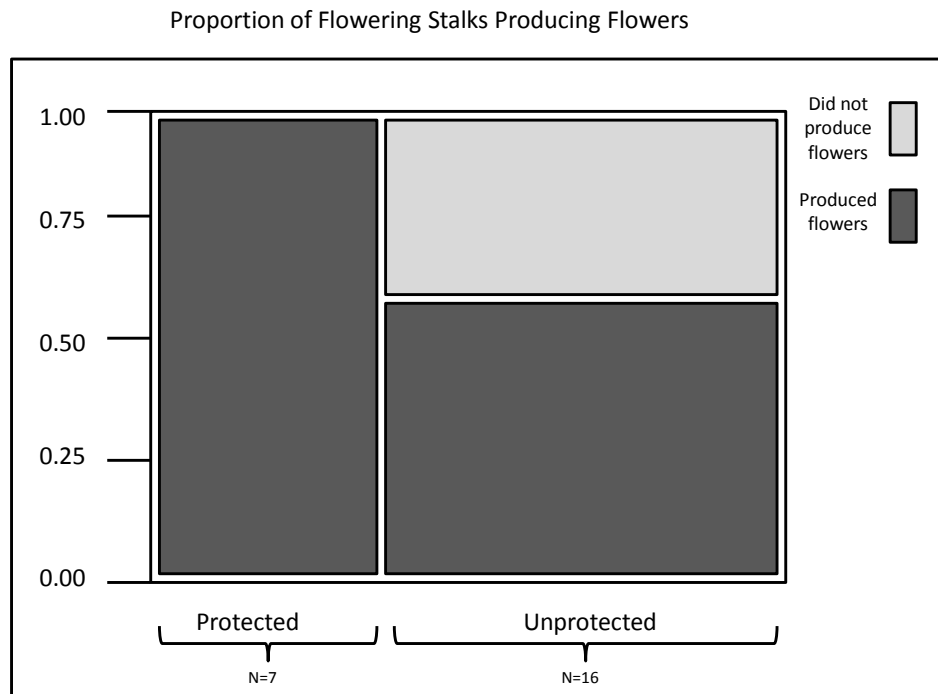


Fig. 9. Proportion of flowering stalks which produced flowers is lower for unprotected plots than for protected plots. This mosaic plot is based on log transformed data (to approximate a normal distribution). Fisher's exact test shows that the probability of producing a flowering stalk is greater for protected than unprotected *Spiranthes spp.*  $P=0.01$

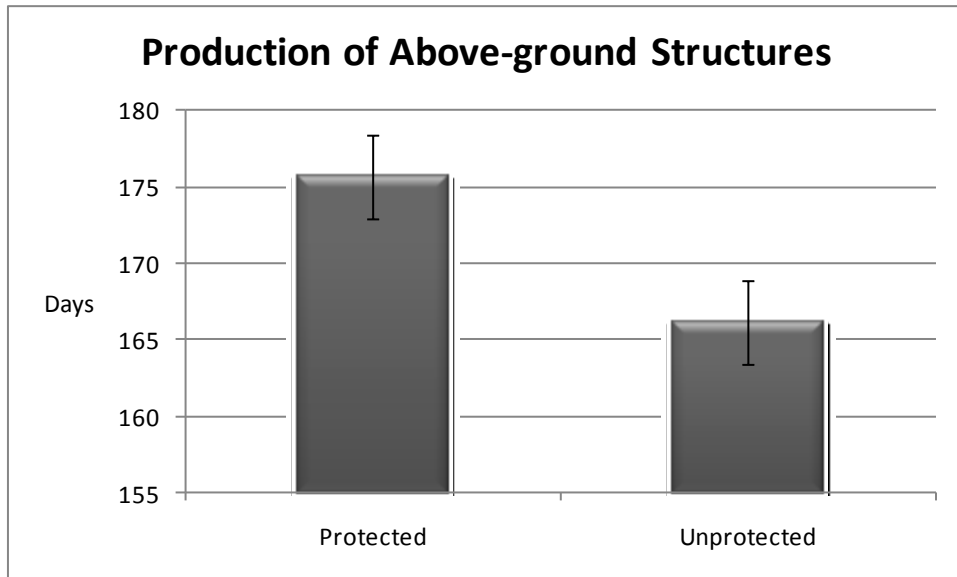


Fig. 10. Average number of days *Spiranthes* spent in above-ground life stages.  $t\text{-ratio}=2.46$   $p=0.02$

### *Life-stage Model*

We used deterministic stage-matrix model in order to explore the relative difference in life cycle transitions for protected and unprotected *Spiranthes spp.* We used a conservative estimate for recruitment of 0.3 individuals per capsule produced. One capsule is produced by each mature *Spiranthes spp.* flower, and each capsule contains thousands of seeds. For purposes of this study, we assume that capsules contain approximately the same number of seeds, although number of seeds produced may fluctuate based on the energy dynamics of the individual. Other potential recruitment rates were explored and each projected similar relative results. *Spiranthes spp.* in protected plots produced a greater number of capsules on average (Figure 11). We included this data in our parameterization of the reproductive transitions.

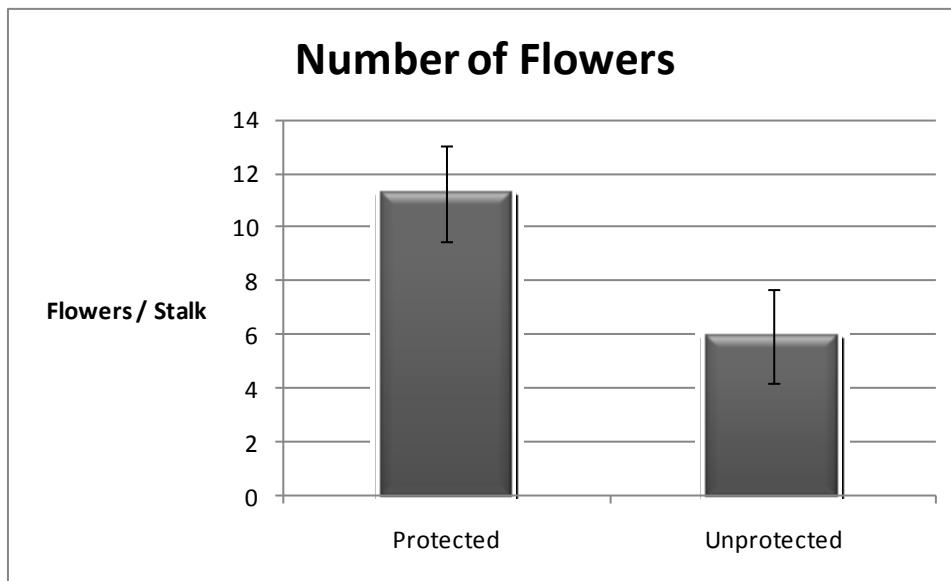


Fig. 11. *Spiranthes sp.* in protected plots produced more flowers on average than those in unprotected plots. Each mature flower contains a capsule, so number of flowers = number of capsules.  $t\text{-ratio}=2.186$   $p=0.05$

We created two matrices, one parameterized with data from the protected plots and the other with data from the control plots (Figure 12).  $\Lambda$  is higher for the matrix parameterized with data from the protected plots ( $1.24 > 1.21$ ). Elasticities also differed for protected and unprotected matrices. Differences in elasticities can be used to illustrate the difference in relative importance of certain transitions (Figure 13). Both matrices showed the dominant transitions to be D-RE-RS-D. However, RE-RE contributed more to  $\lambda$  for protected orchids, and RE-D contributed more for unprotected orchids. The RE-RE transition results from herbivory of rosettes resulting in reemergence of rosettes. Where rosettes reemerged and were eaten again, which happened more often in unprotected plots, they did not often reemerge a second time. This is expressed in the strong RE-D contribution to  $\lambda$  in unprotected plots.



	Protected					Unprotected					
Projection Matrix											
	D	SE	FE	RE	RS		D	SE	FE	RE	RS
D	0.18	0	0	0.08	1	D	0.23	0	0	0.25	1
SE	0.07	0	0	0	0	SE	0.11	0	0	0	0
FE	0	0.86	0	0	0	FE	0	0.69	0	0	0
RE	0.84	0.14	3.30	0.56	0	RE	0.76	0.31	1.8	0.42	0
RS	0	0	0	0.83	0	RS	0	0	0	0.75	0
$\lambda=1.24$						$\lambda=1.21$					
Elasticity											
	D	SE	FE	RE	RS		D	SE	FE	RE	RS
D	0.04	0	0	0.03	0.22	D	0.06	0	0	0.07	0.19
SE	0.03	0	0	0	0	SE	0	0	0	0	0
FE	0	0.03	0	0	0	FE	0	0.03	0	0	0
RE	0.21	0.01	0.03	0.20	0	RE	0.22	0.01	0.03	0.14	0
RS	0	0	0	0.22	0	RS	0	0	0	0.19	0

Fig. 12. Stage-based matrices for *Spiranthes sp.* protected from large herbivores and unprotected. The projected population growth rate  $\lambda$  was calculated for each matrix. Elasticities were calculated for each matrix as well. They show the relative importance of each matrix component to the dominant eigenvalue ( $\lambda$ ). The stages are dormant (D), flowering stalk emergence (SE), flower emergence (FE), rosette emergence (RE), and rosette senescence (RS).

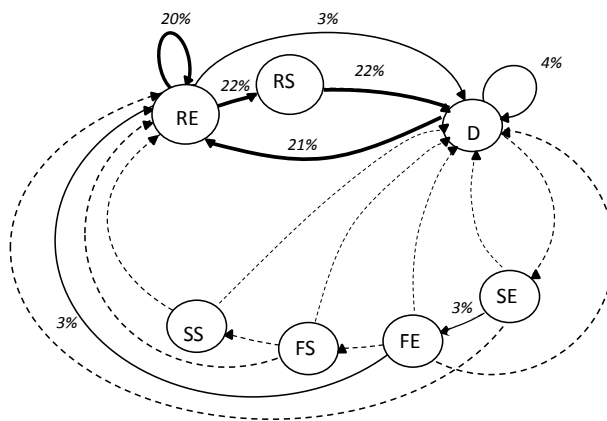
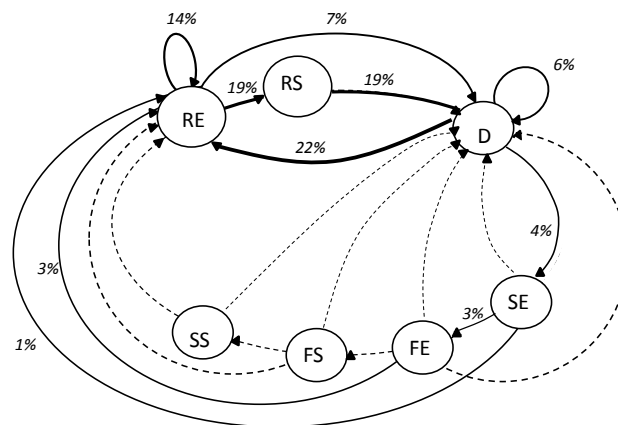
Life-stage Graph for Protected *Spiranthes sp.*Life-stage Graph for Unprotected *Spiranthes sp.*

Fig. 13. Life-stage diagrams for protected *Spiranthes sp.* (above) and unprotected *Spiranthes sp.* (below). The numbers on the arrows indicate the elasticities of the transition. Thicker arrows represent transitions with higher relative contributions to  $\lambda$ . Dotted arrows represent transitions which did not contribute to  $\lambda$ . The stages are dormant (D), flowering stalk emergence (SE), flower emergence (FE), rosette emergence (RE), and rosette senescence (RS).

The reproductive pathway (FE-RE) contributed equally to  $\lambda$  for both protected and unprotected plots. However, the herbivory transition SE-RE contributed to  $\lambda$  in unprotected plots, but not protected plots, rendering D-SE important in unprotected plots as well, suggesting the lower  $\lambda$  in unprotected plots is at least partially driven by a higher incidence of flowering stalk herbivory (Figure 13).

By comparing the unprotected plots (which experience both small and large herbivore impacts), and the protected plots (which experience only small herbivore impacts), we created a hypothetical matrix which represents the herbivory impacts of large herbivores on *Spiranthes spp.* (Figure 14). The elasticities calculated from this matrix highlight the transitions most affected by large herbivore browsing. This allows us to explore herbivore impacts attributable to large herbivores and compare those to the herbivore impacts of small herbivores (represented by the protected matrix.)

The relative importance of the transitions for the matrix associated with large herbivore consumption differs from both protected and unprotected matrices. The most notable difference is the large increase in importance in the RE-D transition, which suggests that rosette herbivory by large browsers strongly affects population growth rates. This is also seen in the reduced importance of the RE-RS and RS-D stages. Moreover, the relative contribution of SE-FE and consequently FE-RE is slightly lower, likely as a result of large herbivore removal of flowering.

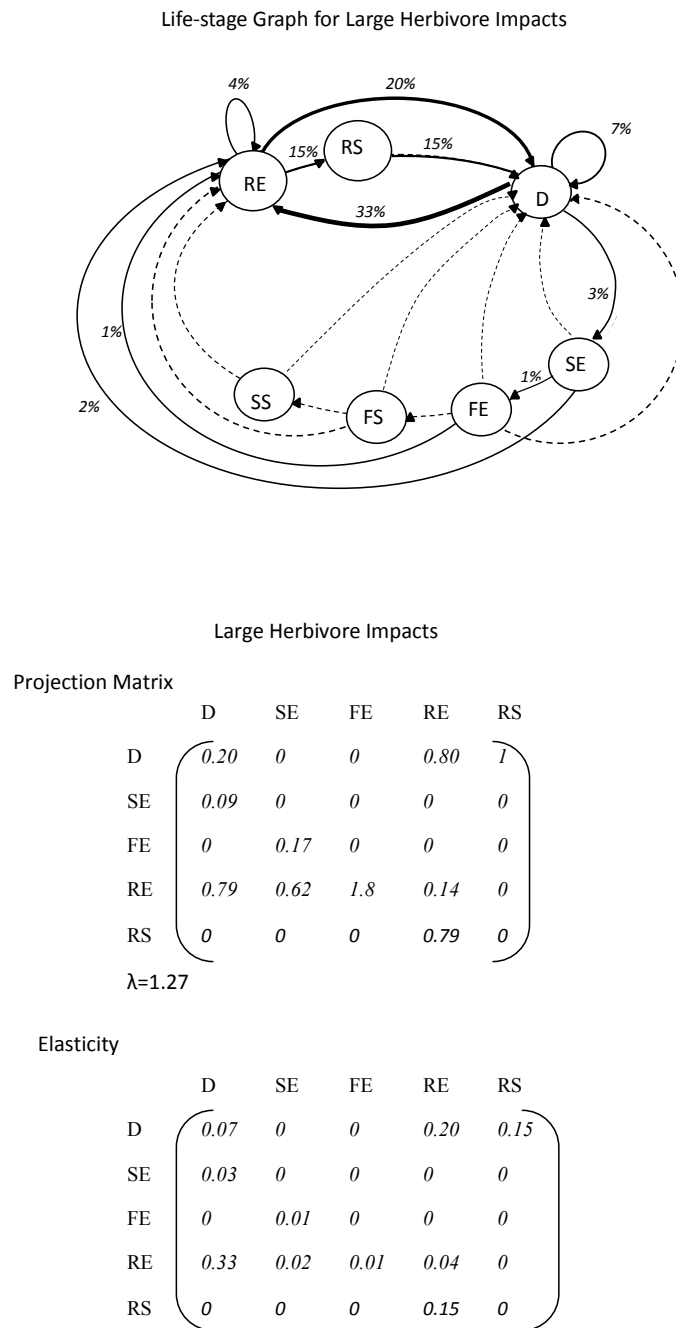


Fig. 14. : Life-stage matrix and elasticities exploring large herbivore impacts on *Spiranthes sp.* (above). Transition diagram showing relative contributions of transitions to  $\lambda$ . Thicker arrows represent greater contributions. Dotted arrows represent no contribution. The stages are dormant (D), flowering stalk emergence (SE), flower emergence (FE), rosette emergence (RE), and rosette senescence (RS).

## Discussion

Significant herbivore reduction of *Spiranthes spp.* rosette leaf area could potentially lead to a reduction in carbon stores for flower production in subsequent growing seasons. This reduced flowering could lower population fecundity, with population growth rates decreasing as a result. Some plants exhibit compensatory growth as a result of herbivore tissue consumption (McNaughton 1983, Trumble et al. 1993). This does not seem to have occurred for *Spiranthes spp.* given the lower maximum leaf areas attained in plots with higher percent herbivory.

Flowering was also affected by herbivore consumption. Only 21 orchids flowered during the data collection period. All of the orchid flowering stalks lost to herbivory were eaten before flower production. This has serious implications for fitness. Herbivores are removing reproductive structures before they have time to flower and produce seeds. These lost reproductive structures act as a sink for carbon reserves, reducing carbon available for the rest of the life-cycle with no positive reproductive value.

Despite the small number of whole rosettes removed by herbivory, *Spiranthes spp.* senescence occurred earlier in the growing season on average in plots where higher herbivory occurred. This could potentially impact the fitness of *Spiranthes spp.* by reducing carbon acquisition, and the resulting stores available for reproduction in subsequent growing seasons.

Decreases in population growth rates for *Spiranthes spp.* in unprotected plots suggest that the increase in leaf area, and time above ground resulting from greater

herbivore damage translates to alteration of population dynamics and reduced population viability. This alteration in the life cycle is highlighted by the differences in the relative contributions of transitions to population growth rates resulting from herbivory.

Increases in herbivore pressure over time may serve to reduce the growth rate even further, threatening the population (which could potentially already have a negative growth rate) with extinction. The deed restricted areas at the study site are designed to serve as a refuge for *Spiranthes parksii*. With the cessation of hunting on this land, the potential for population growth in these conservation areas might be limited by increasing large herbivore impacts.

While flowering stalk herbivory does play a role in the reduction of population growth rates, the transition elasticities suggest that rosette herbivory also contributes substantially to population growth rates. These findings comport with many studies showing that the best indicator of leaf area in one year is the prior year's leaf area (Bevill et al. 1999, Kindlmann and balounova 1999, Janecková et al. 2006). Reduced accumulation of carbon due to reduced leaf area for photosynthesis can create a negative feedback loop by which leaf area in a population experiencing heavy yearly herbivory is constantly declining (Huntly 1991, Whigham and Chapa 1999). This suggests that rosette herbivory can have long lasting fitness effects. By comparing the impacts of large and small herbivores we demonstrate that large herbivore rosette consumption plays a far more important role in population growth than small herbivore rosette consumption. Similarly, small herbivore disruption of reproductive processes by

removal of flowering stalk prior to flowering does not occur with enough frequency to affect population growth rates while large herbivore disruption does.

The identity of the herbivore is also important to determining the impacts of consumption on population fitness (Hulme 1996, Warner and Cushman 2002). Different herbivores may have greater impacts at different stages (Hulme 1994). The large herbivores consuming *Spiranthes spp.* at our study site are likely deer and rabbits, the impacts of other large herbivores on *Spiranthes spp.* could differ substantially. Understanding these plant-herbivore interactions and their timing are crucial to conservation for endangered species. We saw from the elasticities of our models that large and small herbivores affected the various *Spiranthes spp.* life stages differently. Further distinction among the large herbivores and their relative impacts to different stage transitions might aid in the development of effective conservation plans which deal appropriately with the effects of the herbivores having the most crucial impact at each stage of the life history.

## **Conclusion**

Using elasticities to target the important life history pathways is an important tool for developing conservation strategies (Menges 1990, Silvertown et al. 1996, Shea and Kelly 1998). Identifying important pathways creates a target which can focus management objectives, and development of matrix models can be used to evaluate the success of a management option. As management plans are developed for *S. parksii*, the importance of herbivore affects on demographic parameters should be considered, and the impacts of management related to herbivores carefully assessed.

CHAPTER IV  
SIMULATED PULSE GRAZING ALTERS COMPETITIVE INTERACTIONS AND  
DEMOGRAPHIC PARAMETERS OF AN ENDANGERED ORCHID (*SPIRANTHES*  
*PARKSII* CORRELL)

**Introduction**

Herbivores affect plant populations directly through consumption of photosynthetic and reproductive tissues (Crawley 1983). In addition to direct herbivore impacts, abundance, distribution, and population dynamics can also be affected indirectly through habitat alteration and a subsequent restructuring of competitive interactions (Pacala and Crawley 1992, Rees et al. 2001). This can benefit an individual if a competitor for limited resources is suppressed. Where this is the case, grazing of dominant neighbors may promote flowering and seed set of unconsumed species by changing microhabitat conditions, such as increasing light availability, and reducing competition for nutrients and water (Mulder and Ruess 1998, Van Der Wal et al. 2000, Coates et al. 2006). Additionally, herbivore activities can increase recruitment by creating a more favorable environment for seedling establishment (Louda 1990, Coates et al. 2006).

While potentially creating more favorable microclimate and competitive conditions for unconsumed plants, grazing can increase the nutrient requirements of the damaged plants, potentially decreasing the availability of resources for undamaged neighbors (Louda 1990, Huntly 1991). Additionally, removal or reduction of the overall



biomass in an area could cause an increase in direct herbivore consumption of previously undamaged species by increasing their visibility in the area for foraging browsers (Milchunas et al. 1988). Both the direction and magnitude of a species' response to removal of competing vegetation by herbivores depends on environmental conditions, including soil nutrient availability (Maschinski and Whitham 1989, Eskelinen 2008).

For some orchid species, abundance and flowering are negatively correlated with biomass of neighboring species (Silvertown et al. 1994). Mowing has positively impacted orchid demographic parameters such as leaf area, individual growth, and frequency of flowering (Coates et al. 2006, Sletvold et al. 2010). Conversely, nutrient additions have had negative effects on terrestrial orchid species (Dijk and Eck 1995). This is primarily assumed to occur as a consequence of reduced root growth and mycorrhizae infectivity following nutrient additions (McKendrick 1996).

Given the complexity of plant-plant interactions, and their mediation by the resource environment, an understanding of plant population responses to indirect herbivore affects along a nutrient gradient is essential to the development of effective conservation strategies for endangered herbaceous plants. The work presented here aims to experimentally investigate the affects of simulated pulse-grazing and altered soil resource conditions on an endangered orchid (*Spiranthes parksii* Correll) in central Texas post oak savannas. We expect to see increased orchid growth and recruitment where competing vegetation is removed due to a reduction in competition and increased light availability. However, if competitive ability is not reduced by grazing, and the

damaged vegetation requires more nutrient inputs, we expect only to see increased orchid growth and abundance if additional nutrients are made available after removal of the neighboring herbaceous vegetation. Any increased orchid growth resulting from biomass reduction of competing vegetation, however, might be offset by browsing due to increased orchid visibility and accessibility. When neighboring biomass is unaltered, we expect lower orchid growth and recruitment where additional nutrients are available, due to increased shading by neighbors fertilized by the nutrient additions.

## **Methods**

### *Focal Species*

Navasota Ladies' Tresses (*Spiranthes parksii* Correll) is a federally listed endangered species which is endemic to east-central Texas. It occurs in thirteen Texas counties with ninety-three percent of known population sites in Brazos and Grimes counties which are located in the Brazos River Valley of east-central Texas. Human population growth and attendant development are increasing throughout the range of *S. parksii*, especially in Brazos and Grimes counties. Oil, natural gas, lignite, and other developments, as well as urban expansion and exurban development pose significant threats to *S. parksii* populations (USFWS 2009).

*S. parksii* is a perennial terrestrial orchid. Individuals produce basal rosettes with one to four leaves between September and May and peak leaf size generally occurs from late February to early March. Aboveground rosette leaves usually senesce by mid-May, but in wet, cool years, they may persist well into the summer months. *S. parksii* flowers may emerge as early as September, but generally emergence peaks in October, with

anthesis and fruiting in October or November and seed dispersal generally occurring in December (USFWS 2009). The plants are dormant from approximately April or May until September as fleshy tuberous roots with no aboveground leaves, stems, or flowers. *S. parksii* leaf production and flowering are highly variable.

*S. parksii* seeds, like many terrestrial orchids, require a mycorrhizal symbiont for protocorm development (Wells 1981a). The symbiotic relationship between orchid and mycorrhizae persists throughout the life of the orchid. The orchid provides carbon to the mycorrhizae which is essential in nutrient acquisition, especially phosphorus (Rasmussen 1995, 2002). Mycorrhizae may also increase orchid water uptake by increasing the surface area of the root tubers (Rasmussen 1995).

#### *Study Area*

This research was conducted on a 246 ha landfill construction site determined to have a large population of *S. parksii* by the United States Fish and Wildlife Service through an ecological assessment. The site is located in west-central Grimes county (96°8'51.66"W 30°35'47.25"N). As mitigation for the destruction of orchids in the landfill footprint, 56ha of land within the site has been set aside in permanent conservation easements (USFWS 2009).

The area receives approximately 100 cm of annual precipitation mainly in spring and fall. The summers are generally dry. The average minimum temperature is 4.32 °C and the average maximum temperature is 35.67 °C (SRCC 1971-2000). The site consists of upland areas of post oak savanna with bottomlands of closed canopy oak thickets. The soils are predominantly well drained loamy fine sands and fine sandy

loams of the Burlewash series (NCSS 2009). The area was used primarily for moderate grazing and game hunting during the past several decades. However, cattle were removed in 2009 and currently there are no domestic livestock on the site.

The study plots are located adjacent to each other in an open oak savanna with little understory brush. Dominant herbaceous vegetation in the study location includes *Chasmanthium laxum* var. *sessiliflorum*, *Schizachyrium scoparium*, *Aristida* sp., *Paspalum* sp., and numerous forbs especially *Asteraceae* sp. Soils sampled from the study area contain 0.8% carbon, 0.07% nitrogen, and 1.5% phosphorus on average.

#### *Field Methods*

We established 32 5mx5m plots with 4m buffer strips between. Each plot was randomly assigned one of four fertilizer treatments: unfertilized control, nitrogen addition, phosphorus addition, and nitrogen and phosphorus additions. We added  $8\text{gm}^{-2}$  of urea to each nitrogen treated plot,  $3.5\text{gm}^{-2}$  of triple super phosphate to each phosphorus treated plot, and both  $8\text{gm}^{-2}$  of urea and  $3.5\text{gm}^{-2}$  of phosphate to each nitrogen and phosphorus treated plot. The fertilizer was added by hand every summer beginning in 2007 before rain events to ensure absorption into the soil. Plots were divided in half, and one half of each plot was randomly assigned one of two biomass removal treatments: control and biomass removal during orchid dormancy. The biomass removal treatment was implemented through clipping all herbaceous biomass to the ground within the subplot annually in August before orchid emergence in October. Biomass was collected, dried and weighed for each plot. Photosynthetically active radiation (PAR) was collected in October during peak flowering at ground level and 1m

above the ground. Orchids located within plots were permanently marked and demographic data were collected. Demographic data include: number of rosettes, rosette length and width, number of flowering stalks, flower height, flower diameter, and number of flowers. These data were collected twice annually (during peak flowering season and peak rosette season) from fall 2007 through spring 2010. In addition to orchid demographic data, we measured PAR from four points within each subplot at two different heights (at ground level and 1m above the ground) yearly each October.

### *Statistical Analysis*

Light and biomass data were analyzed using a split-plot analysis of variance (ANOVA) to explore interaction effects between clipping and nutrient addition as well as individual treatment effects. Leaf area was calculated as a function of the length of the longest leaf axis (L) and maximum leaf diameter (d). The equation  $0.7854Ld$  for the area of an ellipse was used given the roughly elliptical shape of *Spiranthes spp.* rosettes. Rosette area was obtained for each individual by adding the leaf area of each leaf present. The data are reported as plot averages of rosette area. Difference in rosette area was analyzed using Kruskal Wallis tests because the data could not be transformed to meet the assumption of normality. We report the data as they pertain to *Spiranthes spp.* because *S. parksii* occurs on this site with its congener *Spiranthes cernua*. These two species are vegetatively indistinguishable. Many individuals did not flower during the duration of the study, rendering it impossible to definitively identify individuals to species.

To analyze *Spiranthes spp.* responses to treatment, we applied multivariate methods because the low numbers of this rare plant observed precluded the use of more traditional quantitative methods. We performed a canonical correspondence analysis (CCA) of measured *Spiranthes spp.* demographic characteristics constrained by light and biomass measurements. CCA constrains the ordination of a data matrix by a multiple linear regression coefficient of an environmental data matrix. Regression coefficients are calculated as weighted least-squares regressions of plot scores on the light and biomass variables (McCune and Grace 2002). An inertia value is obtained for the ordination which represents the total variance in the demographic data, and the ratio of eigenvalues for each axis to the inertia of the ordination represents the percent of the variance in the demographic data explained by each axis. The dimensions of this multivariate analysis were parameterized with the biannually collected demographic data, including proportions of individuals flowering and producing rosettes each year, proportion of individuals contributing new individuals to each plot (measured as number of newly discovered individuals in a plot divided by the number of known individuals in that plot), flower height (averaged for each plot each year), rosette area (averaged for each plot each year), and number of flowers per stalk (averaged for each plot each year). These data were standardized to the vector length using the equation:

$$Y_{Ai} = \frac{x_{Ai}}{\sqrt{\sum x_{Ai}^2}}$$

$x_{Ai}$  = value of variable I in sample A

This standardization allows for comparison of data measured at different scales by transforming each variable to a comparable unit of measurement.

## **Results**

### *Light*

In 2007, PAR at ground level was higher in unfertilized control plots than in fertilized plots, and higher in nitrogen than phosphorus addition plots. Plots where nitrogen and phosphorus were added together did not differ from plots where these were added individually (Figure 15). As expected, PAR increased in clipped plots for all treatments (Figure 16). In 2008, a significant interaction for light availability occurred between nutrient treatment and clip treatment ( $p=0.05$ ) with the unfertilized, clipped plots having the highest light levels. The unfertilized, unclipped plots had higher light levels than the various nutrient treated plots which were not different from each other (Figure 17). In 2009, PAR was higher in the unfertilized plots than the nutrient treated plots (Figure 18), but there was no difference between clipped and unclipped plots (Figure 19). Table 2 summarizes the statistics for PAR. Unexpectedly, clipped vegetation biomass did not differ by nutrient treatment in any year (Table 3).

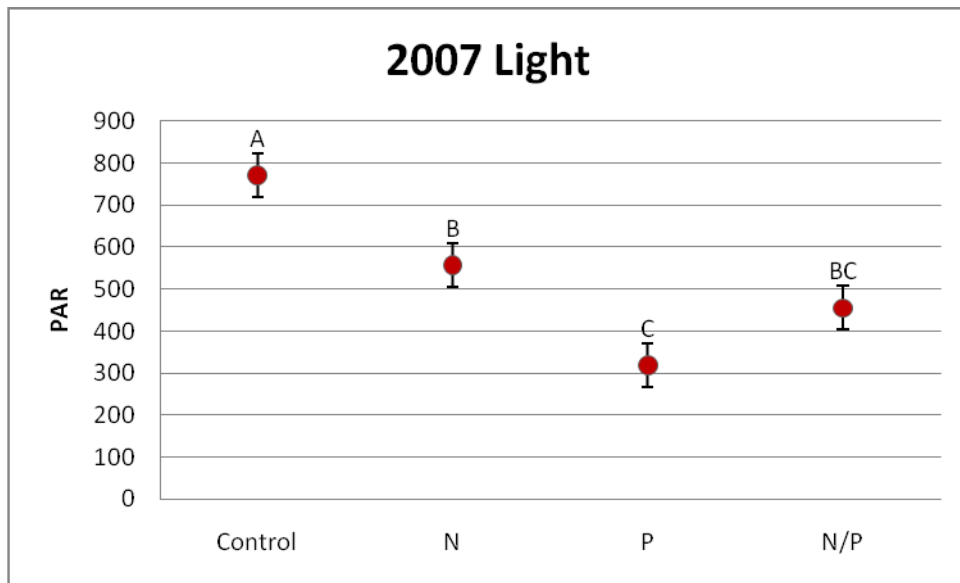


Fig. 15. Analysis of variance (ANOVA) 2007 PAR at ground level by nutrient addition (no interaction effect between nutrient treatment and clip treatment).  $F=13.3$   $P=0.001$

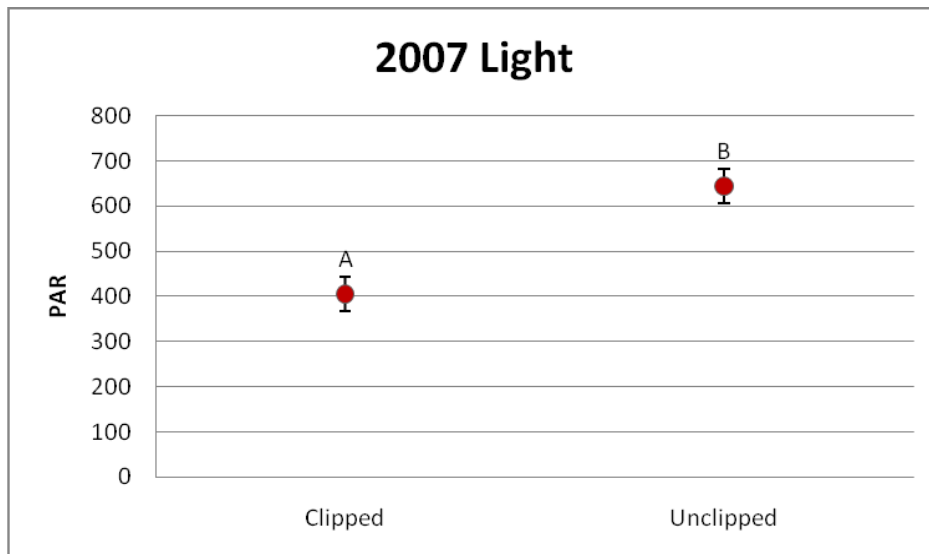


Fig. 16. Analysis of variance (ANOVA) 2007 PAR at ground level by clip treatment (no interaction effect between nutrient treatment and clip treatment).  $F=20.2$   $P=0.001$



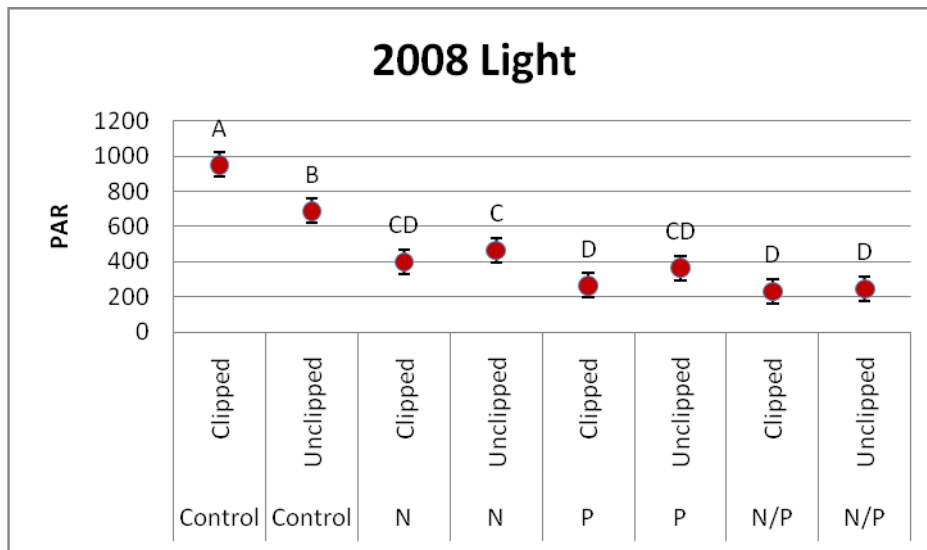


Fig. 17. Analysis of variance (ANOVA) 2008 PAR at ground level by nutrient addition and clip treatment.  $F=2.7$   $P=0.05$

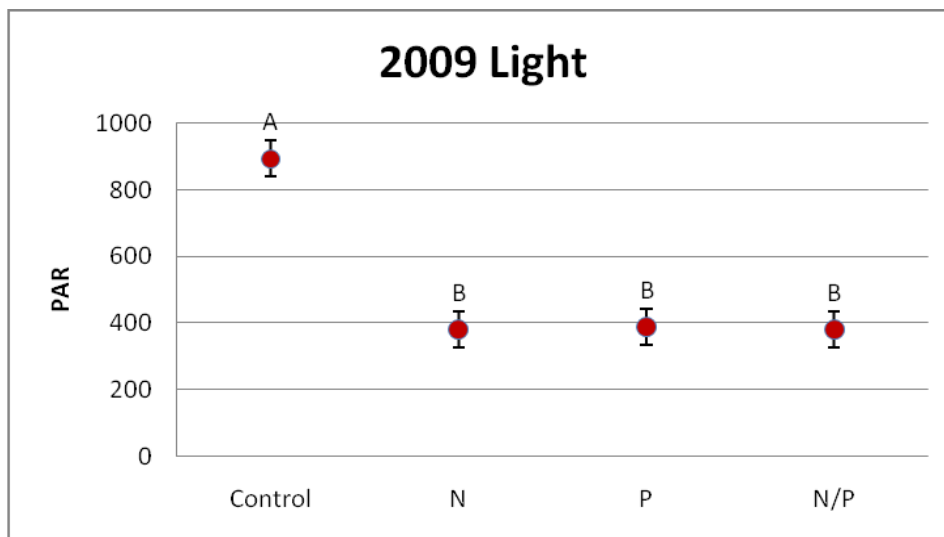


Fig. 18. Analysis of variance (ANOVA) 2009 PAR at ground level by nutrient addition (no interaction effect between nutrient treatment and clip treatment).  $F=10.73$   $P=0.001$

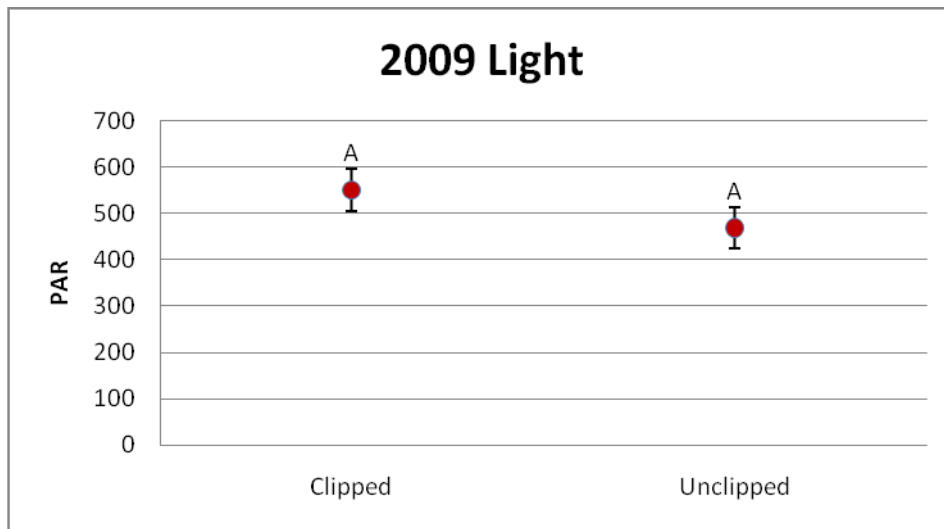


Fig. 19. Analysis of variance (ANOVA) 2007 PAR at ground level by clip treatment (no interaction effect between nutrient treatment and clip treatment).  $F=2.19$   $P=0.14$

Table 2. PAR statistics 2008-2009 for light at ground level.

<b>2007 PAR</b>				
<b>Source</b>	<b>DF</b>	<b>Sum of Squares</b>	<b>F Ratio</b>	<b>Prob &gt; F</b>
Fertilizer trt	3	1743958.0	4.7559	0.0052*
Clipping	1	566074.1	4.6312	0.0359*
Fertilizer trt*clipping	3	198703.7	0.5419	0.6557
<b>2008 PAR</b>				
<b>Source</b>	<b>DF</b>	<b>Sum of Squares</b>	<b>F Ratio</b>	<b>Prob &gt; F</b>
Fertilizer trt	3	2876705.8	7.3973	0.0003*
Clipping	1	75547.0	0.5828	0.4485
Fertilizer trt*clipping	3	356264.3	0.9161	0.4393
<b>2009 PAR</b>				
<b>Source</b>	<b>DF</b>	<b>Sum of Squares</b>	<b>F Ratio</b>	<b>Prob &gt; F</b>
Fertilizer trt	3	3092695.3	7.5447	0.0003*
Clipping	1	2604.5	0.0191	0.8907
Fertilizer trt*clipping	3	402703.8	0.9824	0.4080

Table 3. Biomass differences among treatments.

<b>2007 Biomass</b>				
<b>Source</b>	<b>DF</b>	<b>Sum of Squares</b>	<b>F Ratio</b>	<b>Prob &gt; F</b>
Fertilizer trt	3	2337021	0.8331	0.4815
Clipping	1	32788750	35.0676	<.0001*
Fertilizer trt*clipping	3	7366073	2.6260	0.0596
<b>2008 Biomass</b>				
<b>Source</b>	<b>DF</b>	<b>Sum of Squares</b>	<b>F Ratio</b>	<b>Prob &gt; F</b>
Fertilizer trt	3	353583.4	0.5151	0.6737
Clipping	1	5642660.1	24.6590	<.0001*
Fertilizer trt*clipping	3	446920.8	0.6510	0.5858
<b>2009 Biomass</b>				
<b>Source</b>	<b>DF</b>	<b>Sum of Squares</b>	<b>F Ratio</b>	<b>Prob &gt; F</b>
Fertilizer trt	3	704143.4	1.7909	0.1599
Clipping	1	2681640.4	20.4614	<.0001*
Fertilizer trt*clipping	3	510537.0	1.2985	0.2844

Table 4. Variation explained by CCA.

	Eigenvalues	% Variance explained	Cumulative
CCA1	0.23	19.1	19.1
CCA2	0.14	12.0	31.1
CCA3	0.03	3.0	34.1

### CCA

In the CCA, clipped plots are represented by open circles and unclipped plots by closed. We used black circles for unfertilized control plots, red for nitrogen addition plots, blue for phosphorus addition, and purple for nitrogen+phosphorus plots. Light and biomass are represented as black arrows with light labeled L and biomass labeled B.

The length of each arrow represents the strength of the correlation between that environmental variable and the demographic data. Light and biomass measurement are included for each year of the study, labeled 07, 08, and 09 respectively (Figure 20). CCA axes 1 and 2 explained 34 percent of the variation in the treatment effects on *Spiranthes spp.* population dynamics (Table 4). Light and biomass data correlates with the demographic data along one dominant axis for 2008 and 2009. Light and biomass for 2007, when the treatments began correlate along a different axis. Biomass for 2007 shows the least correlation with the demographic data (shortest arrow). For phosphorus and nitrogen+phosphorus treated plots, clipped and unclipped plots separate in ordination space along the axis of light and biomass measurements for 2008 and 2009. Nitrogen addition and unfertilized control plots separate in ordination space from phosphorus and phosphorus+nitrogen plots along an axis similar to 2007 biomass. However, there is little separation between clipped and unclipped plots within the nitrogen and control plots.

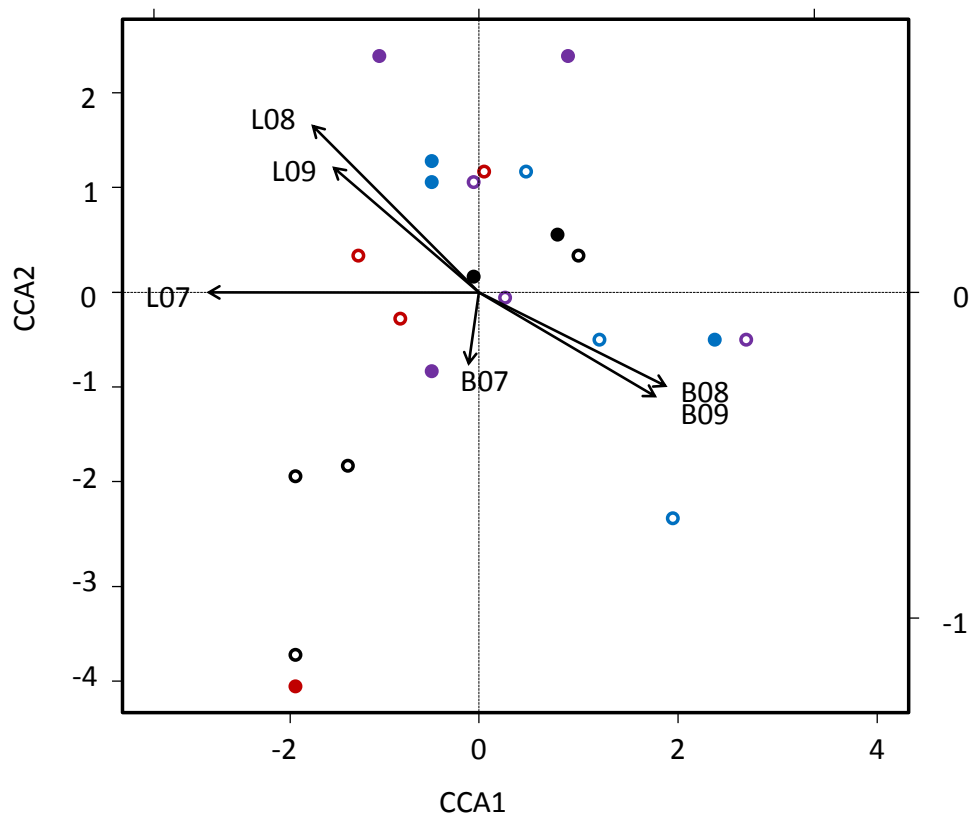


Fig. 20. Canonical correspondence analysis (CCA) of *Spiranthes spp.* demographic characteristics using vector length standardization. Inertia = 1.18. Eigenvalues: CCA1= 0.23, CCA2=0.14, CCA3=0.03, CCA4=0.02) Open circles = clipped; closed circles = unclipped. Black = control; red = nitrogen addition; blue = phosphorus addition; purple = nitrogen+phosphorus addition. Black arrows indicate environmental variables L=light and B=biomass. Plots containing no orchids were not included in the analysis.

### *Precipitation*

Precipitation for 2007 was lower than average for August and September and higher for October. For 2008 it was higher in August and lower in September and October. 2009 followed a pattern similar to 2007, but with higher than average

precipitation in both September and October (Figure 21). Precipitation remained lower than normal throughout most of the *Spiranthes spp.* growing season in 2008 (Figure 22).

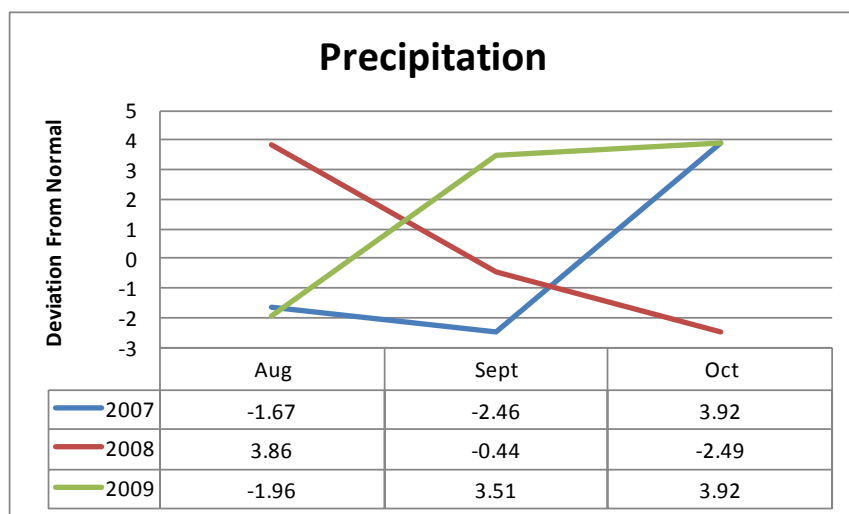


Fig. 21. Deviation from normal precipitation in August, September, and October for the 3 years of the study. (Precipitation data from Easterwood Airport weather station in College Station TX.)

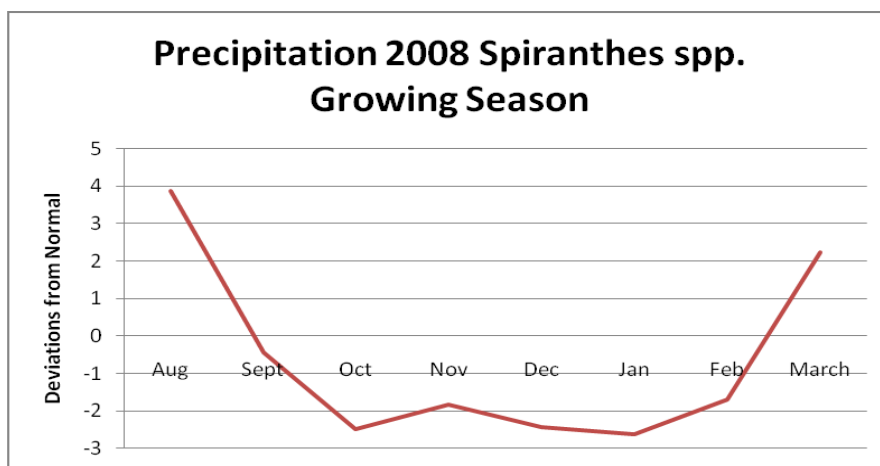


Fig. 22. Deviation from normal precipitation for the 2008 *Spiranthes spp.* growing season. (Precipitation data from Easterwood Airport weather station in College Station TX.)

## Discussion

We would expect orchid demographic parameters to respond to increased resource availability. The alteration of resource availability is affected by herbivore grazing (Crawley 1997). This alteration is influenced by the existing environmental conditions, such as nutrient and water availability (Maschinski and Whitham 1989).

Given the removal of large amounts of biomass in the clipped plots, we expected to see a marked increase in the PAR for clipped plots, but for the most part, this was not the case. In 2007, clipped plots received more light than unclipped plots for all nutrient treatments, but in 2008 and 2009 clipped plots only exhibited higher PAR in unfertilized conditions. This could be due to the timing of the clipping in combination with other environmental factors, especially precipitation. The biomass was removed each year in early-mid August. PAR was measured during peak flower production in mid-late October allowing the vegetation to grow for two months following the clipping treatment. The lack of difference between the light levels in the clipped plots receiving nutrient additions is potentially due to the more rapid growth of these plots following fertilization. The biomass likely grew more slowly following clipping in the unfertilized control plots. The discrepancy in this pattern in 2007 can be explained by precipitation patterns. During the 2007 growing season there was higher than normal precipitation in August followed by lower than normal precipitation in September and October. This may have reduced the availability of water such that all plots were water-limited and even the fertilized plots could not compensate for the biomass removal by October, resulting in differences in PAR for that year. Phosphorus plots had lower light than

nitrogen addition plots in 2007 suggesting that phosphorus had more of an effect on vegetation growth than nitrogen. This might be indicative of greater phosphorus limitation than nitrogen limitation in the study area. During the 2008 growing season there was lower than average precipitation in August and higher than average in September and October. Abundance of precipitation in the months following clipping could account for the small differences between light in the clipped and unclipped plots in 2008 as vegetation grew quickly between August and October due to the favorable conditions. The climatic conditions were similar in 2009.

While the nutrient treatments may accelerate growth following biomass removal, increased growth is not reflected in our biomass measurements. One explanation for this is compensatory growth (McNaughton 1983). Plants in clipped plots may take advantage of the increased nutrient levels to recover from clipping, growing rapidly until another limit to growth is encountered. Biomass measurements were taken each year in August, after a year of growth following the previous year's clipping. While the vegetation likely responded more quickly in fertilized plots, as is indicated by higher PAR in control plots earlier in the year, by the end of the year, fertilized plot biomass had not exceeded unfertilized plot biomass.

The patterns in the ordination of plots by demographic parameters indicates that phosphorus and nitrogen+phosphorus plots are most different from the unfertilized control plots and nitrogen addition plots. This separation occurs in a different direction from the correlation of light and biomass to the demographic variables. This result suggests that the demographic characteristics used to parameterize the ordination differ



according to fertilization treatment but that those differences are not related to light availability and the amount of competing herbaceous vegetation in the plot. Within the phosphorus and phosphorus+nitrogen treated plots, the separation in ordination space of clipped from unclipped plots along a similar axis to light and biomass suggests these variables have an effect on orchid demographic parameters with respect to simulated grazing, although this separation is not as pronounced as the separation by fertilization treatment. Biomass from 2007 correlates less with the major distribution of plots by demographic characteristics than biomass in 2008 and 2009. However, this biomass measurement was taken directly after the implementation of nutrient addition, before the vegetation had adequate time to respond to fertilization.

Mycorrhizal symbiosis may give *Spiranthes spp.* a competitive advantage in nutrient acquisition in low nutrient environments (Arditti 1967a, Hartnett et al. 1993). This potentially serves as a disadvantage where nutrients are readily available. This could explain why we did not observe a greater increase in orchid growth and recruitment (represented by more marked separation by fertilization treatment in the ordination) due to fertilizer treatment. However, timing of both fertilization and nutrient addition might play a role in orchid response to fertilization. Our experiment was designed to explore the effects of simulated pulse-grazing. As a potential management option, it is more likely to be implemented during orchid dormancy given potential direct impacts of grazing on orchids if pulse-grazing occurred concurrently with aboveground orchid production. However, increasing the light environment and

reducing competition during the orchid growing season could produce different results relative to altered soil nutrient availability.

## **Conclusion**

The interaction between indirect herbivore impacts and soil resource conditions has important conservation implications. Grazing may significantly improve the microhabitat conditions for *S. parksii* growth and establishment. However, timing of grazing could alter dynamics of nutrient competition. Grazing throughout the growing season might result in greater light availability in fertilized plots while orchids are photosynthesizing, increasing the difference in orchid growth and development under conditions of greater nutrient availability. However, we did not explore whether biomass removal had an effect on herbivory of orchids. Creating more open areas around orchid flowering stalks may increase plant visibility and encourage native browsers to consume orchid reproductive and photosynthetic tissues. Effective conservation must include management strategies developed with a more complete understanding of the factors related to the impacts of grazing across nutrient gradients. Conservation will be most effective where it considers the interaction between plant responses to grazing and the interaction of those responses with environmental factors.

## CHAPTER V

### CONCLUSION

Both direct consumption of the orchid and removal of neighboring vegetation alter *S. parksii* demographics. Changes in demographic parameters have the potential to result in alterations of lifecycles and population dynamics (Maron and Crone 2006). While this work has illustrated the importance of both types of herbivore impacts to *S. parksii*, more information regarding herbivore-orchid interactions is needed to make management recommendations for effective conservation.

An exploration of herbivore impacts on *S. parksii* at larger scales might help to clarify differences in herbivore affects unexplained at the small plot level, since spatial dynamics could play a role in herbivore selectivity (Huntly 1991, Leibold et al. 2004). Additionally, the exploration of interactive affects between herbivore browsing of orchids, and grazing of surrounding vegetation, is necessary for a complete understanding of the potential impacts of grazing in areas of *S. parksii* establishment. Our own exploration of simulated-pulse grazing could be improved by establishing plots in areas of high orchid abundance ensuring adequate numbers of flowers for analyzing demographic parameters with traditional quantitative methods. Also, additional experimentation regarding small herbivore browsing and root predation is necessary to fully understanding *S. parksii* responses to herbivory.

While this work provides a step toward understanding herbivore impacts on *S. parksii* population dynamics, more detailed information including elucidation of

environmental factors which alter orchid-herbivore dynamics, would increase the effectiveness of a management plan focused on reducing or altering herbivore impacts, and facilitate successful *S. parksii* conservation.

## LITERATURE CITED

- Abrams, M. D. 1992. Fire and the development of oak forests. *BioScience* 42:346-353.
- Archer, S., C. Scifres, C. R. Bassham, and R. Maggio. 1988. Autogenic succession in a subtropical savanna: Conversion of grassland to thorn woodland. *Ecological Monographs* 58:111-127.
- Arditti, J. 1967a. Factors affecting the germination of orchid seeds. *The Botanical Review* 33:1-97.
- Arditti, J. 1967b. Factors affecting the germination of orchid seeds. *The Botanical Review* 33:1-97.
- Arditti, J. 2000. Numerical and Physical Properties of Orchid Seeds and their Biological Implications. Blackwell, Oxford.
- Ariza, M. 2010. Personal communication.
- Augustine, D. J. and S. J. McNaughton. 1998. Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. *The Journal of Wildlife Management* 62:1165-1183.
- Bai, E. and F. E. Smeins. 2007. Assessment of the habitat suitability and potential occurrence of *Spiranthes parksii* in Brazos and Grimes counties, TX. Texas A&M University.
- Batty, A. L., W. K. Dixon, M. C. Brundrett, and K. Sivasithamparam, editors. 2002. Orchid Conservation and Mycorrhizal Associations. Kluwer Academic Publishers, Dordrecht, Germany.
- Bevill, R. L., S. M. Louda, and L. M. Stanforth. 1999. Protection from natural enemies in managing rare plant species. *Conservation Biology* 13:1323-1331.
- Bomar, G. W., editor. 1983. Texas Weather. University of Texas Press, Austin, TX.
- Bowles, M. L. and J. L. McBride. 1998. Vegetation composition, structure, and chronological change in a decadent midwestern North American savanna remnant. *Natural Areas* 18:14-27.
- Breshears, D. D. 2006. The grassland-forest continuum: Trends in ecosystem properties for woody plant mosaics? *Frontiers in Ecology and the Environment* 4:96-104.

- Brigham, C. A. and M. W. Schwartz, editors. 1997. Population Viability in Plants: Conservation Management and Modeling of Rare Plants. Springer, New York.
- Brzosko, E., A. Wróblewska, and M. Ratkiewicz. 2002. Spatial genetic structure and clonal diversity of island populations of lady's slipper (*Cypripedium calceolus*) from the Biebrza National Park (northeast Poland). *Molecular Ecology* 11:2499-2509.
- BVCOG. 2010. Brazos Valley economic and demographic information. Brazos Valley Council of Government.
- Caswell, H. 1982. Stable population structure and reproductive value for populations with complex life cycles. *Ecology* 63:1223-1231.
- Caswell, H., editor. 2001. Matrix Population Models: Construction, Analysis and Interpretation. Sinaur Associates Inc. , Sunderland, MA.
- Catling, P. M. 1982a. Breeding systems of North American *Spiranthes* (Orchidaceae). *Canadian Journal of Botany* 60:3017-3039.
- Catling, P. M. 1982b. Pollination of northeastern North American *Spiranthes*(Orchidaceae). *Canadian Journal of Botany* 61:1080-1093.
- Catling, P. M., and K. L. McIntosh and K. L. McIntosh. 1979. Rediscovery of *Spiranthes parksii* Correll. *Sida* 8:188-193.
- Coates, F., I. D. Lunt, and R. L. Tremblay. 2006. Effects of disturbance on population dynamics of the threatened orchid *Prasophyllum correctum* and implications for grassland management in south-eastern Australia. *Biological Conservation* 129:59-69.
- Côté, S. D., T. P. Rooney, J.-P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35:113-147.
- Crawley, M. J., editor. 1983. Herbivory. University of California Press, Berkeley CA.
- Crawley, M. J. 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* 34:531-562.
- Crawley, M. J., editor. 1997. Plant Herbivore Dynamics. Blackwell Scientific, Cambridge, MA.

- Crawley, M. J. and G. J. S. Ross. 1990. The population dynamics of plants [and discussion]. *Philosophical Transactions: Biological Sciences* 330:125-140.
- Cyr, H. and M. L. Pace. 1993. Allometric theory: Extrapolations from individuals to communities. *Ecology* 74:1234-1245.
- de Kroon, H., A. Plaisier, J. van Groenendael, and H. Caswell. 1986. Elasticity: The relative contribution of demographic parameters to population growth rate. *Ecology* 67:1427-1431.
- Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of Growth and Extinction parameters for endangered species. *Ecological Monographs* 61:115-143.
- Dijk, E. and N. Eck. 1995. Axenic in vitro nitrogen and phosphorus responses of some Dutch marsh orchids. *New Phytologist* 131:353-359.
- Doak, D. F. 1992. Lifetime impacts of herbivory for a perennial plant. *Ecology* 73:2086-2099.
- Dueck, L. A. and K. M. Cameron. 2007. Sequencing re-defines *Spiranthes* relationships, with implications for rare and endangered taxa. *Lankesteriana*. 7:190-195.
- Eskelinen, A. 2008. Herbivore and neighbour effects on tundra plants depend on species identity, nutrient availability and local environmental conditions. *Journal of Ecology* 96:155-165.
- Hammons, J. R. 2008. Demographic, life cycle, habitat characterization and transplant methods for the endangered orchid, *Spiranthes parksii* Correll. Texas A&M University, College Station, TX.
- Hammons, J. R. 2010. Personal communication.
- Hammons, J. R., F. E. Smeins, and W. E. Rogers. 2010. Transplant methods for the endangered orchid *Spiranthes parksii* Correll. *North American Native Orchid Journal* 16:38-46.
- Hartnett, D. C., B. A. D. Hetrick, G. W. T. Wilson, and D. J. Gibson. 1993. Mycorrhizal influence on intra- and interspecific neighbour interactions among co-occurring prairie grasses. *Journal of Ecology* 81:778-795.
- Hulme, P. E. 1994. Seedling herbivory in grassland: Relative impact of vertebrate and invertebrate herbivores. *Journal of Ecology* 82:873-880.

- Hulme, P. E. 1996. Herbivory, plant regeneration, and species coexistence. *Journal of Ecology* 84:609-615.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* 22:477-503.
- Janecková, P., K. Wotavová, I. Schödelbauerová, J. Jersáková, and P. Kindlmann. 2006. Relative effects of management and environmental conditions on performance and survival of populations of a terrestrial orchid, *Dactylorhiza majalis*. *Biological Conservation* 129:40-49.
- Kaye, T. N. and D. A. Pyke. 2003. The effect of stochastic technique on estimates of population viability from transition matrix models. *Ecology* 84:1464-1476.
- Kindlmann, P. and Z. balounova. 1999. Energy partitioning in terrestrial orchids: a model for assessing their performance. *Ecological Modelling* 119:167-176.
- Kotanen, P. M. 1995. Responses of vegetation to a changing regime of disturbance: effects of feral pigs in a Californian coastal prairie. *Ecography* 18:190-199.
- Krupnick, G. A., A. E. Weis, and D. R. Campbell. 1999. The Consequences of floral herbivory for pollinator service to *Isomeris arborea*. *Ecology* 80:125-134.
- Larson, K. S. and R. J. Larson. 1990. Lure of the locks; showiest ladies-tresses orchids, *Spiranthes romanzoffiana*, affect bumblebee *Bombus spp.*, foraging behavior. *Canadian Field-Naturalist* 104:519-523.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601-613.
- Lloyd, D. G. 1988. Benefits and costs of biparental and uniparental reproduction in plants. Pp. 233-252 in R.E. Michod and B.R. Levin, eds. *The Evolution of Sex*. Sinauer, Sunderland, MA.
- Louda, S. M., K.H. Keeler, R.D. Holt, editor. 1990. *Herbivore Influence on Plant Performance and Competitive Interactions*. Academic Press, San Diego, CA.
- Luer, C. A., editor. 1975. *The Native Orchids of the United States and Canada Excluding Florida*. W.S. Cowell Ltd., Ipswich, UK.
- Mack, M. C. and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology & Evolution* 13:195-198.



- Manhart, J. R. and A. E. Pepper. 2007. A genetic study of the rare and endangered orchid *Spiranthes parksii* Correll in a comparative context. Texas A&M University, College Station, TX.
- Manning, J. T. 1981. The “survivor effect” and evolution of parthenogenesis and self-fertilization. *Journal of Theoretical Biology* 93:491-493.
- Maron, J. L. and E. Crone. 2006. Herbivory: Effects on plant abundance, distribution and population growth. *Proceedings: Biological Sciences* 273:2575-2584.
- Marquis, R. J. 1992. The selective impact of herbivores. Pages 301-325 in R.S. Fritz and E. L. Simms, editors. *Plant Resistance to Herbivores and Pathogens. Ecology, Evolution, and Genetics*. University of Chicago Press, Chicago, IL.
- Maschinski, J. and T. G. Whitham. 1989. The continuum of plant responses to herbivory: The influence of plant association, nutrient availability, and timing. *The American Naturalist* 134:1-19.
- McCune, B. and J. B. Grace, editors. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR.
- McKendrick, S. L. 1996. The effects of fertilizer and root competition on seedlings of *Orchis morio* and *Dactylorhiza fuchsii* in chalk and clay soil. *New Phytologist* 134:335-342.
- McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40:329-336.
- Menges, E. S. 1990. Population viability analysis for an endangered plant. *Conservation Biology* 4:52-62.
- Mesipuu, M., R. Shefferson, and T. Kull. 2009. Weather and herbivores influence fertility in the endangered fern *Botrychium multifidum*. *Plant Ecology* 203:23-31.
- Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist* 132:87-106.
- Morrow, P. A. and V. C. LaMarche, Jr. 1978. Tree ring evidence for chronic insect suppression of productivity in subalpine eucalyptus. *Science* 201:1244-1246.
- Mulder, C. P. H. and R. W. Ruess. 1998. Effects of herbivory on arrowgrass: Interactions between geese, neighboring plants, and abiotic factors. *Ecological Monographs* 68:275-293.

- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution* 10:58-62.
- NCSS. 2009. Digital soil survey for Grimes County. National Cooperative Soil Survey.
- Nielsen, S., C. Kirschbaum, and A. Haney. 2003. Restoration of midwest oak barrens: structural manipulation or process-only. *Conservation Ecology* 7:10.
- Olf, H. and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* 13:261-265.
- Ozinga, W. A., R. M. Bekker, J. H. J. SchaminÉ, and J. M. Van Groenendael. 2004. Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology* 92:767-777.
- Pacala, S. W. and M. J. Crawley. 1992. Herbivores and plant diversity. *The American Naturalist* 140:243-260.
- Parker, K. M. 2001. A compendium on *Spiranthes parksii*, Correll (Navasota ladies' tresses). Tejas Ecological Services, College Station, TX.
- Pelchat, C. 2000. *Spiranthes parksii* Correll-Navasota Ladies' Tresses. *North American Native Orchid Journal* 6:268-279.
- Poole, J. M., W. R. Carr, D. M. Price, and J. R. Singhurt, editors. 2007. Rare Plants of Texas. Texas A&M University Press, College Station, TX.
- Rabinowitz, D. 1981. Seven forms of rarity. *in* H. Synge, editor. *The Biological Aspects of Rare Plant Conservation*. John Wiley & Sons, Chinchester, UK.
- Rasmussen, H. N. 1995. *Terrestrial Orchids*. Cambridge University Press.
- Rasmussen, H. N. 2002. Recent developments in the study of orchid mycorrhiza. *Plant and Soil* 244:149-163.
- Rasmussen, H. N. and F. N. Rasmussen. 2007. Trophic relationships in orchid mycorrhiza – diversity and implications for conservation. *Lankesteriana* 7:334-341.
- Rasmussen, H. N., editor. 1995. *Terrestrial orchids - from seed to mycotrophic plant*. Cambridge University Press, Cambridge, UK.

- Rausher, M. D. and P. Feeny. 1980. Herbivory, plant density, and plant reproductive Success: The effect of *Battus philenor* on *Aristolochia reticulata*. *Ecology* **61**:905-917.
- Rees, M., R. Condit, M. Crawley, S. Pacala, and D. Tilman. 2001. Long-term studies of vegetation dynamics. *Science* **293**:650-655.
- Ritchie, M. E. and D. Tilman. 1995. Responses of legumes to herbivores and nutrients during succession on a nitrogen-poor soil. *Ecology* **76**:2648-2655.
- Rosenthal, J. P. and P. M. Kotanen. 1994. Terrestrial plant tolerance to herbivory. *Trends in Ecology & Evolution* **9**:145-148.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* **5**:18-32.
- Schmidt, J. M. and A. E. Antlfinger. 1992. The level of agamospermy in a Nebraska population of *Spiranthes cernua* (Orchidaceae). *American Journal of Botany* **79**:501-507.
- Scholes, R. J. and S. R. Archer. 1997. Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**:517-544.
- SCS. 1979. General soil map of Grimes county. Soil Conservation Service.
- Shea, K. and D. Kelly. 1998. Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications* **8**:824-832.
- Sheviak, C. J. 1976. Biosystematic study of the *Spiranthes cernua* complex with emphasis on the prairies. Harvard University, Cambridge, MA.
- Sheviak, C. J. 1982. Biosystematic study of the *Spiranthes cernua* complex. New York State Museum, Albany, NY.
- Sheviak, C. J. 1991. Morphological variation in the compilospecies *Spiranthes Cernua* (L.) L.C.Rich.: ecologically-limited effects of gene flow. *Lindleyana* **6**:228-234.
- Siemann, E., J. A. Carillo, C. A. Gabler, R. Zipp, and W. E. Rogers. 2009. Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. *Forest Ecology and Management* **258**:546-533.
- Silvertown, J., M. Franco, and E. Menges. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. *Conservation Biology* **10**:591-597.

- Silvertown, J., D. A. Wells, M. Gillman, M. E. Dodd, H. Robertson, and K. H. Lakhani. 1994. Short-term effects and long-term after-effects of fertilizer application on the flowering population of green-winged orchid *Orchis morio*. *Biological Conservation* 69:191-197.
- Singer, F. J., W. T. Swank, and E. E. C. Clebsch. 1984. Effects of wild pig rooting in a deciduous forest. *The Journal of Wildlife Management* 48:464-473.
- Sipes, S. D. and V. J. Tepedino. 1995. Reproductive biology of the rare orchid, *Spiranthes diluvialis*: Breeding system, pollination, and implications for conservation. *Conservation Biology* 9:929-938.
- Sletvold, N., D.-I. Øien, and A. Moen. 2010. Long-term influence of mowing on population dynamics in the rare orchid *Dactylorhiza lapponica*: The importance of recruitment and seed production. *Biological Conservation* 143:747-755.
- Soule, M. E. and K. A. Kohm, editors. 1989. *Research Priorities for Conservation Biology*. Island Press, Washington, D.C.
- SRCC. 1971-2000. Cimograph for College Station, TX: Temperature and precipitation normals Southern Regional Climate Center.
- Strauss, S. Y. 1991. Direct, indirect, and cumulative effects of three native herbivores on a shared host plant. *Ecology* 72:543-558.
- Strauss, S. Y., R. E. Irwin, and V. M. Lambrix. 2004. Optimal defence theory and flower petal colour predict variation in the secondary chemistry of wild radish. *Journal of Ecology* 92:132-141.
- TMPA. 1991. Amended Navasota Ladies' Tresses management plan.
- Tremblay, R. L. 1992. Trends in the pollination ecology of the Orchidaceae: evolution and systematic. *Canadian Journal of Botany* 70:642-650.
- Trumble, J. T., D. M. Kolodny-Hirsch, and I. P. Ting. 1993. Plant compensation for arthropod herbivory. *Annual Review of Entomology* 38:93-119.
- TSDC. accessed 2010. Texas populations and projections program. Texas State Data Center.
- USFWS. 1984. Navasota Ladies' Tresses recovery plan. Page 61, Albuquerque, NM.

- USFWS. 2006. Final biological opinion for the proposed first phase of construction of the Brazos Valley Solid Waste Management Agency (BVSWMA) landfill in Grimes County, Texas and its effects on the federally listed endangered Navasota ladies' tresses (*Spiranthes parksii*).
- USFWS. 2009. Navasota Ladies' Tresses (*Spiranthes parksii*) 5-year review: Summary and evaluation. . United States Fish and Wildlife Service, Southwest region, Albuquerque, MN.
- Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31:197-215.
- Van Der Wal, R., M. Egas, A. v. d. Veen, and J. Bakker. 2000. Effects of resource competition and herbivory on plant performance along a natural productivity gradient. *Journal of Ecology* 88:317-330.
- Walters, C. 2005. Genetic relationships among *Spiranthes parksii* and congeneric species. Texas A&M University, College Station, TX.
- Warner, P. and H. Cushman. 2002. Influence of herbivores on a perennial plant: variation with life history stage and herbivore species. *Oecologia* 132:77-85.
- Wells, T. C. E., editor. 1981a. *Population Ecology of Terrestrial Orchids*. John Wiley & Sons Ltd., Chinchester.
- Wells, T. C. E. 1981b. Population ecology of terrestrial orchids. *in* H. Synge, editor. *The Biological Aspects of Rare Plant Conservation*. John Wiley & Sons Ltd, Chinchester, UK.
- Whigham, D. and A. Chapa. 1999. Timing and intensity of herbivory: Its influence on the performance of clonal woodland herbs. *Plant Species Biology* 14:29-37.
- Wilson, H. D. 2002. Proposed recovery plan revision for Navasota Ladies' Tresses.

## APPENDIX A

NUMBER OF *SPIRANTHES SPP.* FOUND IN NUTRIENT ADDITION AND  
SIMULATED PULSE GRAZING EXPERIMENT PLOTS

Plot	Treat	07 Rosettes	08 Flowers	08 Rosettes	08 Flowers	09 Rosettes	09 Flowers	10 Rosettes	Total Plants
1u	N/P	1	0	1	0	0	0	0	1
1c	N/p	0	0	0	0	1	0	1	0
2u	N/p	0	0	0	0	0	0	0	0
2c	N/p	0	0	0	0	1	0	1	1
3u	N/p	0	0	8	1	3	0	0	9
3c	N/p	2	1	18	5	4	0	3	18
4c	C	0	0	1	0	0	0	0	1
4u	C	0	0	2	0	0	0	0	2
5u	N	0	0	0	0	0	0	0	0
5c	N	0	0	1	0	0	0	0	1
6c	P	0	0	0	0	0	0	0	0
6u	P	0	0	0	0	0	0	0	0
7u	N/P	0	0	0	0	0	0	0	0
7c	N/P	0	0	9	2	5	0	2	9
8c	P	0	0	0	0	0	0	0	0
8u	P	0	0	0	0	0	0	0	0
9c	N/P	0	0	0	0	0	0	0	0
9u	N/P	0	0	0	0	0	0	0	0
10c	C	0	0	4	0	1	0	0	4
10u	C	0	0	0	0	0	0	0	0
11c	N	0	0	19	0	5	1	1	21
11u	N	0	0	1	0	1	0	0	1
12u	P	0	0	0	0	0	0	0	0
12c	P	0	0	0	0	0	0	0	0
13c	P	2	0	1	0	2	0	1	2
13u	P	0	0	1	0	0	0	0	1
14u	C	0	0	1	0	0	0	0	1
15c	N	0	0	7	1	2	0	0	8
16c	C	2	0	0	1	1	1	0	4
16u	C	0	0	2	0	1	0	0	2
17c	N	0	0	0	0	0	0	0	0

Plot	Treat	07 Rosettes	08 Flowers	08 Rosettes	08 Flowers	09 Rosettes	09 Flowers	10Rosettes	Total Plants
18u	C	0	0	0	0	0	0	0	0
18c	C	0	0	0	0	0	0	0	0
19u	P	2	1	31	2	1	1	2	38
19c	P	1	0	7	0	0	1	5	10
20c	C	0	0	0	0	0	0	0	0
20u	C	0	0	0	0	0	0	0	0
21c	N	0	0	0	0	0	0	0	0
21u	N	0	0	0	0	0	0	0	0
22u	N	0	0	0	0	0	0	0	0
22c	N	0	0	0	0	0	0	0	0
24u	P	0	0	0	0	0	0	0	0
24c	P	0	0	0	0	0	0	0	0
25c	P	0	0	0	0	2	0	0	0
25u	P	0	0	2	1	0	0	0	2
26u	P	0	1	17	0	1	0	4	18
26c	P	0	0	0	0	1	0	1	2
27u	C	0	0	0	0	0	0	0	0
27c	C	0	0	0	0	0	0	0	0
28c	N/P	0	0	0	0	0	0	0	0
28u	N/P	0	0	0	0	0	0	0	0
29c	N/P	0	0	0	0	0	0	0	0
29u	N/P	0	0	0	0	0	0	0	0
30u	N	0	0	0	0	1	0	0	0
30c	N	0	0	0	0	0	0	0	0
31c	N/P	0	0	1	0	0	0	1	1
31u	N/P	0	0	0	0	0	0	0	0
32u	C	0	0	0	0	0	0	0	0
32c	C	0	0	0	0	0	0	0	0

u – unclipped side of plot  
c – clipped side of plot

C – unfertilized control  
N – nitrogen addition  
P – phosphorus addition  
N/P – nitrogen and phosphorus addition

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