FACILITATION AND COMPETITION BETWEEN A NITROGEN-FIXING PERENNIAL LEGUME, *LESPEDEZA CUNEATA*, AND AN ANNUAL, *HETEROTHECA SUBAXILLARIS*, IN A SOUTH CAROLINA OLD FIELD

by

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(Under the direction of Rebecca R. Sharitz)

ABSTRACT

Facilitation and competition are recognized as important interactions structuring plant communities. This dissertation investigates the relationship of *Lespedeza cuneata* and *Heterotheca subaxillaris* in an old field in South Carolina. *Heterotheca*, an annual plant, is often found associated with *Lespedeza*, a perennial, nitrogen-fixing legume. The relationship between the two species was explored through a pattern analysis and by modeling the dependency of the positions of *Heterotheca* on the density of *Lespedeza*. Results of a Ripley's K analysis revealed that the two species were clustered, which suggested a potential positive interaction. Further modeling indicated that the intensity of *Heterotheca* was maximized at moderate densities of *Lespedeza*. Heights and biomasses of *Heterotheca* showed a slight yet significant increase as *Lespedeza* density increased. Mortality also had a slight increase with increasing *Lespedeza* density. It is thought that *Lespedeza* may affect its environment in terms of local resources. Soil nutrients, soil moisture, canopy openness, and soil temperature were measured in plots of varying *Lespedeza* density. Increasing density of *Lespedeza* led to decreased canopy openness and temperatures, and increased levels of NO_3^- and NH_4^+, although results of a net nitrogen

mineralization study found no significant differences between *Lespedeza* density. High densities of *Lespedeza* led to higher soil moisture immediately following rain, but lower temperatures thereafter; moderate densities led to higher soil moisture at the 20 cm depth.

Germination of *Heterotheca* seeds was not affected by the presence of *Lespedeza* soil or litter. The growth of *Heterotheca* responded positively to increases in nitrogen, and while growth was hindered by shade, reproductive output was not negatively affected by shade.

These results suggest that there are complex interactions between *Heterotheca* and *Lespedeza*. At high densities, *Lespedeza* likely competes with *Heterotheca* for light resources, but the benefits of *Lespedeza* to soil nutrients and moisture at moderate densities may contribute to the success of *Heterotheca*.

INDEX WORDS: Facilitation, competition, legume, spatial statistics, modelling, old field, *Heterotheca subaxillaris*, *Lespedeza cuneata*

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DEDICATION

I would like to dedicate this dissertation to my family: my parents, Addie and Cleatus Turner, my sister Debbie Hudson, and my wonderful nieces, Katie and Chelsea, for their love, support and encouragement through these past years.

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CHAPTER 1

INTRODUCTION

Understanding biological interactions is a major focus of ecological research because both positive and negative interactions can have significant effects on plant and animal community structure. Studies of negative interactions, or competition, however, have long dominated the literature (Connell 1983, Schoener 1987). Theories surrounding the structure and dynamics of plant communities have focused primarily on negative interactions between plants (Grime 1979, Tilman 1988). Competition between plants for resources such as space, light and soil nutrients has been considered the primary driving force of plant community dynamics and structure (Tilman 1988).

Although less common in the literature, positive interactions, also known as facilitation, have been the focus of a resurgence in interest in factors that structure plant communities (Callaway 1995, Bruno 2000, Callaway and Pennings 2000). Facilitation occurs when the presence of individuals of one species benefits individuals of the same or a different species. The idea that early colonizing species change the environment to promote the establishment of other species was first proposed as a major mechanism for succession by Clements (1916). Later, Connell and Slatyer (1977) proposed facilitation as one of three testable models for explaining species replacement during succession. Facilitation has been found to be a significant factor in both primary (Chapin et al. 1994, Bellingham et al. 2001, Walker et al. 2001a) and secondary succession (Raffaele and Veblen 1998, Rousset and Lepart 1999) where the environments are stressful with low nutrients, soil moisture, or organic matter, or with high

herbivory pressure. Facilitation has not been found, however, to be important to successional dynamics in typical old fields abandoned from agriculture (Keever 1950, Hils and Vankat 1982, Armesto and Pickett 1986), where soils are well established and nutrients are not low (Chapin et al. 1994). Hils and Vankat (1982) dismissed the facilitation model of succession in old fields after finding no decline in perennial biomass after the removal of annuals and biennials. Miller (1994) found limited facilitation of some old-field species; however, these were due to indirect effects resulting from competition.

In addition to studies concerning succession, much early work on positive interactions between plants focused on desert ecosystems. In these habitats, shrubs or trees serve as "nurse plants" and promote the establishment and growth of other species by ameliorating microclimatic and soil nutrient conditions (Shreve 1931, Muller 1953). Questions addressed why annual herbs and perennial seedlings were found under the canopy of only certain shrub species. Shreve (1931) measured microclimatic variation both under and away from desert shrubs and hypothesized that the shade of shrubs offered both protection from physical injury and amelioration of multiple environmental factors. Descriptive work by Went (1942) noted that nutrients might be more important than physical factors because annuals were often associated with remnants of dead shrubs. Muller (1953) speculated that a build up of organic debris was responsible for the presence of herbs under shrubs such as *Franseria dumosa*.

The "nurse plant" phenomenon in deserts has continued to be a focus of study of positive interactions (Franco and Nobel 1988, 1989, Holzapfel and Mahall 1999, Brittingham and Walker 2000, Tielborger and Kadmon 2000a, Forseth et al. 2001, Tewksbury and Lloyd 2001, Walker et al. 2001b, Schenk and Mahall 2002, Schenk et al. 2003). Salt marsh and coastal dune systems have also received much attention (Kellman and Kading 1992, Bertness and Shumway 1993,

Bertness and Hacker 1994, Callaway 1994, Bruno 2000, Callaway and Pennings 2000, Shumway 2000, Franks 2003, Rudgers and Maron 2003). In addition to coastal and desert systems, facilitation has been observed in a wide range of other habitats. These include calcareous grasslands (Rousset and Lepart 1999), subtropical savannas (Vetaas 1992, Barnes and Archer 1996, Couteron and Kokou 1997, Barnes and Archer 1999), oak woodlands (Callaway and D'Antonio 1991, Callaway et al. 1991, Callaway 1992) and high Andean terraces (Nunez et al. 1999).

Facilitation has now found a place alongside competition and is recognized as an important biological interaction in stressful ecosystems. There is a trend towards recognizing that both positive and negative interactions are important and often co-occur within the same community (Franco and Nobel 1988, Bertness and Shumway 1993, Haase et al. 1996, Barnes and Archer 1999, Callaway and Pennings 2000, Franks 2003). Current work focuses on elucidating the responsible mechanisms, targeted life stages, or intensity of interactions (Callaway 1992, Callaway and Walker 1997, Bruno 2000, Rousset and Lepart 2000, Franks 2003).

Mechanisms of facilitation among plant individuals occur primarily through habitat improvement and amelioration. In many habitats, increased soil nutrients and shade, leading to decreased solar radiation, lower temperatures and higher soil moisture, are key mechanisms (Radwanski and Wickens 1967, Franco and Nobel 1989, Valiente-Banuet et al. 1991, Kellman and Kading 1992, Raffaele and Veblen 1998, Shumway 2000, Tielborger and Kadmon 2000b, Lenz and Facelli 2003). In coastal systems, amelioration of salt or water stress and substrate stabilization are important means of facilitation (Bertness and Shumway 1993, Bertness and Hacker 1994, Bruno 2000). Additional mechanisms include protection from predation stress

(Valiente-Banuet and Ezcurra 1991, Rousset and Lepart 1999). Facilitation is most important in stressful habitats, and the importance of facilitation is predicted to increase as stress increases (Bertness and Hacker 1994, Holmgren et al. 1997, Tewksbury and Lloyd 2001), while the importance of competition may increase as stressors are limited (Bertness and Shumway 1993).

The density or size of the benefactor species may also impact either the intensity of facilitation or the balance between competition and facilitation (Callaway and Walker 1997, Tewksbury and Lloyd 2001). In a deglaciated Alaskan habitat with low soil nutrients, Chapin et al. (1994) found that thickets of alder (*Alnus tenuifolia*) facilitated establishment of spruce (*Picea glauca*) seedlings, while Walker and Chapin (1986) noted that thickets of alder in a less stressful Alaskan floodplain habitat suppressed establishment of other species, including spruce. Kellman and Kading (1992) found facilitation of pine seedlings in sand dune succession only at or beyond a "threshold" of oak canopy size. Size is not always important, however, as McAulliffe (1984) found no correlation between the trunk size of a large cactus, *Opuntia fulgida*, and the number of small cacti found under its canopy.

Facilitation can also occur at different life history stages. Walker and Chapin (1986) found that although thickets inhibited seedling establishment, individuals of alder promoted the growth of established spruce seedlings. Growth but not germination was favored under conditions of shade for perennial herbs growing under trees or desert shrubs (Shreve 1931). Lenz and Facelli (2003) found similar results with an Australian shrub that facilitated growth but not germination or establishment of a perennial succulent. Franco and Nobel (1988) found the opposite to be true in their study of *Agave* growing under the desert bunchgrass *Hilaria rigida*; seedling establishment was facilitated by *H. rigida*, but competition for light and water reduced seedling growth. In this case, temperature was the key factor that inhibited seedling

establishment outside of the canopy (Nobel 1984). In salt marshes, the stabilization of the soil by *Spartina alterniflora* facilitated seedling establishment of two annual cobble beach species, but adult transplants of the annuals had high survival rates regardless of their proximity to *S. alterniflora* (Bruno 2000). In a coastal sand dune, the nitrogen fixing shrub *Myrica pennsylvanica* was found to facilitate both seedling establishment as well as adult growth of two perennial species, *Solidago sempervirens* and *Ammophila breviligulata* (Shumway 2000). Rudgers and Maron (2003) also found facilitation at multiple life history stages of one coastal dune shrub, *Lupinus arboreus*, by another, *Baccharis pilularis*. In this case *B. pilularis* benefited seedling establishment, seedling survival, and growth of *L. arboreus*. Rousset and Lepart (2000) found higher seed germination rates, and higher rates of survival of downy oak, *Quercus humilis*, under shrub canopies than in the open grassland. The shrubs, however, did not facilitate the growth of adult oaks.

In this dissertation, I explored the association between two plant species, *Lespedeza cuneata*, a perennial legume, and *Heterotheca subaxillaris*, an annual or biannual forb, found together in old fields of the southeastern USA Coastal Plain. Observations of an old field in Aiken County, South Carolina, suggest that *Heterotheca* individuals are usually found in the presence of *Lespedeza*. Factors such as a hot, dry, climate, coupled with soil low in nutrients, specifically nitrogen, create a stressful environment where positive interactions may take place between the two species. *Lespedeza* is a dominant, nitrogen-fixing, multiple-stemmed plant that could potentially ameliorate these harsh conditions and provide local conditions more favorable to *Heterotheca* than occur in areas away from patches of *Lespedeza*. Alternatively, *Lespedeza* could be a strong competitor of *Heterotheca*, through utilization of soil and light resources. In addition, interactions between *Heterotheca* and *Lespedeza* may be dependent on the density of

Lespedeza. While certain densities of *Lespedeza* may produce favorable conditions for *Heterotheca*, at very high densities the competitive interactions between *Lespedeza* and *Heterotheca* may be more important and serve to exclude rather than facilitate individuals of *Heterotheca*. The dominance of positive or negative interactions could also be dependent on the life cycles of the two species. *Lespedeza* could serve primarily as a facilitator at one stage of the *Heterotheca* life cycle, while competitive interactions might dominate at another life stage. I hypothesized that *Lespedeza* is a facilitator of *Heterotheca* except at high densities where competition for light and soil resources is the predominant interaction. Although *Heterotheca* might also have environmental effects that might influence the distribution and success of *Lespedeza*, the primary emphasis for the purpose of this dissertation was on *Lespedeza'*s status as a facilitator and competitor because it is an established perennial and nitrogen-fixer.

The first goal of this dissertation was to characterize the spatial pattern of occurrence of the two species in the old field, through a second-order spatial analysis using Ripley's K-Functions (Diggle 1983). The presence of spatial patterns among species of plants has come to be a key indicator for the detection of biological interactions such as competition and facilitation (Callaway 1995, Malkinson et al. 2003). Identifying such patterns serves as a useful starting point for further investigation.

Many studies have analyzed spatial patterns, but fewer have attempted to incorporate such analysis into models that provide further insight into the nature of the patterns. After characterizing the pattern between the two species, my second goal was to explore further the relationship between *Heterotheca* and *Lespedeza* density by modelling *Heterotheca* positions as a Poisson process whose intensity was a function of a neighborhood density index of *Lespedeza*.

This yielded information on the relative likelihood of encountering *Heterotheca* across a gradient of *Lespedeza* density.

In order to support the hypothesis that facilitation is potentially occurring, it is important to demonstrate that not only are the two species positively associated, but that the presence of *Lespedeza* improves the performance of *Heterotheca*. It would be possible to imagine a scenario where the results of a pattern analysis yield aggregation of the two species; but on closer observation to find that the largest, hardiest individuals are the ones that are the furthest away from the other species or at the lowest densities. In order to address this question, information on individual *Heterotheca* plant size, seed set, and mortality was analyzed with respect to the neighborhood density index through a logistic regression.

The third goal was to examine how *Lespedeza* modifies the resources within its local environment. Plots of low, medium and high *Lespedeza* density were established across the old field. Soil nutrients, light, temperature, and soil moisture were monitored to detect differences between *Lespedeza* density classes. A net nitrogen mineralization study was also performed in an area where *Lespedeza* was experimentally planted at various densities.

Finally, greenhouse studies investigated the response of *Heterotheca* to changes in environmental conditions that might be brought about by the presence of *Lespedeza*. There are both quantitative and qualitative differences between litter taken from under *Lespedeza* individuals and litter taken in grassy, open areas. The combination of a lower carbon to nitrogen ratio in *Lespedeza* litter and greater quantity of *Lespedeza* litter suggested that there should be a greater pool of available nitrogen in litter under *Lespedeza* plants. It is possible that the presence of this litter, found around *Lespedeza* individuals, may facilitate germination of *Heterotheca* seeds. Soil or litter has been shown to affect germination in other species (Werner 1975, Monk

and Gabrielson 1985, Fowler 1988, Williams et al. 1990, Smith and Capelle 1992, Moro et al. 1997). To investigate such effects on the earliest life stage, the first greenhouse study focused on the germination response of *Heterotheca* to soil and litter taken either distant from or in close proximity to *Lespedeza* in the field.

In the second of the two greenhouse experiments, *Heterotheca* individuals were grown under shaded and unshaded conditions, and at varying levels of soil nitrogen. If facilitation occurred during the growth period of *Heterotheca* through such mechanisms of resource modification, then one would expect to see a response by *Heterotheca* individuals to varying levels of these resources. Increasing soil fertilization has been shown typically to cause increases in biomass and changes in resource allocation (Hunt and Bazzaz 1980, Peace and Grubb 1982, Wilson and Tilman 1991, Huberty et al. 1998). Shade effects may lead to reduced growth and/or reproductive output (Peace and Grubb 1982, Griffith 1998, McKenna and Houle 1999), or may promote survival and growth by tempering a harsh microclimate (Tiedemann and Klemmedson 1977, Rodriguez-Echeverria and Perez-Fernandez 2003).

These studies provide a foundation for understanding the complex interactions between *Heterotheca* and *Lespedeza*. By establishing a positive spatial association between individuals of the two species, demonstrating that *Lespedeza* can affect multiple environmental resources, and showing that *Heterotheca* responds to such changes, particularly soil nitrogen and shade, I showed that *Lespedeza* is both a potential facilitator and competitor of species such as *Heterotheca*.

SITE AND SPECIES DESCRIPTION

The Savannah River Site (SRS) is a federal installation located along the Savannah River in South Carolina. Researchers from the University of Georgia began studying ecosystem processes in several fields across this site shortly after they were abandoned from agriculture in 1951. The field in which I am studying *Lespedeza* and *Heterotheca* has commonly been referred to as "field 3-412" and is located on the Pleistocene Coastal Terrace of the Upper Coastal Plain, about a mile from the Savannah River, in Aiken County, South Carolina (Odum 1960). The soil is Cahaba Loamy-Sand, with an AP horizon composed of roughly 80% sand, 9% silt, and 11% clay (Odum 1960). Nitrogen levels are known to be extremely low and limiting; Odum (1960) reported them as below detection level, and later measurements report nitrogen levels averaging 0.02 $\mu g*g^{-1}$ (Collins and Pinder 1990).

Lespedeza cuneata (Dumont) G. Don is a nitrogen fixing perennial legume (Hoveland and Donnelly 1985). Native to Asia, *L. cuneata* was first introduced to the United States in the late 19^{th} century (Hoveland and Donnelly 1985). It has been used extensively as a forage species and for erosion control (Hoveland and Donnelly 1985, Cripps and Bates 1993) and now is found throughout the southeastern states (Wilbur 1963). *Lespedeza* species are also referred to as bush clover (Blake 1924), and *L. cuneata* is commonly referred to as Sericea (Hoveland et al. 1990).

Lespedeza cuneata individuals each year produce between 1 and 50 stems from the base that reach heights of 1 - 1.5 m. Stems emerge in spring and senesce in the fall, but previous season's stems persist as standing dead throughout the following year. *Lespedeza cuneata* individuals are long lived and drought tolerant (Hoveland et al. 1990). In field 3-412, clusters of individuals frequently form patches of various sizes at a wide range of densities, from areas

where it is so thick that it has excluded most other dominant species, to other areas where it is sparse or non-existent.

Lespedeza has a long history in field 3-412; records of its presence extend back to 1962 (Golley 1965), when it was first collected for studies of biomass. An annual *Lespedeza, L. striata,* may have predated *L. cuneata* in the field as it was listed as an old-field dominant by Odum (1960). Both species were also evident in a twelve-year old field dominated by broomsedge (*Andropogon* sp.) (Golley and Gentry 1965), with *L. striata* having almost twice the standing crop of *L. cuneata.* Both annual and perennial species of *Lespedeza* were found in a nearby one-year field, suggesting that they can quickly spread to neighboring areas. Additional evidence of the "patchy" and transient nature of *L. cuneata* is given by Crapo and Coleman (1972), who report that *Lespedeza* spp. were quickly moving into some areas of field 3-412 by 1970 (19 years after abandonment), but were found at low frequencies in other areas of the field. In some areas, *L. cuneata* can replace the typical broomsedge community after 8-12 years (Wiegert and McGinnis 1975). Since the broomsedge stage occurred 8 years after agricultural abandonment in field 3-412 (Golley 1965), this may imply that *L.cuneata* could become the primary dominant species in areas after 16-20 years.

Currently, 50 years after abandonment of agriculture, there are still areas of field 3-412 that have not yet become dominated by woody species. *Lespedeza cuneata* is still found as a dominant species in much of the area of this field that has retained herbaceous vegetation. The annual *L. striata* species still occurs within the field as well, but at a much lower frequency than *L. cuneata.* This dissertation focuses on *L. cuneata*, hereafter called *Lespedeza*.

Heterotheca subaxillaris (Lam.) Britt. & Rusby, an annual or sometimes biennial composite species found in fields and roadsides (Radford et al. 1964), was also an early

colonizer of the old fields of the SRS. *Heterotheca* is one of the largest annuals found in the field, with heights for the tallest individuals approaching 1.5 meters. Though it can be a biennial, with over-wintering rosettes, in this field it is almost always an annual. This plant germinates in the early spring and persists as a rosette of leaves until the summer when it begins to bolt. Individuals flower and set seed in October and November. Seeds of *Heterotheca* are polymorphic, with both ray and disk seeds. Disk seeds (with a pappus) are wind dispersed and germinate readily, while ray seeds drop close to the parent and remain dormant until the following year (Baskin and Baskin 1976). Despite these differences, there are no differences in genetic diversity between the two types of seeds (Gibson 2002). In field 3-412, *Heterotheca* is reported to have established and been considered a dominant species in the third year after abandonment (Odum 1960). Its dominance in the field was also noted after twelve years (Golley and Gentry 1965). Currently, *Heterotheca* is not found widely in field 3-412 but it can dominate in areas where it is found.

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CHAPTER 2

SPATIAL PATTERN ANALYSIS AND MODELLING OF *HETEROTHECA SUBAXILLARIS* AND *LESPEDEZA CUNEATA* IN A SOUTH CAROLINA OLD FIELD

INTRODUCTION

In ecology, spatial pattern analysis typically is used to identify the scale and intensity of aggregation or regularity within populations or communities. Because competition should lead to a more uniform or regular spacing among individuals between species, and facilitation should lead to a clustering or aggregation of individuals, pattern analysis is often used to infer these potential biotic interactions (Hill 1973, Callaway 1995).

Ripley's K-functions (Diggle 1983) have been used widely for investigating patterns in plant ecology since the mid-1980's (Sterner et al. 1986, Skarpe 1991, Szwagrzyk and Czerwczak 1993, Haase et al. 1996, Scott et al. 1997, Barot et al. 1999, Eccles et al. 1999). The advent of these methods, coupled with the increasing accessibility and capability of computers, has allowed a more thorough analysis of spatially explicit data sets. Previous work on pattern analysis primarily focused on quadrat, transect or nearest neighbor analyses (Hill 1973, Greig-Smith 1979, Yavitt and Smith 1983, Dale and MacIsaac 1989, Wong et al. 1990, Stohlgren 1993, Fransen et al. 1998, Liu 2001).

Many recent ecological studies that incorporate K-function analysis do so with forest or tree species and focus on hypotheses concerning competition (Szwagrzyk 1992, Peterson and Squires 1995, Martens et al. 1997, Moeur 1997, Batista and Maguire 1998). A few studies

employing spatial pattern analysis have examined shrublands or desert plant communities (Haase et al. 1996, Haase et al. 1997, Eccles et al. 1999, Haase 2001). Although clumped or aggregated patterns are frequently seen, they are often attributed to either limited seed dispersal or site heterogeneity (Sterner et al. 1986, Skarpe 1991, Szwagrzyk and Czerwczak 1993, Couteron and Kokou 1997, Barot et al. 1999). Facilitation is rarely mentioned as a possible hypothesis for patterns of aggregation (Martens et al. 1997, Eccles et al. 1999, Haase 2001).

Although spatial analyses have been used to identify the presence of patterns and often infer plant interactions, fewer ecological studies take the next step of modelling the relationships between species to try to further characterize the patterns found. One exception is a study by Batista and Maguire (1998), which used neighborhood and individual variables to model tropical tree ingrowth and mortality as a Poisson process.

The co-occurrence of *Heterotheca subaxillaris* and *Lespedeza cuneata* in a South Carolina old field provided an excellent opportunity to study spatial patterns within the framework of potential biological interactions. In this old field, the annual (or infrequently biennial) *Heterotheca* is usually only found near *Lespedeza,* a nitrogen-fixing perennial legume, suggesting a possible positive association between the two. In addition, the patchy dominant nature of *Lespedeza* within this field, coupled with its perennial status, make it a potential strong competitor, especially at high densities.

The goals of this chapter were to characterize the spatial relationship between the two herbaceous plant species, and to investigate the relationship between *Heterotheca* and *Lespedeza* density. I hypothesized (1) that *Heterotheca* and *Lespedeza* were positively spatially associated and that the degree of this spatial association would increase as *Heterotheca* matured from juveniles to adults, indicating facilitation mechanisms likely operating throughout the growing

season. I also hypothesized (2) that there was a relationship between the densities of *Heterotheca* and *Lespedeza*, and that *Heterotheca* should be more likely found at moderate rather than at either high or low densities of *Lespedeza*. In addition, I hypothesized (3) that both the size and distance of the *Lespedeza* individuals within the neighborhood should be important in determining an index of *Lespedeza* density. The form of this index is similar to the competitive indices discussed by Weiner (1982, 1984), which were designed to provide a measure of crowding of individuals within a neighborhood around a focal individual. The presence of *Lespedeza* should also impact *Heterotheca* survival, growth and reproduction.

I hypothesized (4) that there would be a non-random pattern of *Heterotheca* mortality. Surviving adult *Heterotheca* individuals should be more strongly associated with *Lespedeza* due to its facilitative influence than would be expected if mortality were random. I hypothesized (5) that *Heterotheca* biomass, height, and total seed weight would also be influenced by *Lespedeza* density. *Heterotheca* found at the highest *Lespedeza* densities should have lower biomass and total seed weight than those found at moderate densities due to competition from the larger *Lespedeza*, but plants may be taller due to stem elongation as a response to shading (Ballare 1994). Also, I predicted that *Heterotheca* found at low to moderate densities of *Lespedeza* would show increased biomass, total seed weight and height due to their association with *Lespedeza*.

METHODS

Data Collection

In spring 1999, a 50x20m plot was established in a representative area of the old field containing both species. The plot was gridded at 5m intervals, and all individuals of *Heterotheca*

and *Lespedeza* were mapped using methods of triangulation. Juvenile *Heterotheca* plants were mapped (591 individuals) in April of 1999 and their heights were measured. Heights of surviving mature plants were measured again at the time of seed collection.

During the fall, seeds were harvested on 15 dates, beginning October 15, and continuing through November 16. Seeds were collected for each flowering plant as they matured. *Heterotheca* plants have up to 200 individual flowers, each of which contains upwards of 100 individual seeds, including central disk seeds with a pappus and marginal ray seeds without a pappus. Seeds mature over approximately a one-month period. Flower heads were deemed ready for harvesting when the pappus was fully open and the disk seeds were easily removable. Within an individual plant, flowers matured at different times over the course of this month. This necessitated revisiting individuals on multiple days. Seeds, including the pappus on the disk seeds, were collected in envelopes and weighed.

The 314 individuals that survived were harvested by pulling the plant out of the ground and cutting off the root portion at the nexus between stem and root. After drying to constant weight at 60 C, above ground biomass was measured. Below ground biomass was not measured due to the difficulty of sufficiently removing the roots from the soil.

Lespedeza plants were mapped in November 1999 and the number of stems, basal diameter and height of the tallest stem were recorded. The number of mapped *Lespedeza* individuals was 1290, and 8578 total stems were counted.

Additional data collected for both *Heterotheca* and *Lespedeza* in the same plot in 2001 were used for pattern analysis and regression. At the end of the 2001 growing season, *Heterotheca* and *Lespedeza* individuals were mapped again and *Heterotheca* plants were harvested. Above ground biomass was measured as in 1999. Seeds were not collected this year.

Because mechanisms responsible for spatial pattern may operate at different life stages, examining data sets taken early and late in the growing season can help elucidate timing of potential mechanisms. For both the pattern analysis and the modelling, two *Heterotheca* data sets were compared - one set of positions of juvenile *Heterotheca* taken in early spring 1999, and the second set of surviving adult *Heterotheca* individuals taken in fall of 1999. Those individuals found in the first but not the second data set were presumed to have died and a data set of these individuals was used to test the random mortality hypothesis. All data sets were compared with a single *Lespedeza* data set, measured in the fall.

Pattern Analysis

The *K* function was used to investigate the spatial patterns of *Heterotheca* and *Lespedeza*, as they occurred in the old-field study area. The function *K(t)* characterizes the second-order properties of a strongly stationary, isotropic point process (Diggle 1983). *K(t)* was defined as the expected number of individuals within distance *t* of each focal individual divided by l, the mean number of such events (individuals) per unit area. Because $l|A|$ is the expected number of events found in region *A*, the expected number of pairs of events up to a distance *t* apart (with the first event being found in *A*) is then $l^2|A|K(t)$.

Ripley's $\hat{K}(t)$ was used as the edge-corrected estimator of *K(t)* (Diggle 1983):

$$\hat{K}(t) = n^{-2} \mid A \mid \sum_{i \neq j} w_{ij}^{-1} I_t(u_{ij} \leq t)$$

where $|A|$ is the area of the study plot, n is the total number of events in A, u_{ij} is the distance between the ith and the jth event, I_t is an indicator function, and w_{ij} serves as an edge-correcting factor by weighting each pair by the proportion of the circumference of a circle of radius u_{ij} from the ith event that was in the study plot A (Diggle, 1983). The indicator function, I_t will be equal

to zero unless the condition of $u_{ij} < t$ is satisfied, in which case I_t will be equal to one. This will allow only those pairs of points within the distance class of t to be included in the calculation of $\hat{K}(t)$.

The L function was used to present the results of the data analysis:

$$\hat{L}(t) = \sqrt{\frac{\hat{K}(t)}{p}} - t$$

where $\hat{K}(t)$ is the estimate of Ripley's K function at distance class t. This function is more easily interpreted than the $\hat{K}(t)$ function because its expected mean value at all distances under the hypothesis of complete spatial randomness (CSR) is 0, as the expected mean value of $\sqrt{\hat{K}/p}$ under CSR is t, and because it stabilizes the variance.

The K function was used for investigating patterns within a single species. While I initially considered the degree of spatial patterning within each species, I was more interested in the inter-species patterning that may have arisen from potential interactions between *Heterotheca* and *Lespedeza*. For two species, I defined the Cross $\hat{K}(t)$ function as the expected number of individuals of the target species within distance t of an individual of the focal species divided by l, the mean number of such events per unit area.

$$\hat{K}(t) = n^{-2} \mid A \mid \sum_{i \neq j} w_{ij}^{-1} I_t(u_{ij} \leq t)$$

The definitions of the $\hat{K}(t)$ and Cross $\hat{K}(t)$ functions are the same except that here i and j represent separate species. The Cross $\hat{K}(t)$ function was calculated twice, once with the first species designated as the focal or "i" species, while the second was designated as the target or

"*j*" species, and then once with the opposite designations. These separate calculations were then averaged to yield an overall cross $\hat{K}(t)$ function.

A goodness of fit test was performed on the data set to test for the deviation from CSR. The Cramer - Von Mises statistic was defined as follows:

$$CVM = \int \left(\sqrt{\hat{K}(t)} - \sqrt{\overline{K}(q,t)} \right)^2 dt$$

where $\hat{K}(t)$ is the estimated *K* function for the data and $\overline{K}(q,t)$ is the *K* function under the null hypothesis. Since the expected value of the *K* function, assuming CSR, is $t^2 p$, I substituted this for $\overline{K}$ and so the function becomes:

$$CVM = \int \left(\sqrt{\hat{K}(t)} - t\sqrt{p} \right)^2 dt$$

If the data exhibited characteristics of CSR, this statistic should have been close to 0.

The Cross $\hat{L}(t)$ function was used to present the data. It is similar to the *L* Function in that it is a transformation of the Cross *K* function.

$$\hat{L}(t) = \sqrt{\frac{Cross\ \hat{K}(t)}{p}} - t$$

The above analysis was performed on the mapped data to determine both intra- and inter-species patterning. All analyses were done on both the juvenile and adult *Heterotheca* data sets. First, I estimated $\hat{K}(t)$ for *Heterotheca*, and then I estimated the cross $\hat{K}(t)$ for both *Lespedeza* and *Heterotheca*. Both analyses were done for *t* up to 10m, with a total of 100 distance classes (10 cm intervals).

While the positions of the *Lespedeza* were held constant, 999 sets of *Heterotheca* positions were realized from a Poisson process that exhibited CSR and that had the same original

intensity as the mapped data. The 5% confidence bands were estimated from these simulated data sets. Deviation outside of these bands indicated a significant departure from CSR. A value of the $\hat{L}(t)$ or the cross $\hat{L}(t)$ above the bands indicated a positive spatial association or clustering of individuals.

The Cramer-Von Mises test statistic (CVM) was calculated for the real data as well as for the simulated data sets. The resulting CVM statistics for the data and the simulated data sets were then ranked. A comparison of the rank of the data to that of the simulations would indicate deviation from the null model. If the CVM statistic calculated for the data fell outside of 95% of the CVM statistics calculated for the simulated data sets, then the CVM statistic would be deemed to be significantly different from those of the null model. A *p*-value was calculated by dividing the rank of the data's test statistic by 1000. The data were deemed statistically different from the null model if their *p* - value was greater than .05.

In order to test for non-random mortality, confidence bands were created to reflect the patterns generated by choosing a random subset of juvenile individuals. Individuals of the juvenile data set were randomly selected without replacement until the number of survivors was reached. Confidence bands were computed from the $\hat{L}(t)$ calculated on 1000 of these sets and compared with the $\hat{L}(t)$ computed from the set of surviving (adult) individuals.

Modelling

The positions of the adult *Heterotheca* individuals in 1999 and 2001 were modeled as a Poisson process whose intensity was dependent on the neighborhood density of *Lespedeza*. For the *Lespedeza* density variable, I propose a "Neighborhood Density Index" (NDI). Information on the number, size (as measured by the number of stems), and distance of *Lespedeza* individuals

within a 1-meter radius were incorporated into an index that represents a measure of the intensity of *Lespedeza* at any given location. A 1-meter radius was chosen after initial trials using larger radii yielded poorer fitting models. Information on each *Lespedeza* individual within a set neighborhood was summed together to form an index that increased with increasing density of *Lespedeza*. The contribution to the NDI for each *Lespedeza* individual was proportional to its size and inversely proportional to its distance. That is, a close, large neighbor would have a greater contribution to the NDI than a small, more distant neighbor.

The general form of the model is as follows:

$$l(s;q) = \exp[q' X(s_i)]$$

where s_i represents the spatial position of the individual *Heterotheca* plants in area A, $l(s_i; q)$ is a vector of intensities at position s_i given the vector of parameters q, q is a vector of parameters- (q_0, q_1, q_2…) and $X(s_i)$ is a function representing the neighborhood density index of *Lespedeza*.

The NDI is represented by $X(s_i)$. The general form of the $X(s_i)$ function is as follows:

$$X(s_i) = \sum_{j=1}^{N} \frac{z_j^{\,a}}{d_j^{\,g}}$$

where N is the number of *Lespedeza* individuals within a 1-meter neighborhood of s_i. Size variable z_j denotes the number of stems of the jth *Lespedeza* and d_j denotes the distance from the jth *Lespedeza* to the s_i *Heterotheca* individual. The variables α and γ serve as transformation factors that determine how the *Lespedeza* size and distance variables contribute to the NDI. Values for α were 0, 0.5, and 1; values of γ were 0, 0.5, 1 and 2. The variable α dictates how quickly the index increases with each increase in stem number. The γ dictates how quickly the contribution of the neighbor to the NDI diminishes with increasing distance. The larger the γ,

the more quickly this input drops off. All combinations of (α,γ) were used as possible models (Figure 1).

The simplest model therefore had (α,γ) = (0,0) and represented a count of the number of *Lespedeza* individuals within the neighborhood. Other potential models incorporated a measure of the size of the *Lespedeza* individuals within the neighborhood, and/or a factor that discounted the contributions of far neighbors.

Parameters were estimated for a linear and a quadratic model using common statistical methods programmed in Fortran. Let $\hat{q} = b$.

The linear model was: $l(s_i; b) = \exp\left[b_0 + b_1 * X(s_i)\right]$

The quadratic model was: $l(s_i; b) = \exp\left[b_0 + b_1 * X(s_i) + b_2 * X(s_i)^2\right]$

Parameter estimation was accomplished by finding the set of b that maximizes the following log likelihood function:

$$L(q) = \sum_{i=1}^{N} \log\, l(s_i; q) - \int_A l(s_i; q)\, ds$$

where s_1, $s_2 \ldots s_n$ were locations of the n *Heterotheca* individuals and q was the vector of parameters to be estimated.

An iterative algorithm including the Newton-Raphson Gradient Vector was used to estimate the parameters (Thisted 1988). At each iteration, the parameter vector was updated as follows:

$$\hat{q}^{(t+1)} = \hat{q}^{t} - H(\hat{q}^{t})^{(-1)}\, x\, g(\hat{q}^{t})$$

(0,0)	$\sum_{j=1}^{N} 1$	(0,0.5)	$\sum_{j=1}^{N} \frac{1}{d_j^{.5}}$	(0,1)	$\sum_{j=1}^{N} \frac{1}{d_j}$	(0,2)	$\sum_{j=1}^{N} \frac{1}{d_j^{2}}$
(0.5,0)	$\sum_{j=1}^{N} z_j^{.5}$	(0.5,0.5)	$\sum_{j=1}^{N} \frac{z_j^{.5}}{d_j^{.5}}$	(0.5,1)	$\sum_{j=1}^{N} \frac{z_j^{.5}}{d_j}$	(0.5,2)	$\sum_{j=1}^{N} \frac{z_j^{.5}}{d_j^{2}}$
(1,0)	$\sum_{j=1}^{N} z_j$	(1,0.5)	$\sum_{j=1}^{N} \frac{z_j}{d_j^{.5}}$	(1,1)	$\sum_{j=1}^{N} \frac{z_j}{d_j}$	(1,2)	$\sum_{j=1}^{N} \frac{z_j}{d_j^{2}}$

Figure 1. Combinations of α (0,0.5,1) and γ (0,0.5,1,2) yield the various forms of the Neighborhood Density Index (NDI) shown above and calculated for each *Heterotheca* individual. *Z* represents number of stems of the *j*-th *Lespedeza*, *d* represents the distance between the *j*-th *Lespedeza* and the focal *Heterotheca*. As α increases, the contribution of larger stemmed individuals to the NDI increases. As ? increases, the contribution of distant *Lespedeza* individuals to the NDI decreases.

where *t* is the iteration number, *q* is the vector of parameters, *H(q)* is the Hessian matrix, and *g(q)* is the gradient vector. Let the gradient vector be defined as:

$$g(q) = \frac{d}{dqdq'} L(q) = \sum_{i=1}^{N} \frac{\dot{l}(s_i;q)}{l(s_i;q)} - \int_A \dot{l}(s_i;q)ds$$

where $$\dot{l}(s_i;q) = \frac{d}{dq} l(s_i;q)$$

The first part of the gradient reduces, in matrix notation, to:

$$\sum_{i=1}^{S_n} \frac{\dot{l}(s_i;q)}{l(s_i;q)} = \begin{bmatrix} S_n \\ \sum_{i=1}^{S_n} X(s_i) \end{bmatrix} \quad \text{Linear Model}$$

$$\sum_{i=1}^{S_n} \frac{\dot{l}(s_i;q)}{l(s_i;q)} = \begin{bmatrix} S_n \\ \sum_{i=1}^{S_n} X(s_i) \\ \sum_{i=1}^{S_n} [X(s_i)]^2 \end{bmatrix} \quad \text{Quadratic Model}$$

The set of locations, s_i, used in this part of the gradient are based on the locations of *Heterotheca* individuals in the study area. The second part of the gradient reduces to:

$$\int_A \dot{l}(s_i;q) = T(s_i)' * \exp[b * X(s_i)]$$

where $T(s_i) = [1 \quad X(s_i)]$ for a linear model and $T(s_i) = [1 \quad X(s_i) \quad X(s_i)^2]$ for a quadratic model. For the second part of the gradient, $X(s_i)$ is calculated using 5000 randomly selected locations in the study area.

H(q), the Hessian matrix, is defined as:

$$H(q) = \frac{d}{dqdq'} L(q) = \sum_{i=1}^{n} \left\{ \frac{\ddot{l}(s_i;q)}{l(s_i;q)} - \frac{\dot{l}(s_i;q)\dot{l}(s_i;q)'}{l(s_i;q)^2} \right\} - \int_A \ddot{l}(s_i;q)ds$$

which reduces to:

$$H(q) = -\int \frac{\dot{l}(s_i;q)\,\dot{l}(s_i;q)'}{l(s_i;q)}\,ds$$

This is also known as the Fisher Information statistic, which can be estimated by the inverse of the variance-covariance matrix of *X(s)* calculated using the *Heterotheca* data set. The code for calculating the inverse is found in Press (1992).

After initial estimation using the above algorithm, parameter estimates were further refined through the use of the Robbins-Monroe dampening algorithm. The same parameter estimation program was run, with the following changes. At each successive iteration, an increasing number of random points equal to $5000(t^{.25})$ was chosen to calculate the second part of the gradient. Once parameters were estimated and refined, tests were done to determine whether each parameter value was significantly different from 0.

A likelihood ratio test was performed to compare the quadratic and linear models within each data set. Taking the difference between the linear and quadratic models (of the same NDI and data set) and multiplying by two yielded the test statistic. This test statistic was chi-square distributed with one degree of freedom under the hypothesis of no quadratic effect. Therefore, in order to be significant at the .05 level, this value had to be greater than 3.84.

Assessment of model fit was done through the calculation of a Cramer - Von Mises test statistic, and by comparing the cross $\hat{L}$ functions calculated for the collected data with a confidence interval calculated from simulated data. Simulated realizations of the final parameterized models were generated through rejection sampling. Data sets were again created by holding the *Lespedeza* constant and generating random points for the *Heterotheca* data set, but each random point was accepted into the final simulated data set with a probability equal to

the ratio of the calculated $\lambda(s;\beta)$ to the maximum λ. A cross $\hat{L}$ function was calculated for each of these 999 simulated data sets. The real data set was compared with the confidence envelope calculated from the 999 simulated data sets.

The Cramer - Von Mises statistic used as the goodness of fit statistic is as follows:

$$CVM = \int \left(\sqrt{\hat{K}(t)} - \sqrt{\overline{K}(\theta,t)} \right)^2 dt$$

In this case, no substitution was made for $\overline{K}(\theta,t)$ as was for the case where CSR was the null model. A CVM statistic was obtained for the data sets with $\overline{K}(\theta,t)$ determined by averaging the $\hat{K}(t)$ calculated for all simulations. When the CVM statistic was calculated for each simulation, the $\overline{K}(\theta,t)$ was calculated by averaging the $\hat{K}(t)$ over all other simulated data sets. Again, CVM statistics for the data set and simulations were ranked and the data were deemed to be statistically different from the modeled data if their p – value was greater than .05.

Frequency and Regression Analysis

The form of the NDI chosen as a result of the modelling was a continuous variable representing the localized density of *Lespedeza* for each individual *Heterotheca*. A comparison was made between the frequency distribution of *Heterotheca* across *Lespedeza* density and the expected frequency distribution given random placement of *Heterotheca*. Measures of *Heterotheca* growth and seed production were regressed against this NDI. Separate analyses were performed for both 1999 and 2001. *Heterotheca* individuals less than one meter from the edge of the plot were not included in the regression analyses. Biomass values and seed weights were log transformed in order to stabilize variances and thus reduce heteroskedasticity of the residuals. Both a linear (NDI) and a quadratic (NDI^2) term were used as independent variables. A logistic regression of mortality was performed on the 1999 data set.

RESULTS

In 2001, *Heterotheca* were larger and taller at the end of the growing season than individuals from 1999 ($p<.001$) (Table 1). *Lespedeza* individuals also had more stems and were on average taller than *Lespedeza* individuals from 1999 ($p <.001$). Of these 1159 *Lespedeza* individuals in 2001, 943 were most likely surviving individuals from 1999, based on their mapped positions. The average heights of the two species at the end of the season were similar in each year.

The $\hat{L}(t)$ functions for the juvenile and adult *Heterotheca* data sets for 1999 were plotted against lag distance, *t* (Figure 2). The expectation for *L(t)* under CSR was 0, therefore deviation from 0 indicated deviation from CSR. The 2.5 and 97.5 percentiles from simulated CSR data sets were computed for each lag distance to produce one-at-a-time 95% confidence bands. This provided a means for determining whether there was statistically significant deviation from CSR. Both the juvenile and adult data sets showed a significant departure from CSR as the $\hat{L}(t)$ function lay above the confidence band at all lag distances. A high degree of spatial clustering within the *Heterotheca* population was seen at all scales. The scale of maximum clustering occurred around 3 meters for the juvenile data set and around 3.5 meters for the adult data set.

The calculated cross $\hat{L}(t)$ functions for the juvenile and adult data sets for 1999 are also shown overlain on the confidence bands generated from simulated CSR data sets (Figure 3). Again, both the juvenile and adult data sets showed significant departure from CSR at all spatial scales. A positive spatial correlation between *Heterotheca* and *Lespedeza* was seen as the cross $\hat{L}(t)$ for the data lay above the confidence interval at all lag distances. This association was seen most strongly at scales between 2 and 4 meters and above 6 meters. For the juvenile *Heterotheca* data, there was an initial rise and peak of the cross $\hat{L}(t)$ function around 3 meters, a

Table 1. Size of *Heterotheca* and *Lespedeza* plants at the end of the growing season. a) Height, biomass and seed weight of *Heterotheca* plants in 1999 and 2001. b) Number of stems and height of each *Lespedeza* plant measured in 1999 and 2001.

a.

	1999			2001		
Heterotheca	N	Mean ± 2 S.E.	Range	N	Mean ± 2 S.E.	Range
Height (cm)	229	63.1 ± 2.90	19 - 1.24	477	80.8 ± 2.8	12 - 175
Vegetative Biomass (gm)	314	4.59 ± .574	0.07 - 29.0	476	11.89 ± 1.75	0.06 - 169.7
Seed Biomass (gm)*	288	0.538 ± 0.080	0.015 - 4.27	-	-	-

* weight of all seeds per plant

b.

	1999			2001		
Lespedeza	N	Mean ± 2 S.E.	Range	N	Mean ± 2 S.E.	Range
No. of Stems/plant	1290	6.74 ± 0.35	1 - 77	1159	7.66 ± 0.43	1 - 111
Height (cm)	1290	67.4 ± 1.49	6 - 135	1159	70.5 ± 1.20	5 - 137

a.

b.

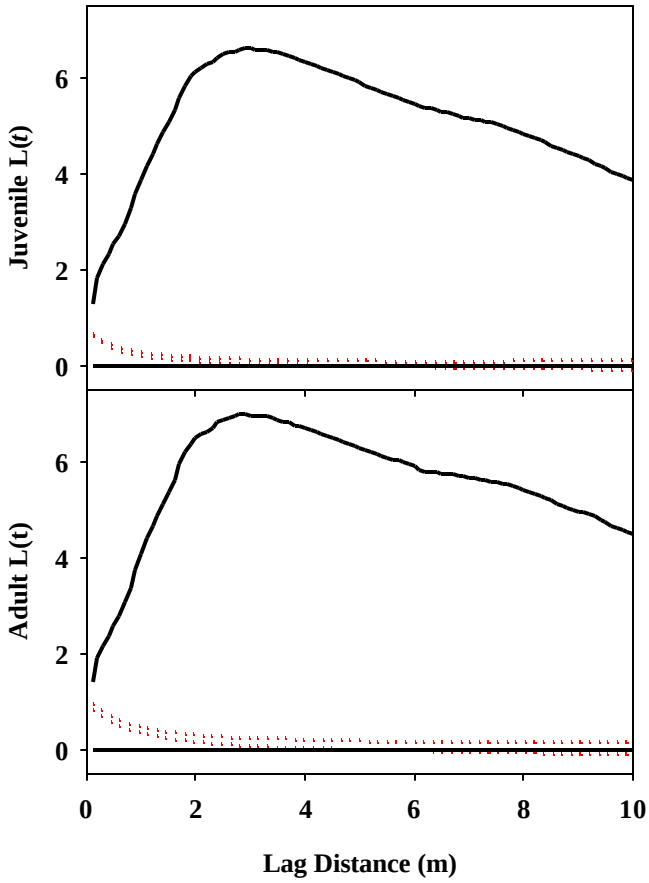

Figure 2. $\hat{L}(t)$ function plotted for the (a) Juvenile and (b) Adult *Heterotheca* data set measured in 1999. Dashed red lines represent upper and lower, one-at-a-time 95% confidence bands generated under the null hypothesis of complete spatial randomness (CSR).

a.

b.

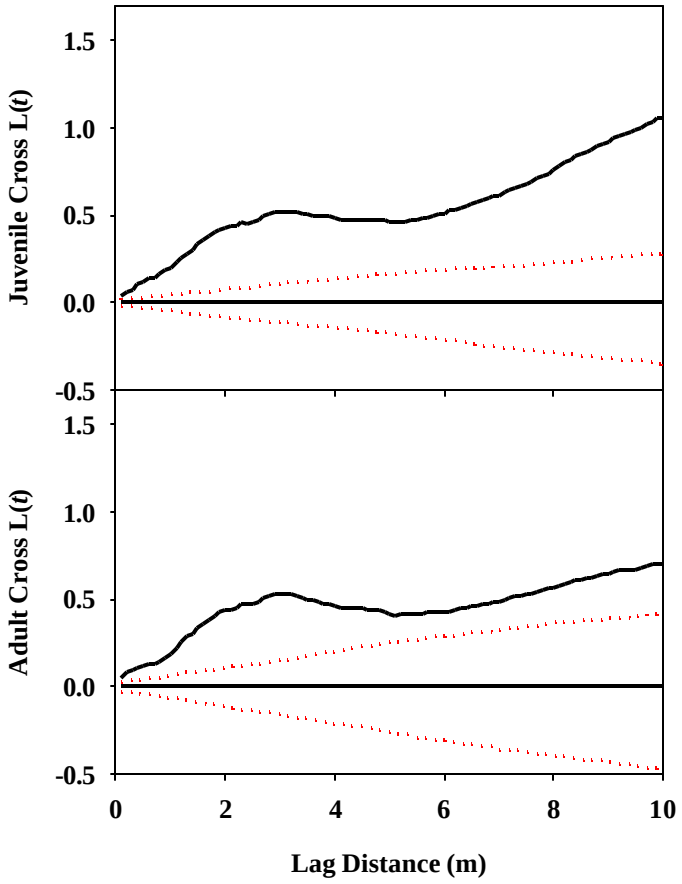

Figure 3. Cross $\hat{L}(t)$ function plotted for the a) Juvenile and b) Adult data, measured in 1999. Dashed, red lines represent upper and lower, one-at-a-time 95% confidence bands generated under the null hypothesis of complete spatial randomness (CSR).

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drop at around 5 meters and then an increase at around 6 meters. In the adult *Heterotheca* data set, the function behaved similarly; there was an initial rise as distance increased to around 3 meters, followed by a slight decline and then slight increase after 6 meters. In 2001, the *Heterotheca* $\hat{L}(t)$ function showed strong clustering with a peak at a scale of between 3 and 4 meters (Figure 4). While the overall pattern was similar to that of 1999, the intensity of the clustering was much less in 2001. The cross $\hat{L}(t)$ function also showed a significant degree of clustering between individuals of the two species.

Modelling

Both the juvenile and adult data sets were modeled using the 12 different NDI's and with both a linear and quadratic relationship. The linear and quadratic models with the same NDI and within the same data set were compared using the likelihood ratio test. Here the null hypothesis that $\beta_2 = 0$ was tested against $\beta_2 \neq 0$. The null hypothesis for each pair was rejected, indicating that the quadratic models performed significantly better than the linear models ($p < .001$) (Table 2).

The choice of the best NDI in the quadratic model was where the log likelihood was maximized (Table 3). Rankings indicated that the best model for both the adult and juvenile *Heterotheca* data was where $(\alpha,\gamma) = (0.5,0)$. In this case, the NDI is equal to the sum (for all *Lespedeza* individuals within the neighborhood) of the square root of the number of *Lespedeza* stems. Plots of the cross $\hat{L}(t)$ function for the juvenile and quadratic adult forms of this model indicate where the data deviates from the 95% confidence bands of the simulated data (Figure 5). The Cramer –Von Mises (CVM) statistic calculated for the juvenile quadratic model where $(\alpha,\gamma) = (0.5,0)$, was 29.69 ($p$ =.006), and for the adult quadratic model it was 36.22 (p=.046). Neither

a.

b.

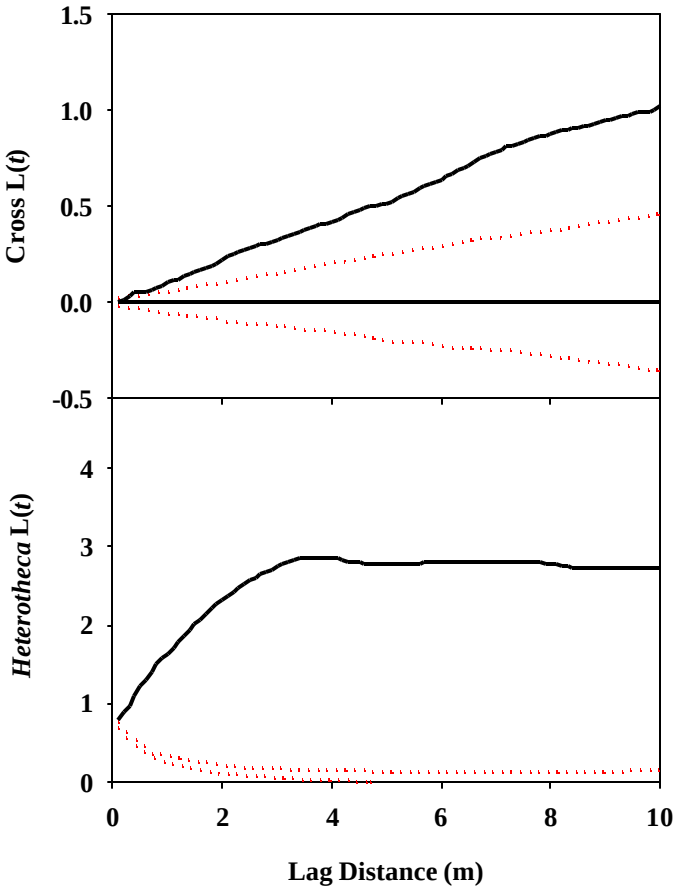


Figure 4. a) Cross $\hat{L}(t)$ function and b) *Heterotheca* $\hat{L}(t)$ function for 2001 data. Dashed red lines represent upper and lower, one-at-a-time 95% confidence bands generated under the null hypothesis of complete spatial randomness (CSR).

Table 2. Ratio Likelihood Test for β_2, juvenile and adult *Heterotheca* data sets. All values are significant at the $p<.001$ level. Values shown are 2 * (Juvenile Log Likelihood – Adult LogLikelihood) and are χ^2 distributed with 1 d.f.

Juvenile *Heterotheca* Data Set

		Distance (γ)			
		0	.5	1	2
Size	0	195.17	156.43	91.22	22.74
(α)	.5	233.99	204.14	131.28	21.66
	1	210.60	190.10	130.53	31.90

Adult *Heterotheca* Data Set

		Distance (γ)			
		0	.5	1	2
Size	0	94.15	79.88	47.43	18.14
(α)	.5	139.36	128.86	72.55	11.57
	1	140.82	135.89	76.63	13.94

Table 3. Comparison of Log-likelihood values for linear and quadratic models within the juvenile and adult *Heterotheca* data sets. Rankings (within parentheses) were used for model selection, with lower rankings indicating increasing likelihood.

Juvenile, Linear

Size (α) \ Distance (γ)	0	0.5	1	2
0	-863.16 (3)	-861.08 (2)	-860.80 (1)	-873.03 (7)
0.5	-871.54 (6)	-869.12 (5)	-867.89 (4)	-877.41 (9)
1	-880.77 (11)	-878.23 (10)	-877.22 (8)	-886.03 (12)

Adult, Linear

Size (α) \ Distance (γ)	0	0.5	1	2
0	-675.42 (4)	-673.26 (2)	-671.59 (1)	-676.14 (5)
0.5	-680.16 (8)	-677.77 (7)	-675.02 (3)	-676.27 (6)
1	-684.45 (12)	-682.32 (11)	-680.46 (9)	-680.46 (10)

Juvenile, Quadratic

Size (α) \ Distance (γ)	0	0.5	1	2
0	-765.57 (2)	-782.87 (5)	-815.20 (9)	-861.65 (10)
0.5	-754.54 (1)	-767.05 (3)	-802.25 (7)	-866.58 (11)
1	-775.47 (4)	-783.18 (6)	-811.96 (8)	-870.08 (12)

Adult, Quadratic

Size (α) \ Distance (γ)	0	0.5	1	2
0	-628.35 (5)	-633.32 (6)	-647.88 (9)	-667.07 (10)
0.5	-610.48 (1)	-613.34 (2)	-638.74 (7)	-670.48 (11)
1	-614.04 (3)	-614.38 (4)	-642.14 (8)	-673.49 (12)

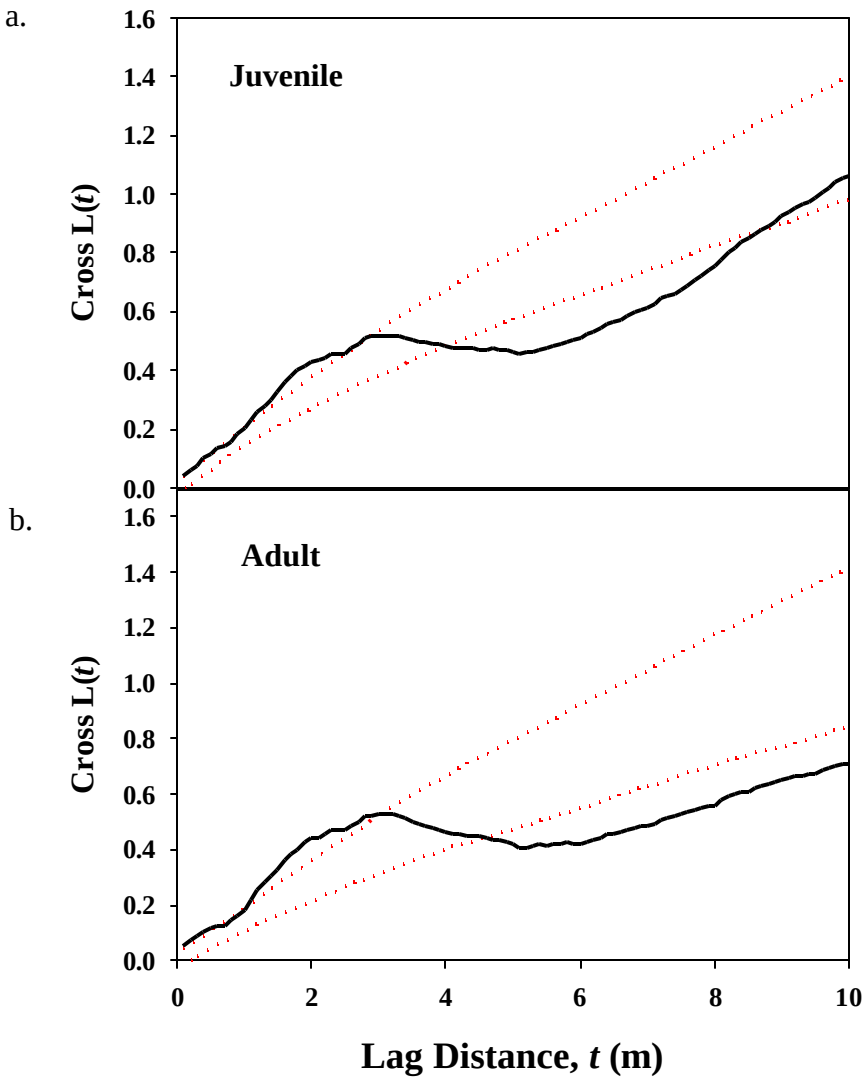


Figure 5. Cross $\hat{L}(t)$ function plots for a) juvenile and b) adult quadratic models of form (α,γ) = (0.5,0). Black lines represent the data, red dotted lines represent the 95% confidence bands for the simulated data.

was within the 95% range of values of the simulations, which indicated a general lack of fit of the data.

Frequency and Regression Analysis

The relative frequency of *Lespedeza* density for each adult *Heterotheca* individual plotted against the relative frequency of *Lespedeza* density for randomly distributed points in both 1999 and 2001 indicated an overall non-random distribution of *Heterotheca* individuals with respect to *Lespedeza* density (Figure 6). In both years there were fewer *Heterotheca* individuals found below an NDI of 10 than would be expected given the random frequency distribution. More *Heterotheca* individuals than expected were found between an NDI value of 10 and 20.

The frequency distribution pattern for random points was very similar between the two years, whereas the pattern for *Heterotheca* was less similar. While only a very small proportion of the population was found at an NDI value of 0 in 1999, over 20% of the 2001 population was found at this lowest index level. Similarly, less than 20% of the 1999 *Heterotheca* population was found at or below an NDI value of 5, but in 2001 this range of *Lespedeza* density accounted for around 40% of the population. *Heterotheca* plants in 2001 were also found at the other end of the density range; in 1999 no individuals occurred above an NDI value of 40, but in 2001 individuals were found up to an NDI value of 60.

Final height, biomass, and seed weight of *Heterotheca* individuals in 1999 increased as the *Lespedeza* NDI increased (Figure 7). The initial heights of *Heterotheca* individuals, measured in March, decreased with increasing *Lespedeza* NDI. Both linear and quadratic (including an extra NDI^2 term) regression models were examined. All linear models were significant ($P < .01$), whereas quadratic models proved not to be suitable. Overall, r^2 values were

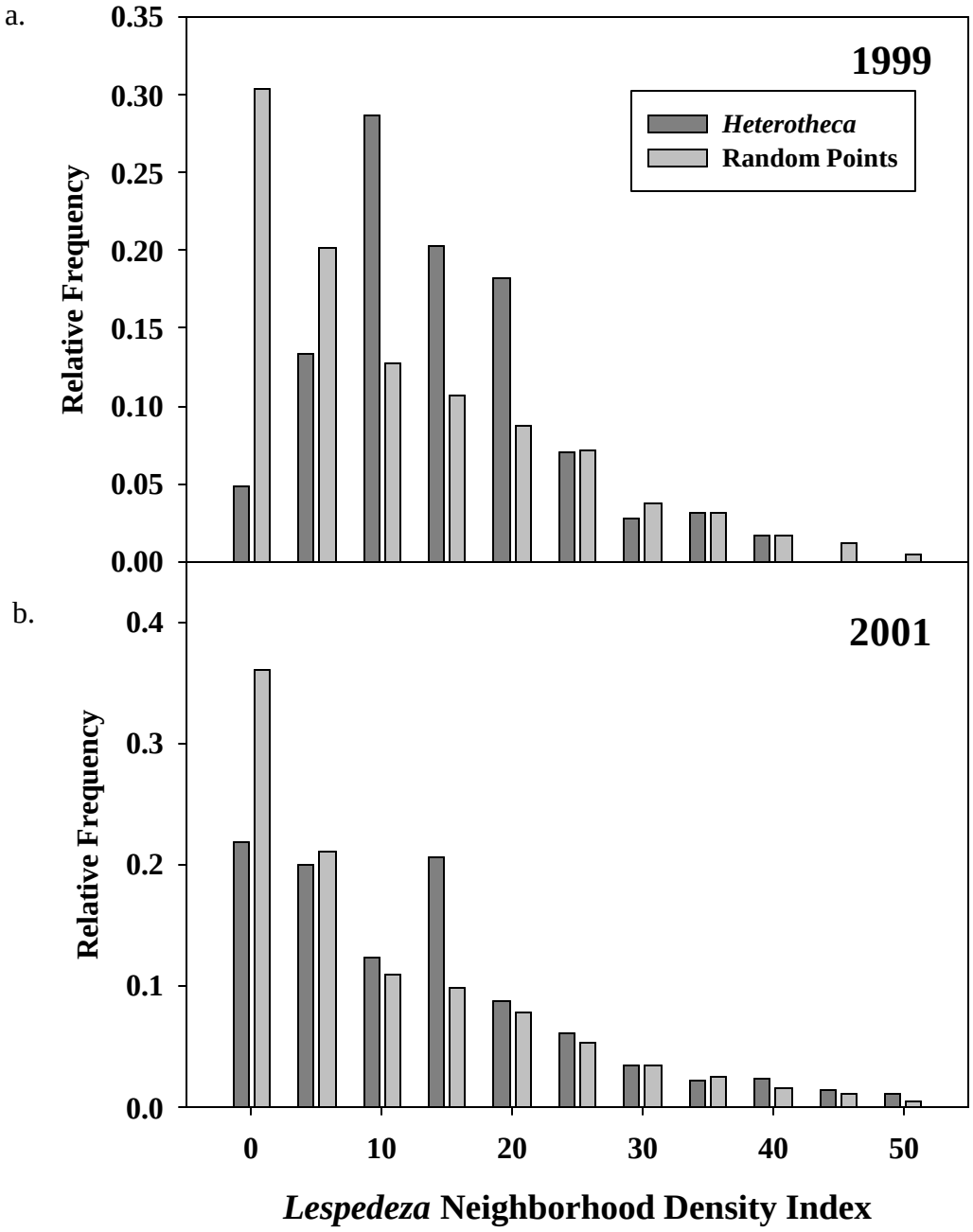


Figure 6. Relative frequencies of the *Lespedeza* densities for each *Heterotheca* individual versus the frequency of *Lespedeza* density for a similar number of randomly distributed points in a) 1999 and b) 2001. The *Lespedeza* density index is calculated as the square root of the number of stems summed over all individuals within a 1m radius.

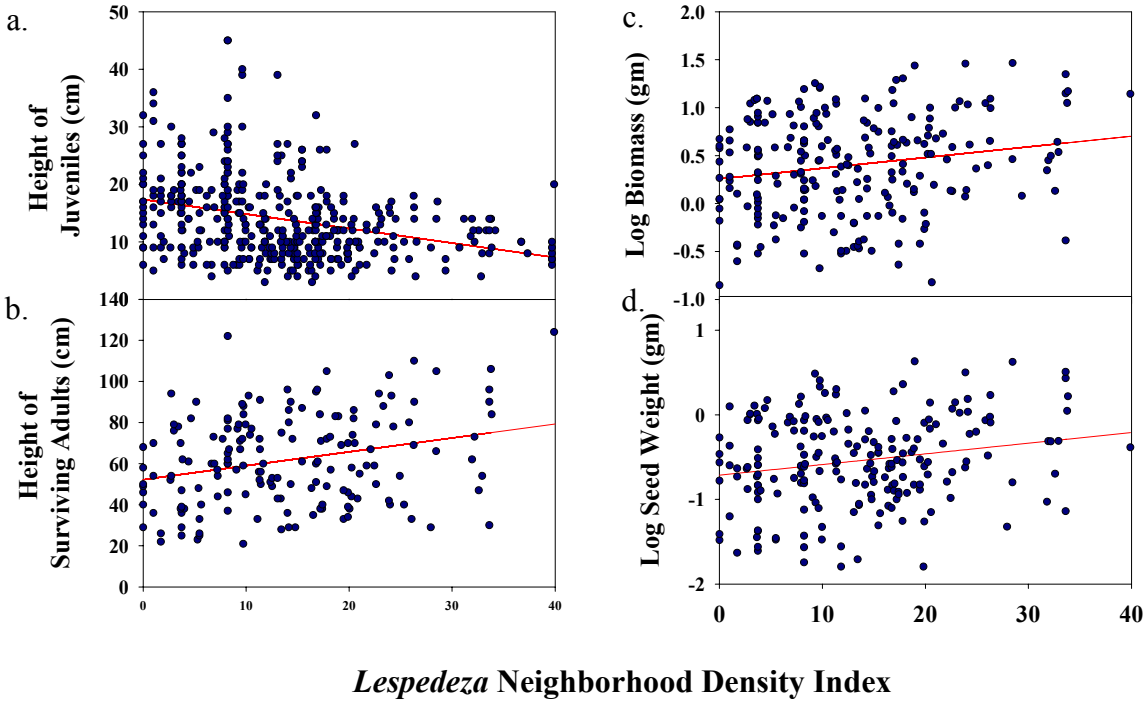


Figure 7. *Heterotheca* a) Juvenile height, b) Surviving Adult height, c) biomass and d) seed weight as a function of the *Lespedeza* NDI for 1999 data. Regression lines are shown in red. The *Lespedeza* neighborhood density index is calculated for each *Heterotheca* individual as the square root of the number of *Lespedeza* stems summed over all *Lespedeza* within a 1m radius.

low. For the height variable, the *Lespedeza* NDI explained 10.9% of the total variation for the juvenile heights, and 7.4 % of the total variation of the surviving adults' heights. For biomass (log), it explained 3.6%, and for seed weights, it explained 4.1% of the total variation. Patterns for biomass and height of *Heterotheca* as a function of the *Lespedeza* NDI were similar in 2001 (Figure 8). Here, the *Lespedeza* NDI explained 5.7% of the total variation of height and explained 5.3% of the total variation of *Heterotheca* log biomass.

Confidence bands reflecting the expected pattern resulting from random mortality were overlain on the adult *Heterotheca* data for 1999 (Figure 9). The cross - $\hat{L}(t)$ function showed significantly less clustering than would have been expected given random mortality. This difference is most apparent at scales of less than 3 meters, however, at scales of between approximately 2 and 3 meters there is a slight increase in clustering between individuals of the two species. A logistic regression of mortality as a function of the *Lespedeza* NDI indicated a higher probability of mortality as the *Lespedeza* NDI increased ($P<.05$).

DISCUSSION

The hypothesis (1) that there was a positive spatial association between *Heterotheca* and *Lespedeza* was supported by the pattern analysis. There was a significant degree of spatial clustering between the two species. Both the juveniles and the adults of *Heterotheca* showed similar patterns as evidenced by the cross $\hat{L}(t)$ plots. The presence of a spatial association between the two species for the juveniles as well as the adults of *Heterotheca* suggested that this pattern of clustering occurred early in the life cycle of *Heterotheca*.

This clustering between *Heterotheca* and *Lespedeza* early in the season suggests that facilitation mechanisms may operate at an early life stage in *Heterotheca*, such as the time of

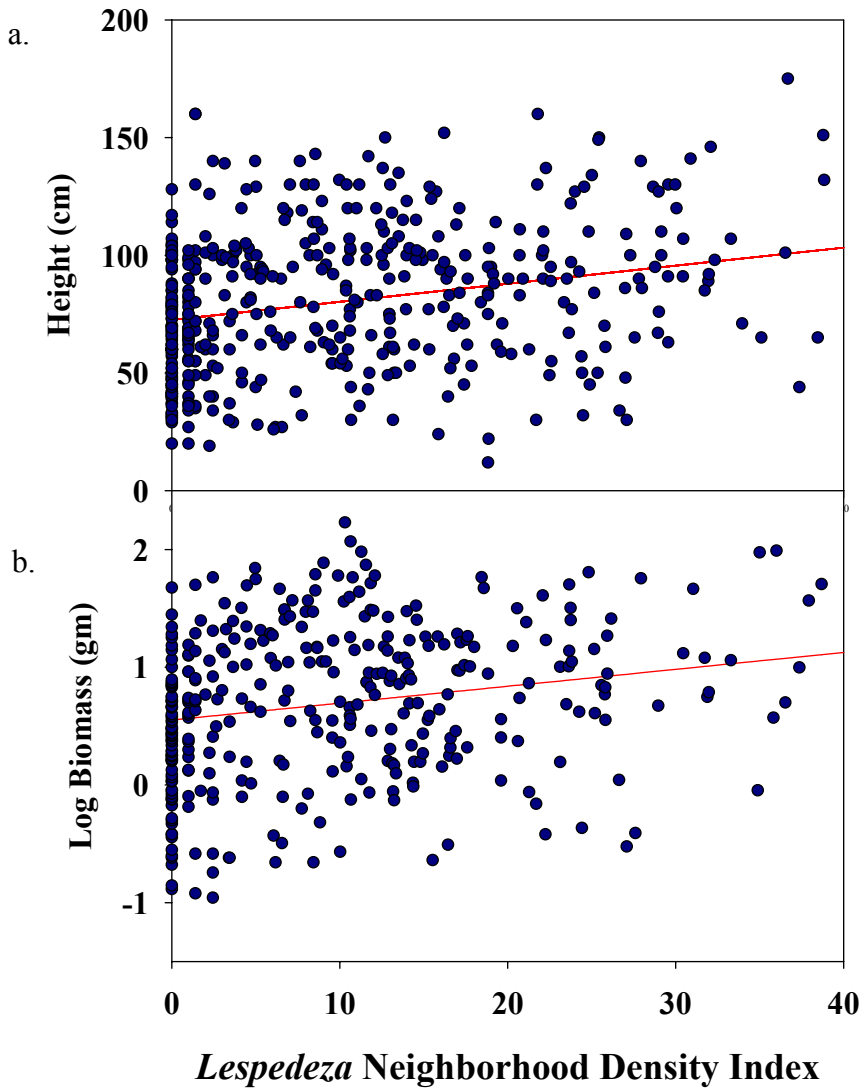


Figure 8. *Heterotheca* a) height and b) biomass as a function of the *Lespedeza* Neighborhood density index for 2001 data. Regression lines are shown in red. The *Lespedeza* neighborhood density index is calculated for each *Heterotheca* individual as the square root of the number of *Lespedeza* stems summed over all *Lespedeza* within a 1m radius.

a.

b.

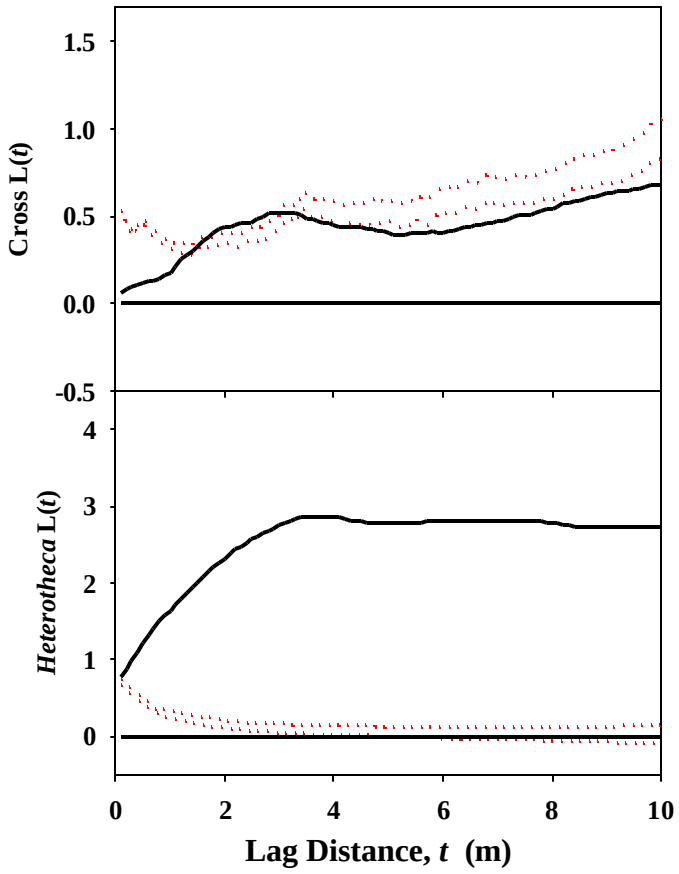


Figure 9. a) Cross - $\hat{L}(t)$ function and b) *Heterotheca* $\hat{L}(t)$ function for surviving (adult) individuals in 1999. Dashed red lines represent upper and lower, one-at-a-time 95% confidence bands for data simulated under the hypothesis of random mortality.

seed dispersal, germination, or seedling establishment. The decrease in clustering for the adults suggests that competitive mechanisms (rather than facilitation) operate during the growing season. This pattern of clustered young individuals is commonly seen in forest systems and often attributed to patchy or limited seed dispersal (Sterner et al. 1986, Skarpe 1991).

Few studies have incorporated spatial pattern analysis with a modelling approach. Moeur (1997) used stochastic, spatially explicit forest models to show a transition in pattern from clustered seedlings to regularly spaced adults. These patterns were then compared with, and deemed generally consistent with, the patterns of their field data. Jeltsch et al. (1999) explored the dynamics of Kalahari trees through stochastic, spatially explicit models in addition to an examination of field data. For both the simulated data and field data, they compared the $\hat{L}(t)$ generated from a K analysis to null models of complete spatial randomness. That is, they compared results of the modelling to confidence envelopes generated from simulations displaying random patterns. Similarly, I am interested in how well the patterns generated from simulated data based on my models capture the pattern of the observed *Heterotheca* distribution. I found that most of the quadratic models generated patterns that did capture the true cross $\hat{L}(t)$ at some range of distance scales, but none captured the exact shape of the cross $\hat{L}(t)$.

The hypothesis (2) that there was a moderate density of *Lespedeza* that maximized the intensity of *Heterotheca* was supported by this modelling. The quadratic models performed significantly better than the linear models in all cases, meaning that the intensity of *Heterotheca* did not increase across all densities of *Lespedeza*. Instead, the function was maximized at a moderate density of *Lespedeza*. As the density of *Lespedeza* increased, the *Heterotheca* intensity increased to a maximum point, and above this point, the intensity of *Heterotheca* decreased with increasing *Lespedeza* density. This is consistent with the hypothesis that both facilitative and

competitive interactions are occurring, with facilitative interactions mostly at moderate densities, and competitive interactions dominating at the highest densities of *Lespedeza*.

The NDI was designed to be a better representation of the local *Lespedeza* environment that was experienced by each individual *Heterotheca* than simple measures of the numbers of *Lespedeza* individuals. As Mack and Harper (1977) asserted, sizes and distances of neighbors are important in considering neighborhood effects on plant growth. Such indices that reflect the relative amount or density of neighboring individuals have been used before in modelling. Weiner (1984) also incorporated various combinations of size and distance of neighboring trees into an index that was used in growth models. He found size to be the most important factor in the index, and distance to be less important. Barot and Gignoux (2003) used a logistic regression to model leaf number increment as a function of several indices that incorporated height and the number of leaves of the neighbor. Wagner and Radosevich (1998) devised an index of shrub competition incorporating optimum and maximum heights raised to a varying exponential form. In each of these studies, determining which form of the index produced the best results yielded information on what types of factors were ecologically important.

One of my goals (3) was to find the NDI with the combination of the size and distance variables for *Lespedeza* that provided the best fitting model of *Heterotheca* intensity. For the quadratic models for both the adult and juvenile *Heterotheca*, the best form of the NDI includes a value of 0.5 for the size variable, α; this suggests that while size is important, the contribution to the overall density index of each *Lespedeza* individual is not directly proportional to its number of stems. Instead, the square root of the number of stems is added to the index. In the initial analysis, 0 and 1 were chosen as the two powers for α. If the power of the distance variable, γ, is 0, this leads to a tally of either the number of individuals within the neighborhood

(α=0), or the total number of stems within the neighborhood (α=1) (Figure 1). Based on the log-likelihood values of the models for the juvenile *Heterotheca* data set where α=0 or 1, the models that ignore size (α=0) performed better than those that include the number of stems in the NDI (Table 3). This result suggests that the presence of the *Lespedeza* individual was more important to juvenile *Heterotheca* plants than its size, which was contrary to the original hypothesis that the size of the *Lespedeza* individuals would be an important component of the models. It was reasoned that simply counting the number of individuals would not be adequate, as there is much variation in the sizes of the individual *Lespedeza* plants. Certainly an individual with 10 stems should contribute more to the crowding by *Lespedeza* than an individual with one or two stems. However, if α = 1, an individual with 10 stems would have a contribution to the NDI 10 times that of a single stemmed individual. A third level of α, 0.5 was then added in the analysis. The NDI still increases as the number of *Lespedeza* stems increases, but by a factor equal to the square root of the number of stems. For the quadratic models, α = 0.5 is better than either α = 0 or α = 1 for both the juvenile and the adult data set. In this case the contribution to the NDI is not directly proportional to the number of stems of *Lespedeza*, instead, the contribution increases by a factor equal to the square root of the number of *Lespedeza* stems.

Distance is the second variable component of the NDI. It was expected that the effect of a *Lespedeza* individual on the focal *Heterotheca* individual would diminish as the distance between the two increased. The contribution to the total NDI of a distant neighbor should therefore be less than that of a near neighbor. The rate at which this contribution diminishes is determined by the power to which the distance is raised. Four powers of distance in the denominator were tried (0, 0.5, 1, 2). With increasing distance, the contribution towards the index diminishes more rapidly with a higher power (i.e., 2) than with a lower power (i.e., 0.5).

Raising the distance to a power of 0 negates the effect of distance for each neighbor; close neighbors have the same contribution to the NDI as distant neighbors of the same size. At the opposite extreme lies $\gamma = 2$; in which case only the closest individuals within the neighborhood have any significant input to the NDI. It was hypothesized that a moderate power would be best; this would allow some discounting of the further neighbors while still retaining an influence of those at moderate distances.

For all quadratic models from the juvenile or adult data set, the poorest fits were found when $\gamma = 2$ (Table 3). This suggests that more than just the closest neighbors were important. For the quadratic models, there was a clear order for the set of γ variables. As γ increased, the log-likelihoods decreased, and a γ of 0 was the best choice at each level of α (Table 3). This suggests that distance was not important; all individuals within the neighborhood had an equal impact on the focal *Heterotheca* regardless of their distance. This may be attributed to the fact that the neighborhood radius was relatively small, at one meter. At this scale, discounting further neighbors was not necessary. For larger radii, it is likely that a different form of the NDI that includes a non-zero power of distance would be needed.

Both the juvenile and adult data sets were modeled in order to determine if there were any differences occurring between the early stages of *Heterotheca* growth and the resulting subset of surviving adults. A common observation is that juvenile plant individuals are aggregated, while adults tend towards regularity (Prentice and Werger 1985, Sterner et al. 1986, Skarpe 1991, Barot et al. 1999). For this study, overall the patterns were similar for the adult and juvenile data sets, with a slight trend towards regularity for the adult data set, suggesting the presence of competitive interactions during the growing season of *Heterotheca*.

By examining how the quadratic models perform at both times, it may be possible to gain information on whether there is a shift in the optimal *Lespedeza* density (that density which gives the maximum *Heterotheca* intensity). Three outcomes are possible (Figure 10). In the first case, the juvenile and adult data sets have similar optimal *Lespedeza* densities (Figure 10a). In this case, mortality operates independently of *Lespedeza* density. In the second case (Figure 10b), there is a shift in the adult response to the right. Surviving adults are more likely to be found at the higher densities of *Lespedeza*. This would lend support to the hypothesis that there may be positive interactions between the two species that lead to increased survival in areas of higher density of *Lespedeza*. In the third case (Figure 10c), the shift of the adult *Heterotheca* response is to the left. This would suggest that competitive interactions over the growing season might cause increased mortality at the higher densities of *Lespedeza*. It is possible that a density of *Lespedeza* that favors the establishment and early growth of *Heterotheca* may have more of a competitive effect later in the season. For the best fitting models, where $(\alpha,\gamma) = (0.5,0)$, there is a slight shift to the left (Figure 11), suggesting that mortality of adult *Heterotheca* plants may increase at higher densities of *Lespedeza*. This was also corroborated by the logistic regression.

The test of the random mortality hypothesis (4) compared the overall pattern of the surviving *Heterotheca* with the expected patterns had mortality been random. At small and large scales, a less aggregated pattern is seen which suggests that surviving *Heterotheca* plants are less closely associated with *Lespedeza* than expected (Figure 9). This may be the result of intraspecific competition as *Heterotheca* individuals are highly aggregated as juveniles, and the surviving *Heterotheca* individuals display much less intraspecific clustering than would be expected if mortality were random. In a descriptive study such as this, it is not possible to separate the effects of intraspecific and interspecific competition.

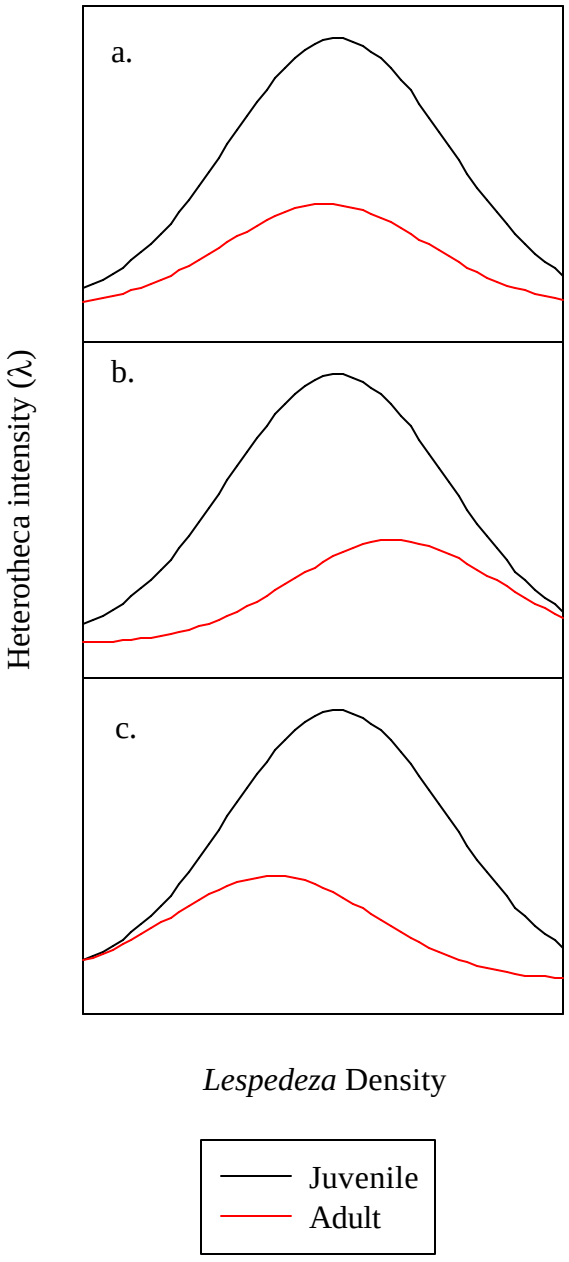
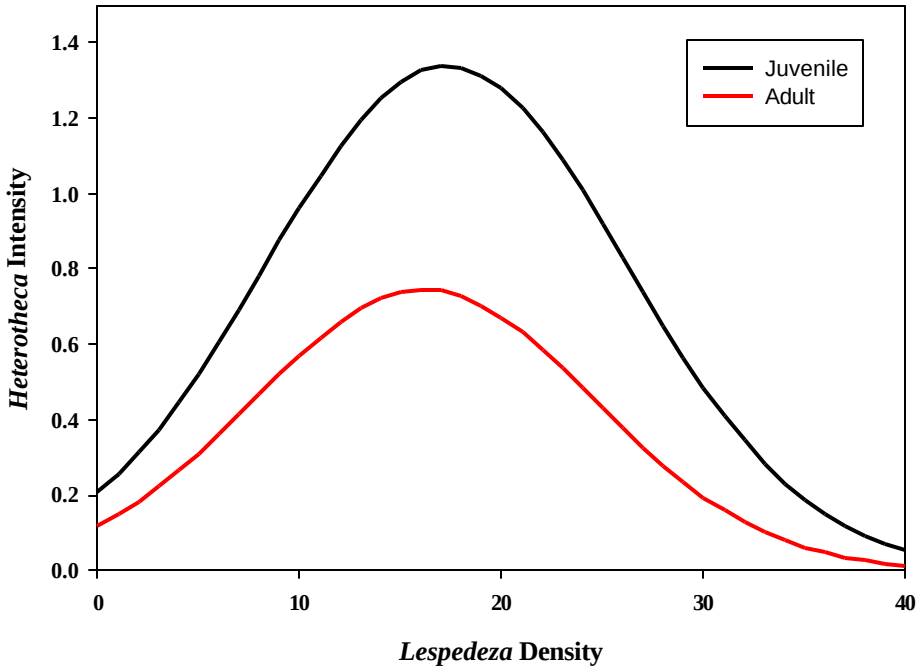


Figure 10 a-c. Graphs showing three potential relationships between adult and juvenile data sets with respect to the *Lespedeza* density yielding the maximum *Heterotheca* intensity.



$$\text{Juvenile : } \textit{Heterotheca} \text{ intensity} = \exp\left(-1.572 + .2161 * X + -.006261 * X^{2}\right)$$

$$\text{Adult : } \textit{Heterotheca} \text{ intensity} = \exp\left(-2.125 + .2268 * X + -.00702 * X^{2}\right)$$

$$X = \text{Lespedeza Density} = \sum_{j=1}^{N} stems^{.5}$$

Figure 11. Model (0.5,0) plotted for the (a) Juvenile and (b) Adult *Heterotheca* 1999 data set.

The pattern analysis revealed a positive spatial association between individuals of *Heterotheca* and *Lespedeza* within the study field, and the modelling demonstrated that *Heterotheca* plants are more likely to be found at moderate densities of *Lespedeza*. The pattern analysis took into account only the positions of individuals of both species, and the modelling evaluated effects of size and density of *Lespedeza* on *Heterotheca* distribution, but neither approach focused directly on the variation in performance of *Heterotheca.* By regressing variables related to *Heterotheca* performance, additional support for hypotheses of facilitative and competitive interactions was gained. If both facilitation and competition between *Lespedeza* and *Heterotheca* were occurring within this system, *Heterotheca* heights and biomass values should have been maximized at a moderate value of the NDI. At the higher densities, competition with *Lespedeza* should have restricted the sizes of *Heterotheca* individuals and increased the likelihood of mortality during the growing season; while at low densities, the absence of *Lespedeza* might also have limited the overall growth and have had similar effects on mortality. All measures of *Heterotheca* performance instead increased over the range of the *Lespedeza* NDI (Figures 7 and 8). Successful individuals were found across a wide range of *Lespedeza* densities. *Heterotheca* was less likely to establish at the lowest and highest values of the *Lespedeza* NDI as evidenced by the frequency diagrams showing the hypothetical distribution of the *Lespedeza* NDI for observed and randomly distributed *Heterotheca* individuals (Figure 6). Individuals that do establish at the lower NDI values are less successful in terms of growth and reproduction than those establishing at the highest values; however, they have a slightly higher probability of survival than their high-density counterparts.

The high standard errors for the various measures of *Heterotheca* emphasize the fact that there is a large amount of variability between individual plants (Table 1). In this field,

Heterotheca grows to a wide range of sizes, from small individuals bearing few or no flowers and standing 20 centimeters tall, to much larger, multiple stemmed individuals which stand over one meter tall. The presence and density of *Lespedeza* explains only a small percentage of this variability.

Although the pattern analysis indicated an overall lack of fit of even the best fitting models to the data, and the regression analysis shows only a small influence of *Lespedeza* density, this may not be surprising when the complexity of the natural system is considered. Many forces are responsible for patterning the two species. Though *Lespedeza* is a dominant species in the study field, there are also many grasses and other forbs that potentially compete with *Heterotheca* (Keever 1950, Pinder 1975). Other biotic factors that may influence pattern include herbivory by deer and insects, and seed dispersal. Barot et al. (1999) attribute the aggregation of juvenile palms to limited seed dispersal. A seed dispersal study indicated no relationship between *Heterotheca* seed density and *Lespedeza* density, however (S.Turner, unpublished). Abiotic factors that may influence pattern include small-scale differences in soil nutrients (independent of *Lespedeza*) or topography, although soil resources were not found to vary significantly due to the presence of grasses in this field (Collins and Pinder 1990). Couteron and Kokou (1997) attributed the aggregation found between woody savannah species to edaphic factors, namely petroferric outcrops that lead to shallow soils in places. Barot et al (1999) suggested that the association of palm trees with termite mounds is in part due to increased nutrients. In addition, there may be remnant effects from previous years or land use history (Stohlgren 1993, Donohue et al. 2000). The pattern from one year to the next may be partially dependent on previous years' patterns of vegetation, including that of *Heterotheca* and *Lespedeza*. The wind-dispersed disk seeds of *Heterotheca* typically germinate the Spring

following seedset, while the ray seeds of *Heterotheca,* which drop close to the parent, typically germinate after spending at least a full growing season in the field (Baskin and Baskin 1976).

The present study finds a non-random pattern of association between *Heterotheca* and *Lespedeza*. *Heterotheca* is more likely to be found at moderate densities of *Lespedeza* than at either low or high *Lespedeza* densities, and this pattern is established early in the life cycle of *Heterotheca*. There is a slight, though significant increase in *Heterotheca* performance with increasing density, though patterns of mortality suggest competition between *Lespedeza* and *Heterotheca*. These results suggest that moderate densities of *Lespedeza* may facilitate the establishment and growth of *Heterotheca*, but high densities of *Lespedeza* may limit the establishment and increase mortality of *Heterotheca*.

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CHAPTER 3

LOCAL RESOURCE MODIFICATION IN A SOUTH CAROLINA OLD FIELD IN AREAS OF VARYING DENSITY OF *LESPEDEZA CUNEATA*

INTRODUCTION

Studying the relationships between plants and their environment is a large focus of plant ecology. The two are inextricably linked, as plants not only respond to, but also affect the conditions of their surroundings. Abiotic factors, such as light, soil nutrients, and soil moisture interact to create environmental conditions that may favor successful establishment or plant growth. These same factors, however, are largely dependent on the vegetation. Tree and shrub species can have significant impacts on the soil environment and microclimate (Zinke 1962, Radwanski and Wickens 1967, Tiedemann and Klemmedson 1973, Barth and Klemmedson 1978, Vetaas 1992). Tiedemann and Klemmedson (1973) found significant differences in soil temperature, moisture and radiation by removing mesquite canopies. Mesquite was also shown to influence patterns of soil nitrogen (Barth and Klemmedson 1978). Soil moisture is influenced by and can vary depending largely on vegetation type (Wilson and Kleb 1996). Forestation can alter soil fertility (Seastedt and Adams 2001) and ultimately cause changes in soil type (Willis et al. 1997).

Because of these complex linkages between plants and their environment, most plant – plant interactions are not direct interactions between individuals but rather are attributable to resource use or modification, with effects occurring between individuals and their environment.

Competition, for example, often occurs when individual plants utilize existing resources in such a way that precludes the use of those resources by other plants (Tilman 1985). Facilitation can occur when individuals change the environment in such a way that allows for increased growth and performance of other individuals (Callaway 1995) . Habitat amelioration may include increasing soil nutrients or moisture, or by other microclimatic alterations (Weltzin and Coughenhour 1990, Callaway 1994, Walker 1994, Pugnaire et al. 1996, Rousset and Lepart 2000).

Plants are a key part of the soil nutrient cycle as they serve to capture, retain, utilize and release nutrients over their life cycle. Nitrogen, in particular, is a key element essential for plant growth. Decomposition of plant litter and roots provides organic nitrogen, which, through nitrogen mineralization, is converted to inorganic forms (NO_3^- and NH_4^+) available for uptake by vegetation. These effects can be species-specific and are largely dependent on litter quality and quantity; litter with a lower C:N or lignen:N, for example, can increase decomposition rates leading to the release of available nitrogen back into the system (Melillo and Aber 1982, Hobbie 1992). Wedin and Tilman (1990) attributed the significant differences in total soil nitrogen and net nitrogen mineralization between soil associated with perennial grasses to species specific differences in litter quality. Stump and Binkley (1993) also found a high correlation between litter quality and quantity and nitrogen mineralization in Rocky Mountain forests. In a semi-arid grassland, however, where mineralization is limited more by water availability, Vinton and Burke (1995) found no significant species-specific differences in nitrogen mineralization.

Several studies have investigated variation in soil nitrogen between open or unvegetated areas and areas with potentially facilitating individuals. For example, Franco and Nobel's (1989) work shows higher levels of soil nitrogen under the canopies of bunchgrass, shrub and tree

species. Schlesinger et al. (1996) also found higher soil nitrogen and PO_4^- under desert shrubs than in the open. Storage of nitrogen in plant tissues which are eventually recycled as litter is a key mechanism by which desert shrubs play a role in increasing soil fertility (Garcia-Moya and McKell 1970). Facilitating plants do not always lead to higher local nutrients, however, as Valiente-Banuet et al. (1991) found lower soil nitrogen under the canopies of several nurse shrubs.

Increased levels of soil nitrogen have been attributed to the presence of nitrogen-fixing plants in many ecosystems. Nitrogen-fixing plants, including many legumes, are particularly important contributors of soil nitrogen in areas undergoing primary succession (Morris and Wood 1989, Vitousek and Walker 1989, Bellingham et al. 2001, Walker et al. 2003), and in forests that have been burned (Hendricks and Boring 1999). In other systems such as grasslands, nitrogen-fixing plants have also been shown to increase soil nitrogen (Birch and Dougall 1967, Robles and Burke 1997, Hooper and Vitousek 1998). The increases in soil fertility are largely attributable to increases in mineralization rates as a result of nitrogen-rich litter. Birch and Dougall (1967) found higher levels of nitrogen mineralization where legumes were present with grasses than where grasses were grown alone and attribute the higher levels of nitrogen mineralization to the legumes' abilities to increase the surface organic horizon through litter inputs. Walker et al. (2003) also found that litter deposited by nitrogen fixers was critical to increasing soil fertility.

When interacting individuals differ in height or canopy size, the response of temperature and soil moisture is thought to be at least partially an indirect effect of increased shading. Both positive and negative interactions between individuals can result from shading. In some environments, particularly those that experience water stress, shading can lead to facilitative

interactions between species as the decreased light can serve to decrease temperatures and overall evapotranspiration (Bertness and Hacker 1994, Shumway 2000). In other systems, shading by neighbors reduces plant performance (Forseth et al. 2001) or increases the intensity of competitive interactions (Weihe and Neely 1997). With higher canopy cover, soil temperatures can be lower and soil moisture levels immediately following a rain event can be higher due to decreases in evapotranspiration.

Lespedeza cuneata, an herbaceous legume found in old fields of the southeastern USA, may affect its local environment in multiple ways. It typically occurs in open sites with grasses and herbaceous vegetation. Because of its relative size and dominance, coupled with its status as a nitrogen fixer, this shrubby perennial may both compete with and facilitate other plants by its modification and utilization of resources. *Lespedeza* may impact local soil nutrients, the light environment, soil moisture, and soil temperature.

This study sought to investigate how *Lespedeza* affected the availability of light, soil nutrients, soil moisture and temperature in an old field. I hypothesized that soil nitrogen and moisture would increase and light and temperature would decrease with increasing density of *Lespedeza*.

METHODS

Resource Plots

In spring 2001, 1 m^2 resource plots were established in five areas of the old field where *Lespedeza* was a patchy dominant. The variation in size of *Lespedeza* plants, combined with variation in clustering of individuals, created a *Lespedeza* density gradient across the areas in which it was found. Plots were of three types - low, medium and high *Lespedeza* density.

Because of the large variability in plant size and number of stems per individual (1 to 42), in this case "density" was defined as the number of *Lespedeza* stems within a standardized area. Incorporating the size of the *Lespedeza* into the measure of density was deemed better than simply counting the number of individuals. To alleviate effects of background environmental variation, care was taken to cluster the plots together in blocks, each with a low, medium and high-density plot separated by only a few meters. Three blocks were established in each of five areas, yielding a total of 15 blocks (45 plots total).

Plots were initially chosen based on a visual perception of *Lespedeza* density. In the fall of 2001, the positions of all *Lespedeza* individuals were mapped to verify that the plots represented varying levels of *Lespedeza* density. Though the actual plots were 1 m^2, mapping was done both within the 1m^2 plot and extended an extra 0.5 m on each side to yield a total 4 m^2 mapped area. Height of the tallest stem of each *Lespedeza* individual was measured, as well as the number of stems and basal diameters. Basal diameter was defined as the diameter where the stems emerge from the soil.

Canopy openness was used as a surrogate variable for light. Measurements were taken at daybreak using a Li-Cor canopy meter placed above and below the *Lespedeza* canopy. Light readings were taken for five positions within each plot over two days in May 2001.

In July of 2001, soil nutrients (nitrogen and phosphorous) were measured within each resource plot. Three soil cores were taken within each plot and composited. A 2 molar solution of KCl was used to extract anions and cations from the soil samples; for each plot, three replicate samples were analyzed. Samples were stored frozen until processing at the University of Georgia Institute of Ecology's soil testing laboratory, where NH_4, NH_3 and PO_4 were measured using continuous flow colorimetry.

Soil moisture was measured using a Dynamax Delta-T soil moisture probe, inserted into moisture tubes established roughly in the center of each resource plot. Care was taken not to place the tubes too close to large individuals of *Lespedeza*. Soil moisture was measured in the early morning daily for 27 days starting in June 2001 at four depths: 10, 20, 30 and 40 cm.

Soil temperature was measured in three of the areas using Thermochron ibuttons. Because the number of ibuttons was limited and the effect of area on temperature was not a focus of study, all buttons were placed within a single area at a time. Each button was placed in a plastic bag and buried to a depth of 10 centimeters. Three buttons were buried in each of the fifteen resource plots in the area, for a total of 45 buttons. Measurements were taken every hour for thirty days. For each day, a maximum and minimum temperature was calculated from the 24 measurements. The coefficient of variation for each button for each day was calculated by dividing the standard deviation by the average temperature of the 24 temperature readings (Sokal and Rohlf 1995).

Nitrogen Mineralization

One of the resource plot sites was an area that had been previously planted with *Lespedeza*. In 1998, 32 2 m^2 plots were established in a powerline right-of-way through the old field. Plots were arranged in two four by four grids with one meter spacing between plots. All vegetation was removed with Round Up ™ and replanted with *Lespedeza* seedlings that had been grown in root tubes in a greenhouse for six months. Three densities of *Lespedeza* (plus a control with no *Lespedeza*) were planted in a replicated Latin square design to control for any natural resource gradients within the field. The densities were achieved by planting 4 (low), 16 (medium) or 36 (high) individuals within each plot in a regular pattern. Some natural

colonization of *Lespedeza* occurred in some of the control plots, but densities in these plots were very low.

A net nitrogen mineralization study was performed in late March and April of 2002. Three soil samples were extracted from each of the 32 experimental plots using a soil auger in March. A portion of each soil sample was placed in a Ziploc bag, sealed, and reburied in the holes created by the auger. The remaining soil was composited and three samples were extracted with 2M KCl and analyzed for NH_4, NH_3 and PO_4 in the manner described previously. After an incubation period of one month, bags left in the field were recovered, soil was composited, and three samples were taken and analyzed as before. Net nitrification is defined as the difference in nitrate between the two time periods, while potential net N mineralization is defined as the sum of nitrate and ammonium at the second date minus the sum of the two at the first date (Satti et al. 2003).

Litter Analysis

Litter was collected in the fall of 2000 underneath and away from patches of *Lespedeza*. The non-*Lespedeza* litter consisted primarily of litter of grass species including *Andropogon virginicus*, *Leptoloma cognatum*, and *Panicum aciculare*. Six samples of each *Lespedeza* and non-*Lespedeza* litter were taken by removing all loose aboveground dead plant material within 1 m^2 quadrats. Litter was collected in bags, weighed, and sent to the University of Georgia Soil, Plant and Water testing facility in Athens, GA where percent nitrogen and carbon were measured.

Data Analysis

Data were analyzed using ANOVAs with *Lespedeza* density treated as a fixed effect and area treated as a random effect. Blocks were nested within area and were also a random effect. In the cases of soil moisture and temperature, a repeated measures ANOVA was used.

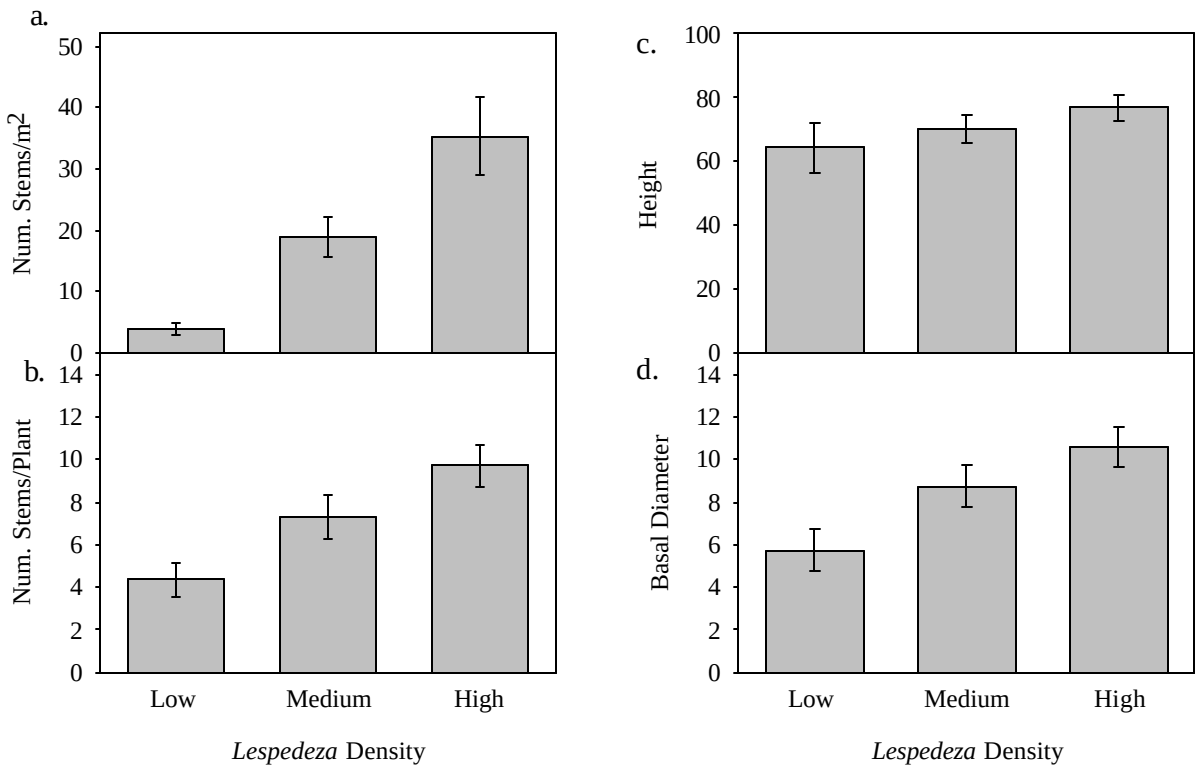
RESULTS

Resource plots

The average number of *Lespedeza* stems per m^2 in the resource plots increased from low to high (Figure 1). Each *Lespedeza* plot density type was significantly different from the others in total number of stems per m^2 based on contrasts generated from a simple one-way ANOVA, treating area and plot density type as fixed effects. In addition, the number of stems per *Lespedeza* individual, height, and basal diameter increased from low to high-density plots (Figure 1). All plot types were significantly different from one another for all metrics except height. Plants in the low and medium density plots types were not significantly different in average height, yet there were significant differences in plant height between the low and high, and the medium and high density plots.

The percent canopy openness was significantly reduced in plots with high density of *Lespedeza* (Figure 2). Contrasts between *Lespedeza* density levels showed significant differences between each plot type. Nitrate and ammonium increased with increasing *Lespedeza* density in the resource plots, but phosphate decreased with increasing *Lespedeza* density (Figure 3). Density was a significant effect for both nutrients.

In the planted experimental plots, patterns were similar to those of the resource plots, with a general increase of nitrate and ammonium and a decline in phosphate as *Lespedeza*

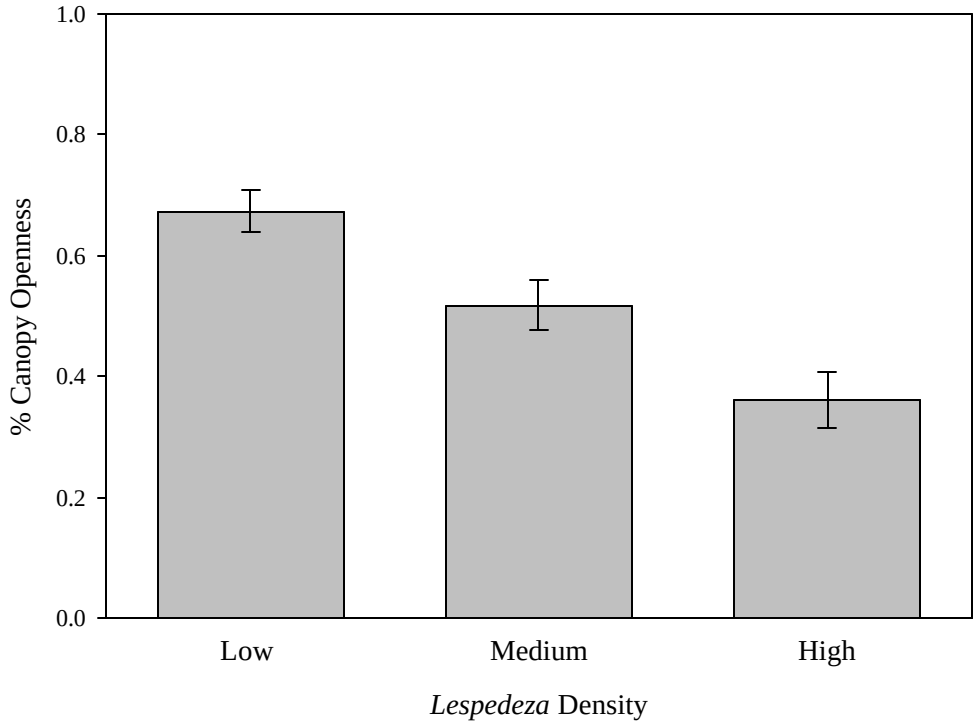


e.

	Lespedeza Number of stems/m^2	*Lespedeza* Height	*Lespedeza* Basal Diameter	Number of Stems per *Lespedeza* Individual
Lespedeza Density Type	Pr >F			
Low vs Medium	< 0.0001	0.4979	0.0013	0.0046
Low vs. High	< 0.0001	0.0060	<0.0001	<0.0001
Med. vs High	< 0.0001	0.0024	0.0037	0.0006

Figure 1. a.) Stem density, b) number of stems per plant, c) height, and d) basal diameter of *Lespedeza* by density type for resource plots. Data shown are means ± 2 S.E. e.) Contrasts between density type are based on an ANOVA including density type and area as effects.

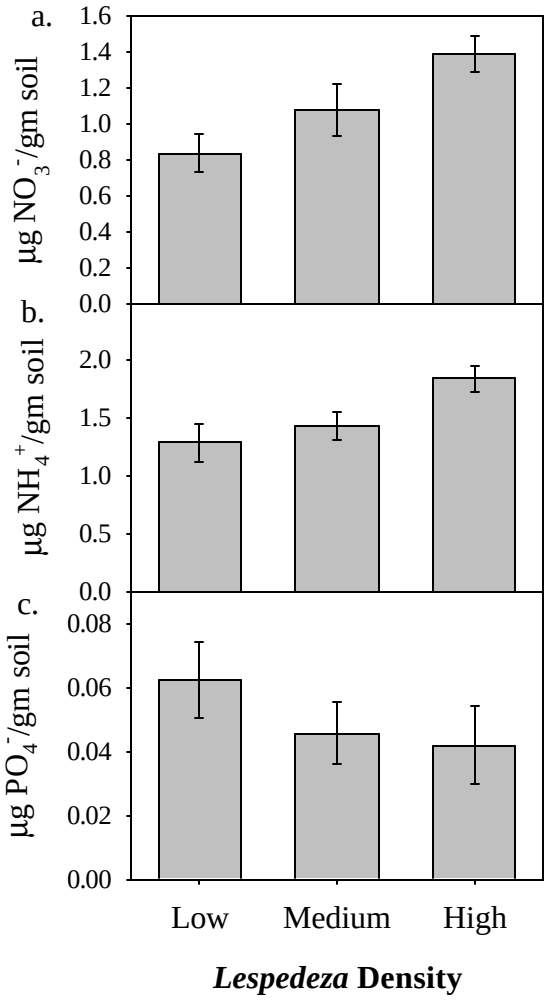
a.



b.

Contrast	Canopy Openness
N Concentration	Pr >F
Low vs. Medium	<0.0001
Low vs. High	<0.0001
Medium vs. High	<0.0001

Figure 2. a) Percent canopy openness as a function of *Lespedeza* density as measured for the resource plots. Data shown are means ± 2 S.E. b) Contrasts between *Lespedeza* density levels for Canopy Openness, based on ANOVA including density type, area and block.



d.

	NO_3^-	NH_4^+	PO_4^-
Contrast		Pr >F	
Low vs. Medium	0.0004	0.2772	0.0040
Low vs. High	<0.0001	<0.0001	0.0002
Medium vs. High	<0.0001	<0.0001	0.4099

Figure 3. a) NO_3^- b) NH_4^+ and c) PO_4^- for all resource plots combined in July 2001 shown as a function of *Lespedeza* density . Data shown are means ± 2 S.E. d) Contrasts between *Lespedeza* density levels for soil nutrients, based on ANOVA including density type and area as effects.

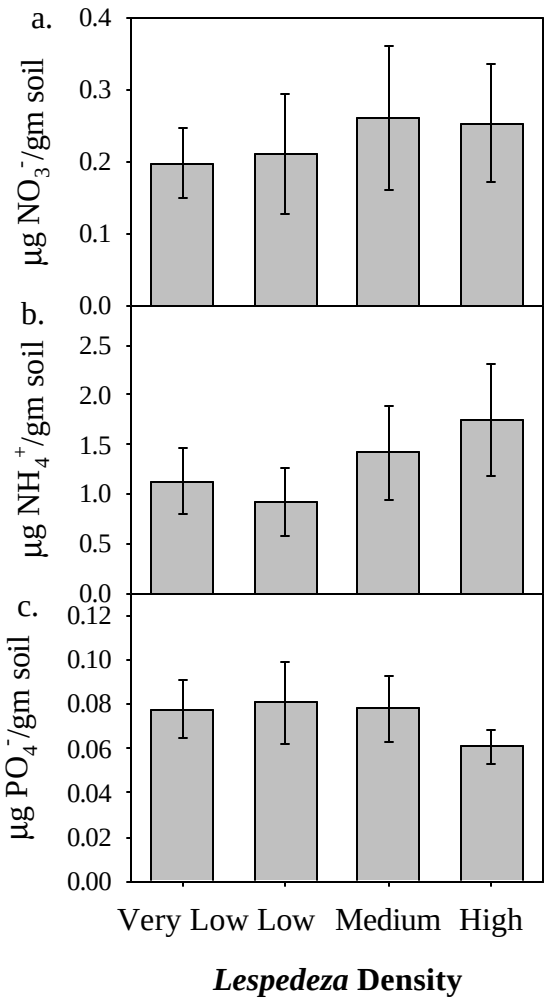
increases (Figure 4). Both ammonium and phosphate were significantly different between low and high densities at the $p < .05$ level, but there were no significant effects of *Lespedeza* density on nitrate. There also were no significant differences between *Lespedeza* densities on the net nitrification or the potential net N mineralization (Figure 5). There was a general pattern increased net nitrification and potential net N mineralization at the high density, but significant differences were not seen due to the high standard errors.

Percent soil moisture was averaged over all plots of similar density type (Figure 6). Data shown are for three major rainfall events and subsequent days. Based on a repeated measures ANOVA, there were no significant differences in soil moisture between densities of *Lespedeza* at any of the four depths measured. However, it is interesting to note that there was a pattern of the high density plots having the lowest percentage soil moisture at the lower depths, and the medium density plots having the highest percent soil moisture at the intermediate depth (20 cm).

Soil temperatures decreased significantly as the density of *Lespedeza* increased (Figure 7). In addition, daily temperature variability was also a function of *Lespedeza* density; and coefficients of variation decreased as *Lespedeza* density increased. For the maximum daily temperature, each level of *Lespedeza* density was significantly different from the others. For the daily temperature variability, the low-density *Lespedeza* plots were significantly different from both the medium and high density plots (Figure 7d).

Litter Analysis

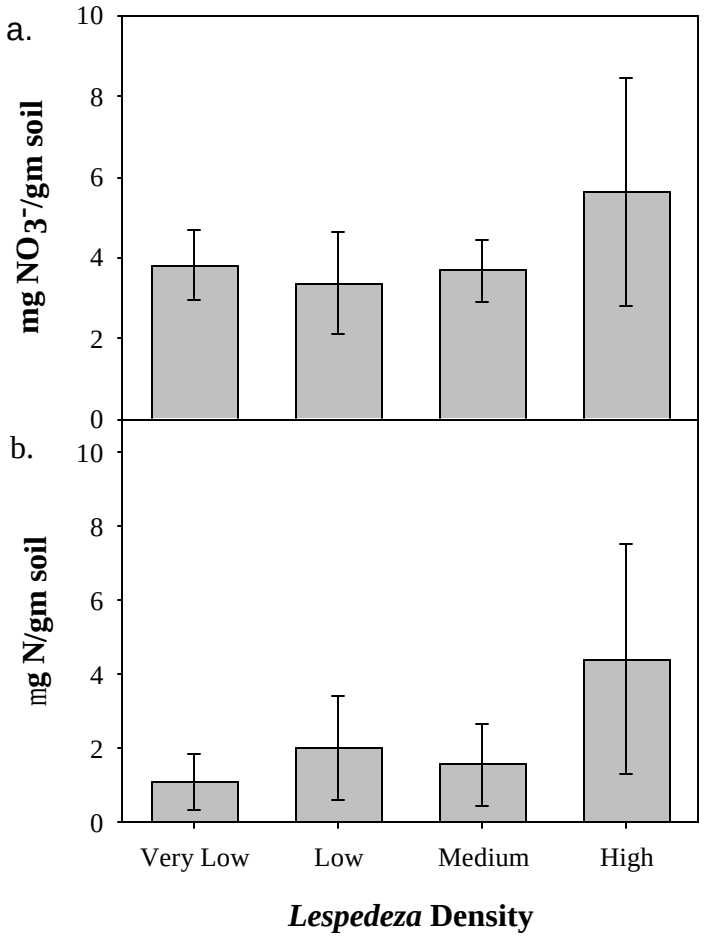
C:N was significantly lower in *Lespedeza* litter than in non-*Lespedeza* litter (Figure 8). This is attributable primarily to differences in percent carbon, which was higher in the non-



d.

Contrast	NO_3^-	NH_4^+	PO_4^-
Lespedeza Density		Pr < F	
Very Low vs Low	0.8282	0.5034	0.7313
Very Low vs. Medium	0.2831	0.3558	0.9808
Very Low vs. High	0.3595	0.0467	0.0313
Low vs. Medium	0.3909	0.1133	0.7495
Low vs High	0.4824	0.0088	0.0132
Medium vs. High	0.8814	0.2752	0.0296

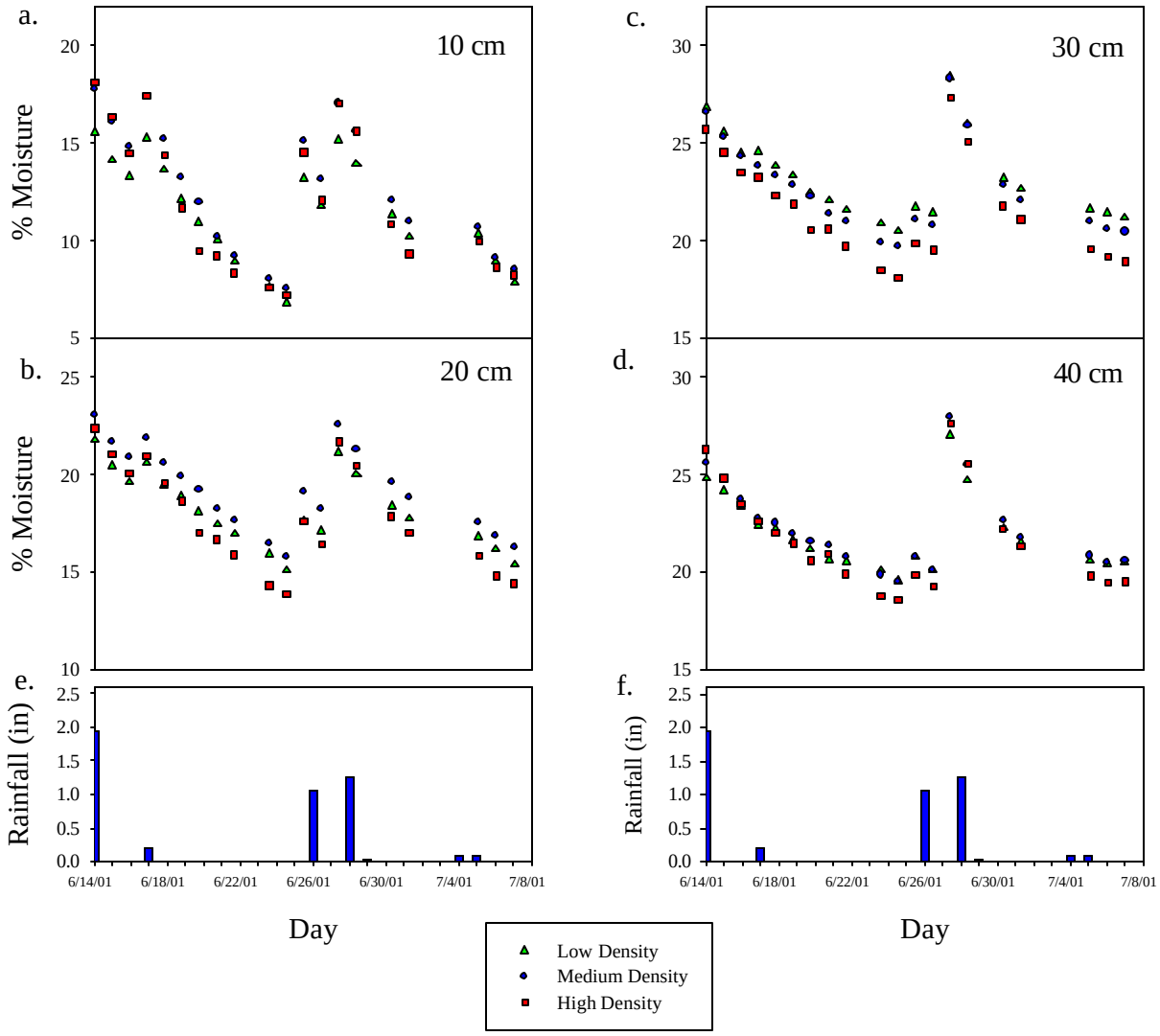
Figure 4. a) NO_3^-, b) NH_4^+ and c) PO_4^- shown for planted *Lespedeza* plots. Data shown are means ± 2 S.E. d) Contrasts between treatment levels of various planted density types of *Lespedeza* for NO_3^-, NH_4^+, and PO_4^+ based on an ANOVA including density type, column and row. Very low densities resulted from natural colonization of *Lespedeza* in some of the unplanted control plots.



c.

Contrast	Net Nitrification	Potential net N mineralization
Lespedeza Density	Pr < F	
Very Low vs Low	0.4547	0.5361
Very Low vs. Medium	0.6696	0.6342
Very Low vs. High	0.4220	0.7296
Low vs. Medium	0.6968	0.8623
Low vs High	0.0777	0.2604
Medium vs. High	0.1542	0.3354

Figure 5. a) Net nitrification and and b) Potential net N mineralization shown for planted *Lespedeza* plots. Data shown are means ± 2 S.E. c) Contrasts between *Lespedeza* density levels based on repeated measures ANOVA including density type, column and row.



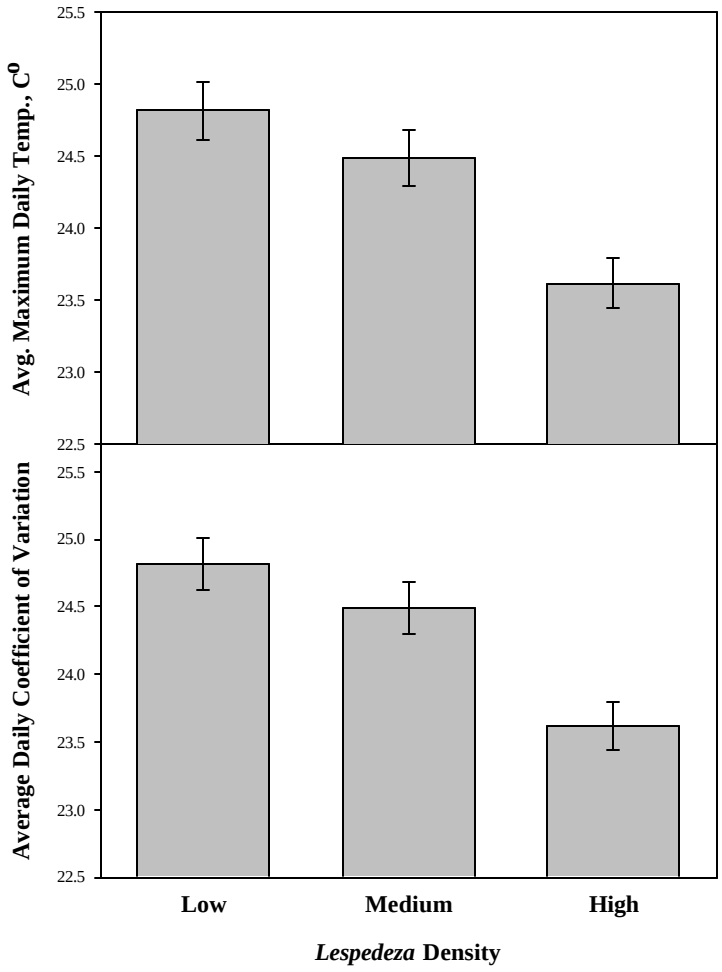
g.

	10 cm	20 cm	30 cm	40 cm
Contrast	Pr >F			
Low vs. Medium	0.0630	0.0586	0.2814	0.2118
Low vs. High	0.0983	0.5699	0.0765	0.6814
Medium vs. High	0.1707	0.0633	0.1025	0.2566

Figure 6. (a-d) Soil moisture profiles for *Lespedeza* resource plots for 10 – 40 cm. Data shown are averages over all areas and blocks. (e-f) Local SRS reported rainfall in g) Contrasts between *Lespedeza* density types for soil moisture, based on ANOVA including density and block as effects.

a.

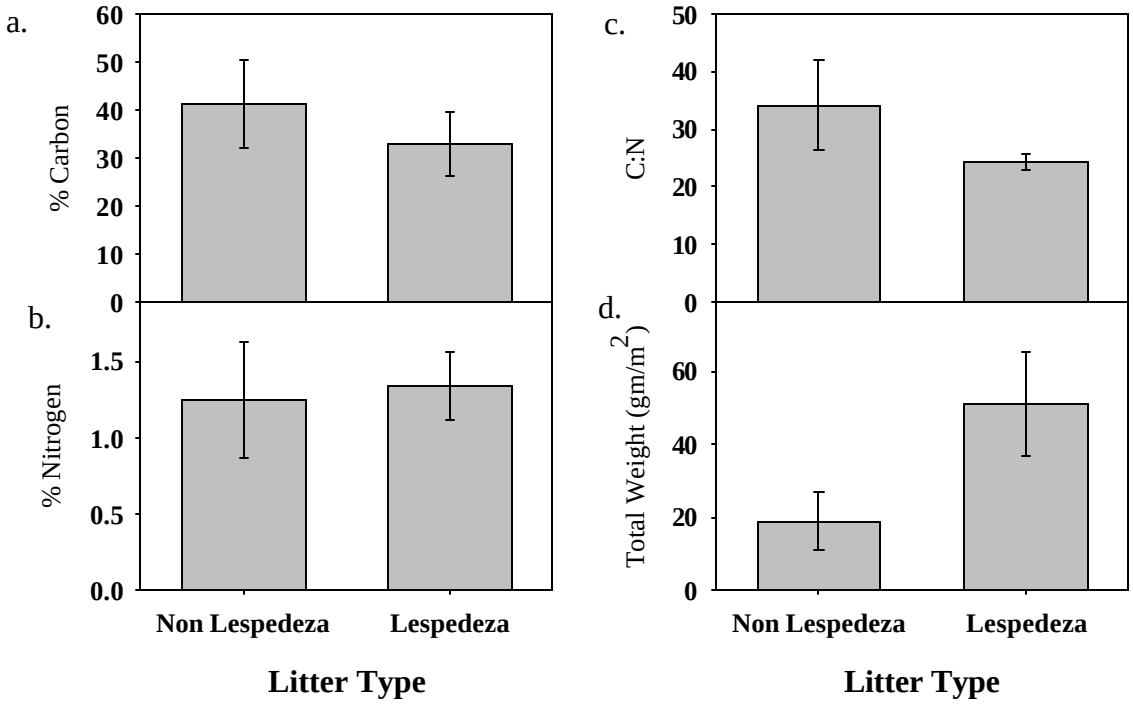
b.



c.

Contrast	Maximum Temperature	Daily Temperature Variation
N Concentration	Pr >F	
Low vs. Medium	0.0003	0.0135
Low vs. High	<0.001	<0.0001
Medium vs. High	0.0033	0.0747

Figure 7. a) Average maximum temperature and b) Coefficient of variation given for Low, Medium and High density *Lespedeza* resource plots. Data shown are means ± 2 S.E. c) Contrasts between *Lespedeza* density levels for Soil Temperatures, based on repeated measures ANOVA including density type, area and block.



e.

	% Carbon	% Nitrogen	C:N	Total Weight
t- test		Pr > t		
Non-*Lespedeza* vs. *Lespedeza* d.f. = 9	.1970	.7002	0.0384	0.0026

Figure 8. (a-d) Mean % C, % N, C:N and total weight of *Lespedeza* and non *Lespedeza* litter. Data shown are means ± 2 S.E. e. Results of a t- test testing the null hypothesis that there is no difference between *Lespedeza* and non *Lespedeza* litter in terms of %C, %N, C:N and Weight vs the alternative that there is a difference between litter types.

Lespedeza litter, rather than to nitrogen differences. In addition, quantity of litter was significantly higher for litter taken under *Lespedeza* plants than in other areas.

DISCUSSION

There is significant variation amongst *Lespedeza* densities for several of the measured variables, including soil nutrients, soil temperature, and canopy openness. Plots with high-density *Lespedeza* had higher soil nitrogen, lower soil phosphorous, lower canopy openness, lower soil moisture except immediately after a rainfall, and lower maximum daily soil temperatures than plots with low density of *Lespedeza*.

I expected to find increasing levels of soil nitrogen with increasing density of *Lespedeza*. Many studies have demonstrated increases in soil nitrogen under perennial plants (Garcia-Moya and McKell 1970, Barth and Klemmedson 1978, Vetaas 1992, Vinton and Burke 1995); in particular, nitrogen fixers can be significant contributors to soil fertility (Birch and Dougall 1967, Vitousek and Walker 1989, Pugnaire et al. 1996, Rodriguez-Echeverria and Perez-Fernandez 2003). Data from the resource plots support this, but only weak evidence suggests higher nitrification and mineralization rates in soils of the highest density of planted *Lespedeza* plots.

That *Lespedeza* litter had a nitrogen content (%) similar to litter taken under perennial grasses may not be surprising, as Garcia-Moya and McKell (1970) also found no variation in nitrogen content of leguminous litter versus non-leguminous shrub litter. What is more important is the C:N ratio, a better measure of litter quality than percent nitrogen (Hobbie 1992). The lower C:N ratio of *Lespedeza* litter should lead to increased nitrogen availability due to

increased rates of decomposition and mineralization (Melillo and Aber 1982, Hobbie 1996, Tateno and Chapin 1997).

The lack of significant differences for the net nitrogen mineralization study were therefore surprising. While measurements of NO_3^- and NH_4^+ reveal current plant available nitrogen, net nitrogen mineralization should better reflect overall soil fertility by indicating the potential supply of nitrogen. Birch and Dougall (1967) found increased mineralization under legumes even when levels of ammonium and nitrate were not significantly different between areas with and without legumes. There were significant differences in NO_3^- and NH_4^+ across density types in the resource plots in July 2001. However, in the planted *Lespedeza* plots, only NH_4^+ differed across *Lespedeza* densities in March 2002. Both net nitrification and net mineralization were higher in the high-density planted plots, but these differences were not statistically significant at $p < .05$ due to high variation among samples.

Levels of phosphate were lower in both the medium and high-density *Lespedeza* resource plots, as well as in the high density planted plots. This result may be expected, however, as Hooper and Vitousek (1998) also found decreases in levels of phosphorous in soil associated with nitrogen fixers, and nitrogen fixers are often phosphorous limited (Vitousek and Howarth 1991). A decrease in phosphate with increasing *Lespedeza* density could reflect this limitation.

Positive effects of a perennial canopy on soil moisture are more important in periods following rain, than during dry periods, as shade effects serve to prolong the high moisture conditions (Shreve 1931). Because of this, I predicted that soil moisture would increase as *Lespedeza* density increases. Patterns of moisture over *Lespedeza* density change as the soil dries out. Immediately after a rainfall, the medium and high density *Lespedeza* plots at depths of 10-20 cm are the wettest, but high density plots several days later become the driest of the plots.

Medium density plots remain the wettest at these depths. This could indicate that moderate densities of *Lespedeza* promote increased soil moisture at these depths. At low *Lespedeza* densities, there may be high evapotranspiration due to higher temperatures and lack of ground cover. At high densities however, the uptake and use of water by *Lespedeza* may overcome the advantages of decreased evapotranspiration. The overall differences in soil moisture between the wetter and drier periods were most pronounced for depths of 10 - 20 cm, the depths were most rooting is occurring. At depths of 30 and 40 cm there is less soil moisture variation, particularly for the low and medium density plots. High-density plots may have lower soil moisture at these lower depths due to deeper root growth resulting from intraspecific competition.

In this old field, plots with *Lespedeza* can have markedly lower soil temperatures during the growing season. Variation in soil temperature under conditions of sun rather than shade has been shown for several ecosystems (Shreve 1931, Parker and Muller 1982, Valiente-Banuet et al. 1991), and may be important to the success of many plants. In deserts, this reduction in temperature by shading may be an important mechanism for facilitation of establishing cacti which, as CAM plants, do not transpire during the day (Valiente-Banuet et al. 1991). Nobel (1984) also found that high temperatures associated with growing in open areas inhibit cacti seedling growth and survival. Nitrogen fixation among legumes has been shown to be temperature dependent, with interspecific differences in optimal soil temperature for nitrogen fixation (Power and Zachariassen 1993). Nitrogen mineralization is also temperature dependent and maximized at moderate temperatures (Goncalves and Carlyle 1994). Soil temperatures in the old field can exceed 40° C (104° F) where there is no shade provided by *Lespedeza*. It is possible that these higher temperatures could negatively impact mineralization, although this was not tested.

It is clear that there are differences associated with plots of varying *Lespedeza* density. Attributing these differences directly to the *Lespedeza* is more difficult. It is not possible to know the full history of the natural areas, as plots were chosen for their current densities and little is known of conditions in prior years. Because *Lespedeza* is a perennial, however, it is likely that the measured density does reflect that of the past several years. For some of the measured resources or conditions this is not a concern; the shading seen is obviously a function of the current *Lespedeza*. Differences in the environmental conditions of soil moisture and temperature, because they are intrinsically related to degree of shading, also can be attributed to the *Lespedeza*. Attributing differences in soil nutrients to differing densities proves most difficult because the question remains as to whether or not the variation in local soil nutrients is an effect of the *Lespedeza* or is a cause of the differences in *Lespedeza* density. The plots in the planted right-of-way provide the best evidence of *Lespedeza*'s role in the modification of its soil resources because they were planted at set densities in an area originally without *Lespedeza*, in a pattern designed to control for underlying environmental gradients.

This study demonstrates that *Lespedeza* does have an impact on local environmental conditions and resources. By altering such conditions, *Lespedeza* may in turn create conditions that may impact the establishment and success of other herbaceous species. Increasing soil fertility and decreasing soil temperatures during the summer could prove beneficial to neighboring plants in the old field. The effects of *Lespedeza* on shading could lead either to facilitation or competition. While the preemption of solar radiation may result in competition, some shading may in turn benefit neighboring plants by causing increased soil moisture and lower temperatures. Whether or not competitive or facilitative effects are dominant is likely due

to the density of *Lespedeza*; with high-density *Lespedeza* having competitive effects and moderate density *Lespedeza* resulting in facilitation.

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CHAPTER 4

RESPONSE OF *HETEROTHECA SUBAXILLARIS* TO POTENTIAL ENVIRONMENTAL MODIFICATION BY *LESPEDEZA CUNEATA*

INTRODUCTION

Facilitation has recently been recognized as an important interaction in plant communities, particularly in environments where the presence of individuals can ameliorate harsh or limiting conditions (Bertness and Callaway 1994, Callaway 1995) . Current theory suggests that both positive and negative plant – plant interactions may occur either simultaneously, or at different life stages (Callaway and Walker 1997, Rudgers and Maron 2003). Resources often mediate these plant-plant interactions. Negative interactions, or competition, may occur when plants preempt nutrient or other resource usage by other individuals (Tilman 1988). Facilitation, on the other hand, can occur when individuals of one species modify their environment in such a way that favors the growth and reproduction of individuals of another or the same species. In systems where facilitation has been shown to be important, the effects of plants on both nitrogen and shade are important facilitative mechanisms (Tiedemann and Klemmedson 1977, Vitousek and Walker 1989, Valiente-Banuet and Ezcurra 1991, Rodriguez-Echeverria and Perez-Fernandez 2003).

Variation in soil nitrogen may have impacts on plant growth, biomass partitioning and reproductive allocation (Lambers et al. 1981, Whigham 1984, Boot et al. 1992, Clabby and Osborne 1997, Puri and Swamy 2001), with increased levels of nitrogen typically leading to an increase in plant biomass, a greater allocation to shoots than to roots, and an increase in seed

production. The most notable effect of shading is to decrease solar radiation. Decreased solar radiation is typically associated with decreases in growth responses by plants, although responses to shading vary depending on plant species and shade tolerance (Dale and Causton 1992, Bloor and Grubb 2003). For shade tolerant species, growth and reproduction can be increased by moderate shading (Packham and Willis 1977, Pitelka et al. 1980, Packham and Willis 1982). Shading can also indirectly impact plant success by altering soil temperatures and soil moisture. This may have more influence on plants grown under harsh conditions. In addition, light and nitrogen are also known to interact, with increasing nitrogen allowing for greater photosynthetic capabilities (Peace and Grubb 1982, De Pinheiro Henriques and Marcelis 2000).

The goal of this chapter was to investigate the response of *Heterotheca subaxillaris* ((Lam.) Britt. & Rusby) to conditions that may result from growing in proximity to *Lespedeza cuneata* ((Dumont) G. Don). A spatial pattern analysis showed interspecific clustering between *Lespedeza* and *Heterotheca* in an old field on the Savannah River Site (SRS), located in Aiken County, South Carolina (chapter 1), and Lespedeza was shown to modify its local environment by decreasing light and increasing soil nitrogen (chapter 2). Demonstrating a response by *Heterotheca* to these conditions may provide supporting evidence of possible mechanisms of interaction between *Heterotheca* and *Lespedeza*. In addition, litter taken from beneath *Lespedeza* differs both qualitatively and quantitatively from litter taken in grassy areas distant from *Lespedeza*. The combination of a lower C:N and greater quantity of *Lespedeza* litter suggests that there should be a greater pool of available nitrogen in litter under *Lespedeza* plants. It is possible that the presence of this litter may affect germination and seedling establishment of *Heterotheca* seeds in the proximity of *Lespedeza* plants.

Two greenhouse experiments were designed to test the effects of an environment characterized by the presence of *Lespedeza* on the germination, growth and reproduction of *Heterotheca*. This study sought to provide additional information on life stages in which potential interactions may be taking place. The first greenhouse experiment focused on the germination response of *Heterotheca* to soil and litter found beneath *Lespedeza*. Does the presence of *Lespedeza* affect the early stages of *Heterotheca* germination and seedling establishment, or do interactions between these species primarily occur later in the *Heterotheca* life cycle? I hypothesized that percent germination would be higher under conditions of *Lespedeza* litter and soil than under conditions of grassy litter and non-*Lespedeza* soil.

The second greenhouse experiment focused on the effects of nitrogen and shading on the growth of *Heterotheca*. If *Lespedeza* modifies these resources, does *Heterotheca* then respond by increases or reductions in growth and flowering? I hypothesized that individuals grown under conditions of increasing nitrogen would have increases in shoot and root weights and an increased number of flowers. Shade effects would decrease the growth and reproductive output of *Heterotheca*; but overall, the positive effects of nutrient additions would be greater than the negative effects of shading.

METHODS

Germination Study

Soil and litter were collected in an old field (field 3-412) on the SRS in the spring of 1999, both directly under *Lespedeza* plants and in areas without *Lespedeza*. Soil was sieved to remove roots and other debris. Seeds of *Heterotheca* were collected from this field in the fall of 1998 and stored outside in a Rubbermaid tub. Ten blocks of four treatments were established in

greenhouse flats: *Lespedeza* soil plus *Lespedeza* litter, *Lespedeza* soil plus non-*Lespedeza* litter, non-*Lespedeza* soil plus *Lespedeza* litter, and non-*Lespedeza* soil plus non-*Lespedeza* litter. Soil to a constant depth of 3 cm was put into each 25 cm by 50 cm flat. One hundred *Heterotheca* disk seeds were placed on top of the soil in a 10 by 10 grid. Approximately 2 cm of litter was placed on top. Disk seeds were used, as ray seeds require an after-ripening period to break dormancy (Baskin and Baskin 1976). Flats were gently watered with a light spray every other day. Germination was checked daily for ten weeks. The germination study was treated as a fixed effects, 2 by 2 factorial experiment with two levels of both soil and litter type.

Shade/N Experiment

Soil for use in this greenhouse experiment was collected in the spring of 2001 from an area of field 3-412 where *Lespedeza* was not present. In addition, there was no visible evidence of *Lespedeza* from the previous year in this area. Soil was dried and sifted in a 5 mm sieve to remove roots and other matter. *Heterotheca* seeds were collected from field 3-412 in the fall of 2000 and stored outside over winter. The greenhouse experiment began in March 2001. Seeds were germinated in flats and 225 seedlings were transferred to root tubes in July, when seedlings were approximately 6-8 cm tall. Five soil nitrogen treatments were randomly assigned to blocks of five root tubes. Nitrogen amendments were made by adding Nitroform ™ to soil prior to transplants. Nitroform ™ is a commercially available slow release nitrogen fertilizer, which provides 38% nitrogen by weight, in the form of urea. For each root tube, soil was mixed with Nitroform™ to produce one of the following concentrations of nitrogen: +0 (control), +25, +50, +100, and +200 ppm.

The shade treatment was not imposed at the beginning of the experiment. During the time that *Heterotheca* is in the seedling stage, the new shoots of *Lespedeza* are just emerging and provide little shade. By mid-summer, *Lespedeza* can significantly reduce canopy openness (Chapter 2) and shade adjacent plants.

In July, the *Heterotheca* plants were transplanted from root tubes into two-gallon pots. Nitroform™ was again mixed with 7kg of field 3-412 soil per pot to yield the correct soil nitrogen amendment. From the surviving seedlings, 180 plants were randomly selected for transplant. Plants were randomly assigned to one of two shade treatments (no shade or shade) and randomly assigned a position in one of two greenhouse rooms. This resulted in 18 replicates of 2 shade treatments and 5 nitrogen addition treatments.

Four shade houses, constructed of PVC pipe and 60% shade cloth, were placed on two diagonally opposite tables arranged to minimize cross shading in each greenhouse room. Shade houses were 1.5 m tall and were not covered on the top. Unshaded plants were placed on open tables in the same rooms. Care was made to position the groups of pots in such a way that the shade treatments had little effect on the non-shade treatments. Plants were well watered from the bottom of the pots throughout the experiment. Periodic measurements of plant height were taken, and plants were harvested after flowering and seed production, in November and December. Harvest times were staggered, as there was variability between plants in the time of bolting and flowering. During harvesting, heights were measured, and the number of flowering stems and flowering heads were counted. Flowering heads were removed, and above and below ground plant portions were separated. Stems were cut off at the soil surface and bagged, and the roots were separated from the soil through washing and bagged separately. Roots and shoots were dried and then weighed separately.

A fixed effects, factorial ANOVA was run on the data treating N concentration and shade as two factors with 5 and 2 levels, respectively. Shade and N concentrations were both treated as fixed effects. There were no significant interactions between the two factors for any of the measures; therefore, they were treated separately throughout the results. Also, there were no effects of location of plants in terms of their placement in either greenhouse room or either side of the room.

RESULTS

Germination Study

There was no significant effect of litter type on the germination of *Heterotheca* seeds (Figure 1). There was a small effect of soil type on germination, though it was not significant at the $p < .05$ levels. The average germination in the *Lespedeza* soil was 50.55 % ± 7.33, while seeds in the non-*Lespedeza* soil had an average germination of 42.7 % ± 7.48. The *p*-value for the difference between these two means was .158.

Shade/N Experiment

Shoot weights were affected by both N concentration and shade treatments, while root weights were affected only by shade treatment (Figure 2). Shoot weights increased as N increased, and both shoot and root weights were lower in the shade treatment. All pairwise comparisons between concentration levels for shoot weight were highly significant ($p<.001$) except for the comparison of 25 and 50 ppm. (Table 1) There was a slight increase in root weight for the 25 and 50 ppm treatments; both of these treatments were significantly higher than the control treatment.

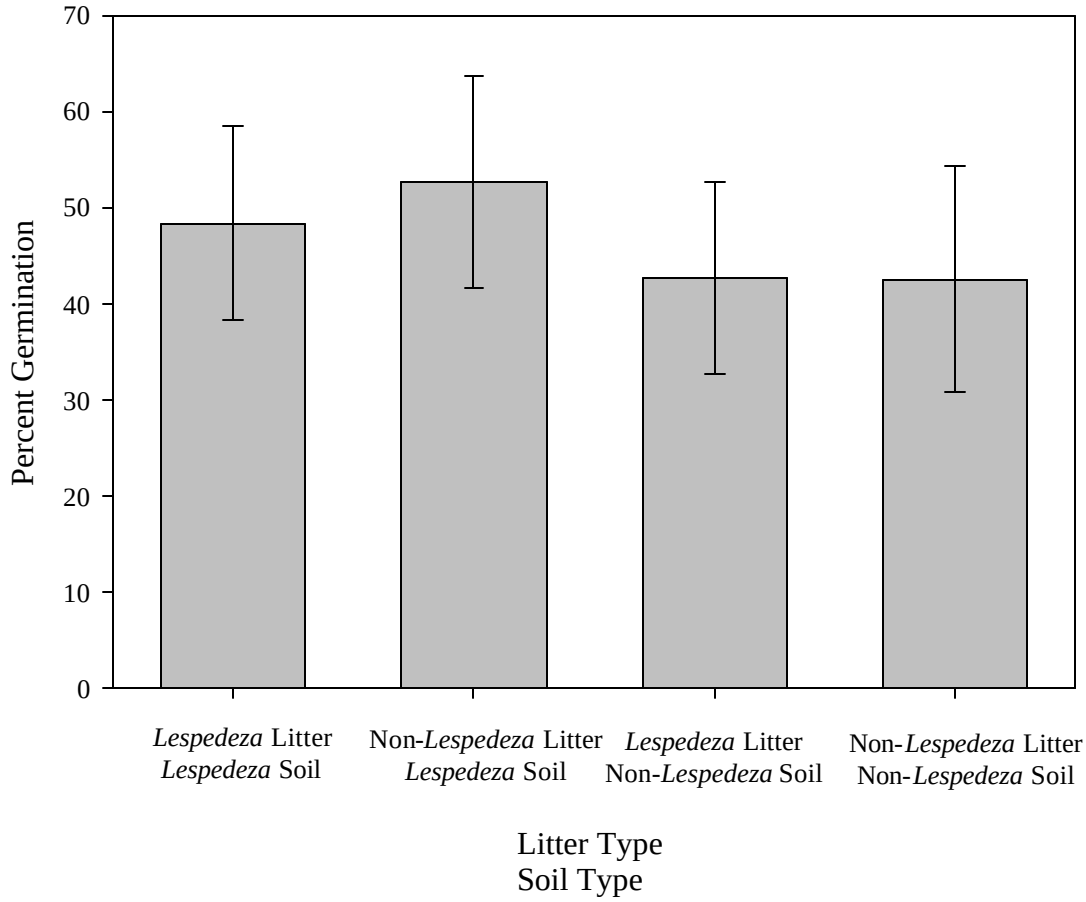

Figure 1. Mean Percent Germination of *Heterotheca* disc seeds for each combination of soil and litter Treatment. Error Bars represent ±2 S.E.

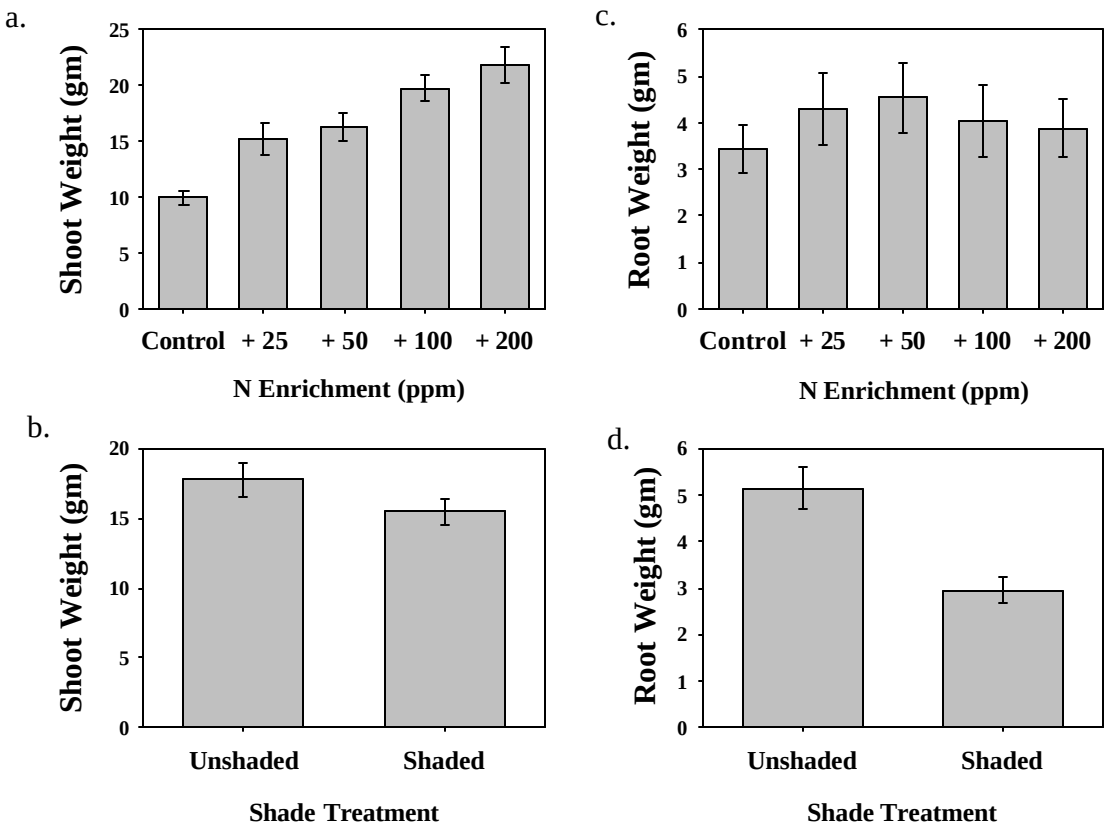

Figure 2. Shoot and root weights of *Heterotheca* individuals under nitrogen amendment and shade treatments. Shown are means ± 2 S.E.

Table 1. Contrasts between treatment levels for shoot and root weight, root:shoot, height, number of flowering heads and number of flowering stalks. Significance indicates differences between individual treatments as indicated. n.s. indicates where two treatments were not statistically different.

Contrast	Shoot Wt.	Root Wt.	R:S	Height	# of Flowering Stalks	# of Flowering Heads
N Concentration	Pr >F					
0 vs. 25	<.0001	0.0399	n.s.	n.s.	0. 0152	0. 0400
0 vs. 50	<.0001	0.0103	0.0095	n.s.	0. 0004	0. 0124
0 vs. 100	<.0001	n.s.	<.0001	n.s.	<.0001	<.0001
0 vs. 200	<.0001	n.s.	<.0001	0.0269	<.0001	<.0001
25 vs. 50	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
25 vs. 100	<.0001	n.s.	0.0010	n.s.	0.0043	0.0327
25 vs. 200	<.0001	n.s.	<.0001	n.s.	0.0047	0.0302
50 vs. 100	<.0001	n.s.	0.0088	n.s.	n.s.	n.s.
50 vs. 200	<.0001	n.s.	0.0003	n.s.	n.s.	n.s.
100 vs. 200	0.0136	n.s.	n.s.	n.s.	n.s.	n.s.
Shaded vs. Unshaded	<.0001	<.0001	<.0001	0.0487	n.s.	n.s.

The root to shoot ratio was significantly affected by both nitrogen amendment and shade treatment (Figure 3). The root to shoot ratio decreases with increasing concentration of N and with added shade, indicating a relatively greater allocation to shoots as N increases and under shade. Height was significantly affected by shade treatment but not by N amendment (Figure 3). The only two N treatments to produce significantly different heights were the control and +200 ppm treatment (Table 1).

The number of flowering stalks and heads significantly increased as a result of N addition and was not affected by shade treatment (Figure 4). Within the N treatment, the effect was seen at small concentrations of N and there were no further differences as concentration increased above 50 ppm (Table 1).

DISCUSSION

Soil and litter beneath shrubs are often enriched in nitrogen (Tiedemann and Klemmedson 1973, Barth and Klemmedson 1978), and data in Chapter 2 suggest that *Lespedeza* soil and litter may be higher in nitrogen than soil and litter elsewhere in the field. However, there was no effect of either *Lespedeza* litter or soil quality on seed germination of *Heterotheca*, and thus no evidence of potential facilitation at that stage of the *Heterotheca* life cycle. It is important to note, however, that while *Lespedeza* soil and litter did not enhance *Heterotheca* germination, it also did not inhibit germination. Many studies have shown that the presence of litter can inhibit seed germination (Werner 1975, Fowler 1988, Williams et al. 1990, Smith and Capelle 1992). In particular, the litter of pine and oak was found to significantly inhibit *Heterotheca* germination in the same field where this study was conducted (Monk and Gabrielson 1985). A similar study also found a slight yet non-significant negative effect of litter

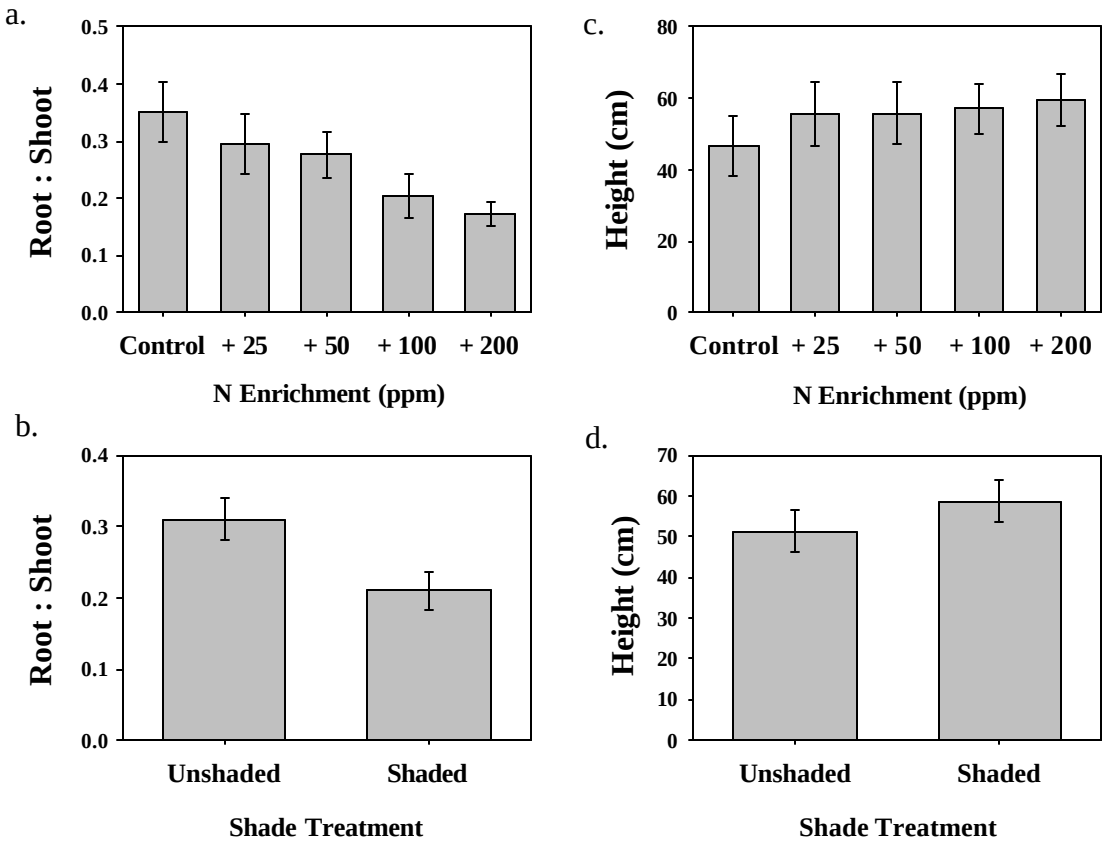

Figure 3. Root : Shoot and heights of *Heterotheca* under nitrogen amendment and shade treatment. Shown are means ± 2 S.E.

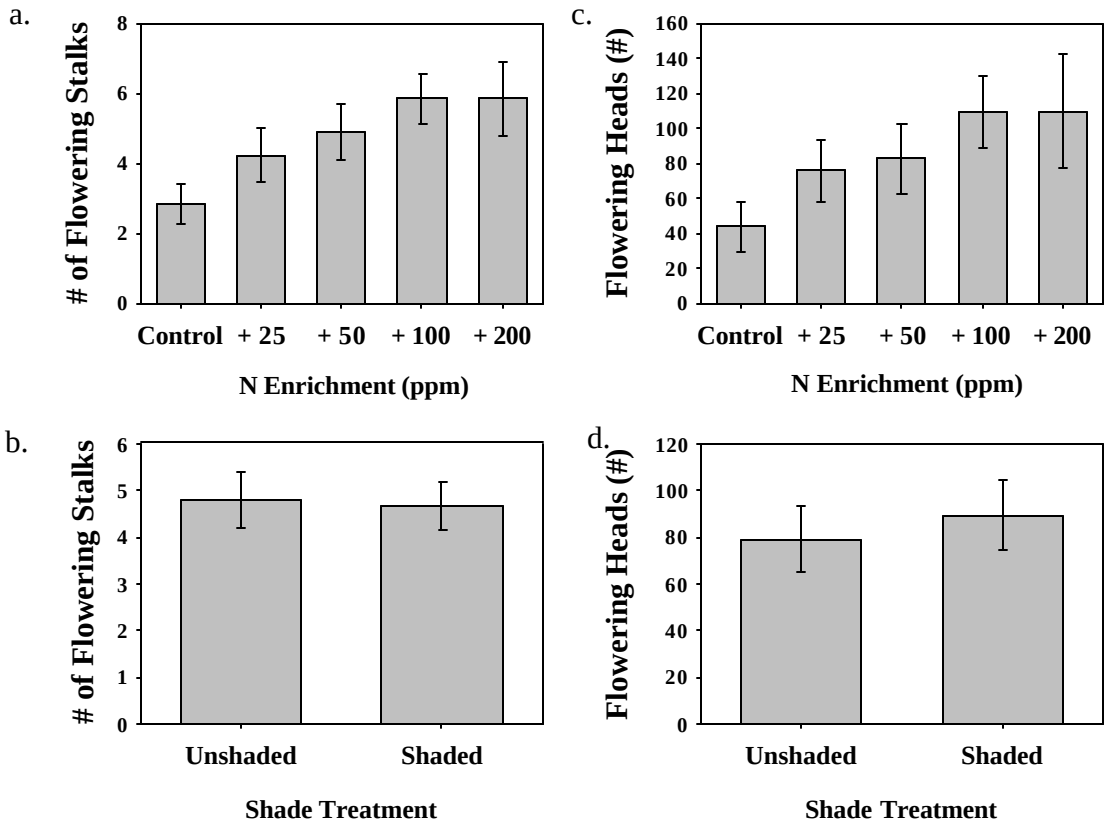

Figure 4. Number of flowering stalks and number of flowering heads of *Heterotheca* individuals under nitrogen amendment and shade treatment. Shown are means ± 2 S.E.

of a nitrogen fixing legume, *Retama sphaerocarpa*, on the germination rate of Barley seeds (Moro et al. 1997).

Plants often respond to changes in resources through differential biomass allocation. With decreasing nutrient availability, plants generally allocate more resources to roots in order to increase nutrient capture, and with increasing shade stress, plants typically allocate more resources to aboveground, photosynthesizing tissue (Gulmon and Chu 1981, Ingestad and McDonald 1989, Aerts et al. 1992, McConnaughay and Coleman 1999). This should lead to increases in root/shoot ratios with increasing shade, and decreases in root/shoot ratios with increasing nutrients. Several studies have demonstrated decreases in root/shoot ratios under nutrient enrichment or fertilization for a wide variety of plants. Hunt and Bazzaz (1980) found greater allocation to roots of unfertilized ragweed as opposed to fertilized ragweed. McConnaughay and Coleman (1999) examined changes in root/shoot ratios for three old-field species across a nutrient and light gradient. Two of the three species in this study showed significant decreases in root/shoot ratios across the nutrient gradient, and increases in root/shoot ratios across the light gradient. Greater root allocation was also seen in *Heterotheca* rosettes grown under nitrate limited conditions (Mihaliak and Lincoln 1985). In this study, the root/shoot ratio of mature flowering individuals behaved predictably in terms of the response to light and nutrients; however, the decreasing root/shoot ratio is attributable to an effect on aboveground allocation, and not on root weight. Increasing nitrogen led to increases in shoot weights across all levels of added nitrogen, but only the control treatment had a lower root weight. At the time of harvesting, pots did not appear to be root bound; nevertheless, roots were still limited to the physical space in the pots and it may not be surprising to see a greater effect on shoots rather

than roots. While nitrogen concentrations in the field were lower than treatment additions, significant differences were seen even at the lowest levels of nitrogen addition.

Reproductive increases as a result of increases in light availability or nutrients have been documented frequently (Pitelka et al. 1980, Whigham 1984, McKenna and Houle 1999). Increasing N increased the number of flowering stalks and heads of *Heterotheca* as predicted, but there were no significant increases above the + 50 ppm treatment. This indicates a moderate increase in reproductive allotment at the lower levels of nitrogen enrichment, but an upper threshold beyond which increasing nitrogen did not have further effects on flowering heads or stalks.

The imposition of a shade treatment produced effects on *Heterotheca* biomass and height, but not on the reproductive measures. There was a slight, though statistically insignificant, increase in flowering heads per plant under the shade treatment. Height increased significantly, suggesting that *Heterotheca* does respond to reduced light by increasing stem length. In this case, while biomass was significantly reduced by shade, there was no effect on the plant in terms of reproductive output. This may suggest that partial light limitation of *Heterotheca* may not be significantly detrimental to its overall fitness.

Many studies have shown interactive effects of light and nitrogen and that differences in plant yields due to increasing nutrients are most pronounced or only seen under conditions of high light (Montoya et al. 1961, Murray and Nichols 1966, De Pinheiro Henriques and Marcelis 2000). Wainhouse et al. (1998) found that root/shoot ratios of young sitka spruce varied less between low and high nitrogen under conditions of low light than under high light. Roots of *Agropyron desertorum,* a perennial grass, responded to nitrogen enriched patches by increasing relative growth rates only under conditions of full light; roots grown under shade conditions did

not respond (Bilbrough and Caldwell 1995). Peace and Grubb (1982), however, did find a growth response of a shade tolerant annual, *Impatiens parviflora,* to increases in nutrients at high levels of shade. Nevertheless, there was an interaction between light and nutrients, as together they produced a greater effect on growth than either alone (Peace and Grubb 1982). These findings would suggest that the *Heterotheca* individuals grown under shade conditions might not have the same response to increases in nitrogen as plants under full light conditions. In this study, however, there were no interactive effects of shade and nitrogen addition for any of the measures. Individuals under full light were larger than their unshaded counterparts at each level of added nitrogen.

While seed germination was not significantly affected by the presence of *Lespedeza* soil or litter, mature *Heterotheca* plants were affected by changes in both soil nitrogen and shade. Increasing nitrogen increased growth and reproductive output; even low additions of nitrogen led to larger individuals with greater numbers of flowers. The addition of partial shade reduced plant biomass but did not affect flower production. In a low nutrient old field where these two species co-occur, *Lespedeza* provides both increased shade and the potential for increased soil nutrients, which could influence both facilitative and competitive interactions with *Heterotheca*. These results suggest that Heterotheca may be facilitated by *Lespedeza* if it causes increases in soil nitrogen. Competition with *Lespedeza* may lead to decreases in overall *Heterotheca* growth, but shading may not reduce fitness.

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CHAPTER 5

CONCLUSIONS

Evidence from this dissertation supported the hypothesis that *Lespedeza cuneata* acts as both a facilitator for, and a competitor with, *Heterotheca subaxillaris* within this old field. Traditionally, competitive interactions have been well studied and are often assumed to be the major interactions structuring plant communities (Tilman 1987). Less attention has been given to facilitation, although interest over the last decade has demonstrated the importance of facilitation in many systems, particularly those where plants experience harsh conditions. Facilitating individuals are typically perennial, established plants such as shrubs and trees that can modify their local environment in such a way as to ameliorate stressful conditions. The positive effect of plants on neighbors has been attributed to such mechanisms as increasing nutrient availability (Tielborger and Kadmon 2000), and amelioration of water and temperature stress through shading (Shumway 2000, Forseth et al. 2001, Maestre et al. 2001). This dissertation focused on a perennial nitrogen-fixing legume in a nutrient poor old field, where there are conditions of stress that create opportunities for moderation by a perennial plant such as *Lespedeza*. This old field has extremely low nitrogen levels (Chapter 2) and during the years of study, a drought led to severe rainfall shortages (Kiuchi 2002). The presence of *Heterotheca*, found typically in the vicinity of *Lespedeza* within this old field, suggested evidence of possible facilitation.

There was a significant degree of clustering between the two species at all spatial scales, and *Heterotheca* was more likely to be found at moderate densities of *Lespedeza* than at either

high or low densities (Chapter 1). These patterns were evident at early stages and persisted through the lifespan of *Heterotheca*, although surviving individuals were less likely to be clustered with *Lespedeza* than predicted by random mortality. These results suggested that *Lespedeza* might facilitate the establishment of *Heterotheca*, but that patterns of mortality may have been influenced by competitive interactions.

Methods of spatial pattern analysis, such as that of Ripley's K, used here, are useful in categorizing the nature of spatial patterns seen amongst individuals. The presence of a spatial pattern has been used to infer the presence of competitive or facilitative interactions (Fowler 1986, Kenkel 1988, Dayong 1990, Martens et al. 1997); however, it is impossible to discern specific interactions from the presence of a pattern.

I would argue that the biological inferences that can be made from pattern analysis alone are limited for two reasons. First, there may be alternative explanations for the patterns seen. Individuals may be clustered simply because of shared resource requirements, underlying environmental heterogeneity, or seed dispersal (Couteron and Kokou 1997, Barot et al. 1999). In this study, the old field was chosen for its apparent uniformity with respect to topography and vegetation, but there still may be small-scale variation in relief and soil quality. Seed dispersal in this case may not be responsible for the patterning as I found no relationship between *Heterotheca* seed density and *Lespedeza* density (data not presented).

Second, pattern analysis only considers the positions of the individuals and does not take into consideration the variation in success of the individuals. Information on the size or reproductive output of individuals may reveal more about the types of interactions taking place. If competition were the predominant interaction between the two species, one would expect to see larger and more successful individuals at the lower ends of the density spectrum. As

Lespedeza density increases, measures of *Heterotheca* success should decrease. If facilitation were the predominant interaction, one would predict increases in the measures of *Heterotheca* success as *Lespedeza* density increases. I found fewer *Heterotheca* individuals, with lower biomass and seed weight, at lower *Lespedeza* densities than at moderate or higher densities (Chapter 1). This supported the hypothesis of facilitative interactions. The probability of mortality increased with increasing *Lespedeza* density; however, which supported the hypothesis of increasing importance of competitive interactions at higher densities. These results supported the hypothesis that both facilitative and competitive interactions co-occurred between *Heterotheca* and *Lespedeza* at my study site.

The results of the pattern analysis suggested that the spatial patterning between the two species primarily occurred early in the life cycle of *Heterotheca*. However, comparing heights of *Heterotheca* taken early in the season to adult *Heterotheca* heights suggested that mechanisms responsible for this positive association may have occurred during the growing season as well as at the beginning. There was no correlation between early heights and *Lespedeza* density, but final heights were slightly positively correlated with *Lespedeza* density. This however, may have been an artifact of competitive interactions. At higher densities, taller, well-established *Heterotheca* had a higher probability of survival.

One potential explanation for the positive spatial association seen between *Heterotheca* and *Lespedeza* is that individuals of *Lespedeza* helped to create local environmental conditions that favored the establishment and growth of *Heterotheca*. I found evidence that *Lespedeza* significantly altered its local resources. For some of the resources tested such as light and temperature, the connection to *Lespedeza* was apparent (Chapter 2). *Lespedeza* caused decreasing canopy openness leading to shadier conditions at increasing density. Higher soil

temperatures were found at the lowest levels of *Lespedeza*. Soil nutrient studies also suggested higher levels of nitrate and ammonium, and lower levels of phosphorous, at higher *Lespedeza* densities. High densities of *Lespedeza* led to lower soil moisture except for several days following a rainfall event, when soil moisture was higher than in plots with low densities of *Lespedeza*. During a drought, when there are fewer rainfall events, this may lead to an increase in the competitive effect of *Lespedeza* on *Heterotheca*.

The combination of a positive growth response by *Heterotheca* to increases in soil nitrogen and the lack of a significant negative effect of moderate amounts of shading supports the contention that facilitation of *Heterotheca* through resource modification by *Lespedeza* is possible (Chapter 3). Increasing the levels of nitrogen in the soil around *Heterotheca* had a positive effect on the growth and reproduction of *Heterotheca*. Increasing shade did negatively affect overall biomass of the individuals, but did not affect the overall reproductive output.

This study takes our understanding of the dynamics of *Lespedeza* and *Heterotheca* one step further and demonstrates that not only do *Heterotheca* individuals occur more often at moderate densities of *Lespedeza*, but that successful individuals are found across the range of the *Lespedeza* Neighborhood Density Index (NDI). Evidence suggests that an increasing NDI favors larger and taller *Heterotheca* individuals with a greater total seed weight, but at the same time decreased the probability of *Heterotheca* survival.

At higher densities of *Lespedeza*, competitive forces may have dominated over facilitative interactions that operated at the moderate densities. At the highest densities there were fewer *Heterotheca* individuals than expected, and those that were at higher densities had a higher probability of mortality. However, those individuals that did survive were likely to be

more successful, achieving slightly greater height and weight than their counterparts at lower densities.

While many studies document plant spatial patterns, few take the next step of incorporating a modelling approach to further investigate the relationships between plant species. This study used a pattern analysis to first document the presence of a positive spatial association between two species, and then explored the occurrence of one species as a function of a neighborhood density measure of the other. This approach, coupled with an investigation of a plant's effect on multiple environmental resources and the subsequent consequences for a species with which it interacts, will help further ecological understanding of the dynamic and complex relationships between facilitative and competitive interactions among plants.

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APPENDICES

```
C   PATTERN ANALYSIS PROGRAM
C   Program to calculate khat and lhat function for the juvenile data
C   Output files are:  origlc.out and origlhs.out
C   This program will read data from the baseget and neighbor data
C   files. The number, x, and y for each observation will be read into
C   2 separate (n x 2) arrays.
C         nlc = number of Lespedeza
C         nhs = number of Heterotheca
C         lxy =1500 x 2 array of Lespedeza data (x, y)
C         Hxy =700 x 2 array of Heterotheca data (x, y)
C         Khat = numt x 2 array containing the distance class and
C         corresponding khat values
C   Initialization of variables
          implicit real*8(a-h,o-z)
          Real*8 les(10000,5), hxy(10000,2),rl1(100,2), rl2(100,2)
          real*8 rl3(100,2),rhs(10000,2),rl4(100,2)
      a = 50d0
      b = 20d0
      area = a*b
      tnum=100
      totm=10
      nlc = 0
      nhs = 0
      rls = 0d0
      rlshs = 0d0
      pi = 4*atan(1.0d0)
      inum=1
      itotsim = 1000
      rlambdahs = 574/(a*b)

C        Declare files to open
      open (unit = 1, file = "lesfin.txt")
      Open (unit = 2, file = "hsdat.txt")
      open (unit = 3, file = "origlc2.out")
      open (unit = 54, file = "origlhs2.out")
      open (unit=55, file = "origlc2.out")
C    Read from files into array
C     Read in Lespedeza data
      Do 100 i = 1,2000
         read (1,10,end=110) les(nlc+1,1),les(nlc+1,2),les(nlc+1,3),
     +             les(nlc+1,4), les(nlc+1,5)
      if (les(nlc+1,1).ge.0d0.and.les(nlc+1,2).ge.0d0.and.
     +     les(nlc+1,1).le.a.and.les(nlc+1,2).le.b) then

           nlc=1+nlc
       endif
  100   Continue
  110   Continue

C     Read in Heterotheca data
```

```
      Do 200 i = 1,700
         read (2,20,end=210), hxy(nhs+1,1), hxy(nhs+1,2)
      if (hxy(nhs+1,1).ge.0d0.and.hxy(nhs+1,2).ge.0d0) then

          nhs=nhs+1
      endif
  200   Continue
  210   Continue

  10    Format (f8.2,4x,f8.2,4x,f8.2,4x,f8.2,4x,f8.2,4x,)
  20    Format (f5.2,5x,f6.2)

C        Call Khat subroutine to calculate the Khat values -
C        first is the baseget species, next is the neighbor species
C        also pass number of each species
C        K array is returned
C  Perform Rkhat cross calculations for two species
        Call rkhatsub(les, hxy, nlc,nhs,a,b,tnum,totm, rl1)
        Call rkhatsub(hxy, les, nhs,nlc,a,b,tnum,totm, rl2)

C  Perform HS-HS khat calculations
        Call rkhatsub(hxy, hxy, nhs,nhs,a,b,tnum,totm, rl3)
        Call rkhatsub( les, les, nlc,nlc,a,b,tnum,totm, rl4)

C  Avg CrossK's and write to files
          Do 300 k = 1, tnum
              rlavg = (rl1(k,2) + rl2(k,2))/2
              rls = rls + (rlavg)**2
              rlshs = rlshs + (rl3(k,2))**2
              rlslc = rlslc + (rl4(k,2))**2
              write (3,301) inum, rl1(k,1), rlavg, rls
              write (54,401) inum, rl3(k,1), rl3(k,2), rlshs
              write (55,401) inum, rl4(k,1), rl4(k,2), rlslc
  300    Continue
  301    Format (i4, 2x, f10.5, 2x, f15.8, 2x, f15.8)
  401    Format (i4, 2x,f10.5, 2x, f15.8, 2x, f15.8)

C  Simulate HS and calc. khat fxns
      Do 500  isim = 2, itotsim
         rls = 0d0

C       Choose Random HS points
        u = ran2(iseed)
        ux = -log(u)/(rlambdahs*b)
        rhs(1,1) = ux
        rhs(1,2) = (ran2(iseed))*b
        inhs = 1

  400      u = ran2(iseed)
           v = ran2(iseed)
           ux = rhs(inhs,1) - log(u)/(rlambdahs*b)
           uy = b*v
             If (ux.le.a) then
                inhs = inhs+1
                rhs(inhs,1) = ux
                rhs(inhs,2) = uy
                Go to 400
```

```
            endif

C  Perform Rkhat cross calculations for two species
        Call rkhatsub(les, rhs, nlc,inhs,a,b,tnum,totm, rl1)
        Call rkhatsub(rhs, les, nhs,nlc,a,b,tnum,totm, rl2)

C  Perform HS-HS khat calculations
        Call rkhatsub(rhs, rhs, inhs,inhs,a,b,tnum,totm, rl3)

C  Avg CrossK's and write to files
          Do 600 k = 1, tnum
              rlavg = (rl1(k,2) + rl2(k,2))/2
              rls = rls + (rlavg)**2
              rlshs = rlshs + (rl3(k,2))**2
              write (3,301) isim, rl1(k,1), rlavg, rls
              write (54,401) isim, rl3(k,1), rl3(k,2), rlshs
  600    Continue
  500    Continue
       end
```

```
C     MODELLING PROGRAM #1
C     Initial Estimation of parameters
C     Program to estimate betas for intensity model – Quadratic model
C     Initialization of variables
            implicit real*8(a-h,o-z)
            Real*8 les(2000,5), hxy(60000,2), hx(60000,3), ss(3,3)
            Real*8 beta(3), g1(3), g2(3), grad(3)
            Real*8 rx(3), ssi(3,3), ssigrad(3)
        iseed = 32664
        pi = 4*atan(1.d0)
        a = 50d0
        b = 20d0
        area = a*b
        nlc = 0
        nhs = 0
        ns = 5000
        itotsim = 2000
        rmlone = 0.0d0

        beta(1) = 0.0d0
        beta(2) = 0.0d0
        beta(3) = 0.0d0
        irns = 5000

C     Declare files to open

        open (unit = 1, file= "lesfin.txt")
        open (unit = 2, file= "hsdat.txt")
        open (unit = 3, file= "nm32par1.out")
        open (unit = 52, file = "var32par1.out")

C     Read from files into array
C       Read in Lespedeza data
        Do 100 i = 1,2000
           read (1,10,end=110) les(nlc+1,1),les(nlc+1,2),les(nlc+1,3),
     +             les(nlc+1,4), les(nlc+1,5)
        if (les(nlc+1,1).ge.0d0.and.les(nlc+1,2).ge.0d0.and.
     +     les(nlc+1,1).le.a.and.les(nlc+1,2).le.b) nlc=1+nlc
  100   Continue
  110   Continue

C       Read in Heterotheca data

        Do 200 i = 1,700
           read (2,20,end=210), hxy(nhs+1,1), hxy(nhs+1,2)
        if (hxy(nhs+1,1).ge.0d0.and.hxy(nhs+1,2).ge.0d0) then

           call lambda(hxy(nhs+1,1),hxy(nhs+1,2),nlc,les,
     +               hx(nhs+1,1),hx(nhs+1,2),hx(nhs+1,3))

        rmlone = rmlone+log(exp(beta(1)*hx(nhs+1,1)+beta(2)*hx(nhs+1,2)
     +              +         beta(3)*hx(nhs+1,3)))
          nhs=nhs+1
        endif
  200   Continue
  210   Continue
```

```
  10    Format (f8.2,4x,f8.2,4x,f8.2,4x,f8.2,4x,f8.2,4x,)
  20    Format (f5.2,5x,f6.2)

C   Initialize or reset g matrix values

           do 300 i = 1,3
               g1(i) = 0d0
            do 400 j= 1,nhs
               g1(i) = g1(i)+hx(j,i)
 400       Continue
 300      Continue

C    Calculate (hx'hx)^-1
        do 600 i=1,3
           do 700 j=1,3
              ss(i,j) = 0.0d0
             do 750 k=1,nhs
              ss(i,j) = ss(i,j)+hx(k,i)*hx(k,j)
  750        Continue
  700      Continue
  600   Continue

        call inverse(ss,ssi,3,3)
        write(52, 520) ssi(1,1), ssi(2,2), ssi(3,3)

  520   Format(f20.15, 2x, f20.15, 2x, f20.15)

C  Iterate procedure of estimation
       do 800 inum = 1,itotsim

            rmlhood = 0
            rmltwo = 0

      do 1000 i = 1,3
         g2(i) = 0.0d0
 1000    Continue

         do 9000 i = 1,irns
            rxx = ran2(iseed)*a
            rxy = ran2(iseed)*b
            call lambda(rxx,rxy,nlc,les,rx(1),rx(2),rx(3))


C  Calculate 2nd part of gradient
        do 40 j=1,3
           temp=0.0d0
          do 30 k=1,3
             temp = temp+beta(k)*rx(k)
  30       Continue
           g2(j) = g2(j) +rx(j)*exp(temp)

           rmltwo = rmltwo+exp(temp)

  40    Continue
 9000      Continue
          do 1300 ig = 1,3
              g2(ig) = (area)*g2(ig)/irns
```

```
            grad(ig) = g1(ig) - g2(ig)
 1300    Continue

C  Calculate new parameters by adding ssgrad to the previous beta
estimate

       do 1400  i = 1,3
        ssigrad(i) = 0d0
         do 1500 j = 1,3
         ssigrad(i) = ssigrad(i)+ssi(i,j)*grad(j)
 1500    Continue
         Beta(i) = beta(i)+ ssigrad(i)/50
 1400  Continue

         rmltwo = (area)*rmltwo/irns
         rmlhood = rmlone-rmltwo

         write(3,301) inum,beta(1),beta(2),beta(3),rmlhood

 301     Format(i5,3x,f13.10,3x,f13.10,3x,f13.10,2x,f15.5)

 800   Continue
        end
```

```
C    MODELLING PROGRAM #2
C    Robbins Monroe Dampening of Parameters
C    Program to fine tune estimation of betas for intensity model
C    Initialization of variables
           implicit real*8(a-h,o-z)
           Real*8 les(2000,5), hxy(60000,2), hx(60000,3), ss(3,3)
           Real*8 beta(3), g1(3), g2(3), grad(3)
           Real*8 rx(3), ssi(3,3), ssigrad(3)
      iseed = 32664
      pi = 4*atan(1.d0)
      a = 50d0
      b = 20d0
      area = a*b
      nlc = 0
      nhs = 0
      ns = 5000
      itotsim = 2000
      beta(1) = -.50918d0
      beta(2) = 0.000655d0
      beta(3) = -0.0000001832d0
      rmlone = 0.0d0

C    Declare files to open

      open (unit = 1, file= "lesfin.txt")
      open (unit = 2, file= "hsdat.txt")
      open (unit = 3, file= "r3par1.out")

C    Read from files into array
C      Read in Lespedeza data
      Do 100 i = 1,2000
         read (1,10,end=110) les(nlc+1,1),les(nlc+1,2),les(nlc+1,3),
     +             les(nlc+1,4), les(nlc+1,5)
      if (les(nlc+1,1).ge.0d0.and.les(nlc+1,2).ge.0d0.and.
     +     les(nlc+1,1).le.a.and.les(nlc+1,2).le.b) nlc=1+nlc
  100   Continue
  110   Continue

C      Read in Heterotheca data

      Do 200 i = 1,700
         read (2,20,end=210), hxy(nhs+1,1), hxy(nhs+1,2)
      if (hxy(nhs+1,1).ge.0d0.and.hxy(nhs+1,2).ge.0d0) then

         call lambda(hxy(nhs+1,1),hxy(nhs+1,2),nlc,les,
     +               hx(nhs+1,1),hx(nhs+1,2),hx(nhs+1,3))
         rmlone=rmlone+log(exp(beta(1)*hx(nhs+1,1)+beta(2)*hx(nhs+1,2)
     +           +beta(3)*hx(nhs+1,3)))
         nhs=nhs+1
      endif
  200   Continue
  210   Continue

  10    Format (f8.2,4x,f8.2,4x,f8.2,4x,f8.2,4x,f8.2,4x,)
  20    Format (f5.2,5x,f6.2)

C   Initialize  or reset g matrix values
```

```
           do 300 i = 1,3
               g1(i) = 0d0
            do 400 j= 1,nhs
               g1(i) = g1(i)+hx(j,i)
 400       Continue
 300      Continue

C    Calculate (hx'hx)^-1
        do 600 i=1,3
           do 700 j=1,3
              ss(i,j) = 0.0d0
             do 750 k=1,nhs
              ss(i,j) = ss(i,j)+hx(k,i)*hx(k,j)
  750        Continue
  700      Continue
  600   Continue

        call inverse(ss,ssi,3,3)

C  Iterate procedure of estimation
       do 800 inum = 1,itotsim

           rmlhood = 0
           rmltwo = 0

          t=(inum)**(.25)
          irns=int(ns*t)

       do 1000 i = 1,3
          g2(i) = 0.0d0
 1000    Continue

         do 9000 i = 1,irns
            rxx = ran2(iseed)*a
            rxy = ran2(iseed)*b
            call lambda(rxx,rxy,nlc,les,rx(1),rx(2),rx(3))


C  Calculate 2nd part of gradient
        do 40 j=1,3
           temp=0.0d0
          do 30 k=1,3
             temp = temp+beta(k)*rx(k)
  30       Continue

           rmltwo = rmltwo+exp(temp)

           g2(j) = g2(j) +rx(j)*exp(temp)
  40    Continue
 9000      Continue
         do 1300 ig = 1,3
             g2(ig) = (area)*g2(ig)/irns
             grad(ig) = g1(ig) - g2(ig)
 1300    Continue
```

```
C  Calculate new parameters by adding ssgrad to the previous beta
estimate

       do 1400  i = 1,3
        ssigrad(i) = 0d0
         do 1500 j = 1,3
         ssigrad(i) = ssigrad(i)+ssi(i,j)*grad(j)
 1500    Continue
         Beta(i) = beta(i)+ ssigrad(i)/(inum+9)
 1400  Continue

         rmltwo = (area)*rmltwo/irns
         rmlhood = rmlone-rmltwo

         write(3,301) inum, beta(1), beta(2), beta(3), rmlhood
 301   Format(i5, 2x, f18.14, 2x, f18.14,2x,f18.14,2x,f12.3)

 800   Continue
        end
```

```
C     MODELLING PROGRAM #3
C     Model Simulations
C      Program to simulate Heterotheca positions using rejection
C      sampling and given the fitted model.  Will also
C      calculate the cross lhats

C      Initialization of variables
            implicit real*8(a-h,o-z)
            real*8 rhs(10000,5), les(10000,5), rl1(100,2), rl2(100,2)
            real*8 rl3(100,2), rk1(100,2), rk2(100,2), rk3(100,2)
        iseed = 32664
        pi = 4*atan(1.d0)
        a = 50d0
        b = 20d0
        area = a*b
        nlc = 0
        nhs = 0
        beta1 = -.51d0
        beta2 = .000665d0
        beta3 = -.0000001862d0
        tnum=100
        totm=10
        numsim=1000
        rls = 0d0
        rlshs = 0d0
        rmaxlam =1.087357

C     Declare files to open

        open (unit = 1, file= "lesfin.txt")
        open (unit = 2, file= "rs321.out")

C     Read from files into array
C       Read in Lespedeza data
        Do 100 i = 1,2000
           read (1,10,end=110) les(nlc+1,1),les(nlc+1,2),les(nlc+1,3),
     +             les(nlc+1,4), les(nlc+1,5)
        if (les(nlc+1,1).ge.0d0.and.les(nlc+1,2).ge.0d0.and.
     +     les(nlc+1,1).le.a.and.les(nlc+1,2).le.b) nlc=1+nlc
  100   Continue
  110   Continue

  10    Format (f8.2,4x,f8.2,4x,f8.2,4x,f8.2,4x,f8.2,4x,)

        Do 200 isim = 1, numsim

C   Sample for simulated HS

          do 250 rhsi = 1, 10000
           do 260 rhsk = 1,2
             rhs(rhsi,rhsk) = 0d0
  260   Continue
  250   Continue

          do 270 rli = 1,100
           do 280 rlk = 1,2
              rl1(rli,rlk) = 0d0
```

```
              rl2(rli,rlk) = 0d0
              rl3(rli,rlk) = 0d0
              rk1(rli,rlk) = 0d0
              rk2(rli,rlk) = 0d0
              rk3(rli,rlk) = 0d0
  280   Continue
  270   Continue

          rls = 0d0
          rlshs = 0d0
          ux=0d0
          nhs = 0

   30      ux = ux - log(ran2(iseed))/(rmaxlam*b)
           uy = (ran2(iseed))*b
           if (ux.le.a) then
             call lambda(ux, uy, nlc, les, sm1, sm2, sm3)
             rlam = exp(sm1*beta1+sm2*beta2+sm3*beta3)
             rpi = rlam/rmaxlam
             u = ran2(iseed)

             if (u.le.rpi) then
               nhs = nhs + 1
               rhs(nhs,1) = ux
               rhs(nhs,2) = uy
             endif

             goto 30
           endif

C  Perform Rkhat cross calculations for two species

        Call rkhatsub(les, rhs, nlc,nhs,a,b,tnum,totm, rl1, rk1)
        Call rkhatsub(rhs, les, nhs,nlc,a,b,tnum,totm, rl2, rk2)

C  Avg CrossK's and write to files

          Do 300 k = 1, tnum
              rlavg = (rl1(k,2) + rl2(k,2))/2
              rls = rls + (rlavg)**2
              rkavg = (rk1(k,2)+rk2(k,2))/2
              write (2,201) isim, rl1(k,1), rlavg, rkavg, rls
  300    Continue
  200    Continue

  201    Format (i4, 2x, f10.5, 2x, f12.8, 2x, f12.8, 2x, f10.5)
  301    Format (i4, 2x, f10.5, 2x, f12.8, 2x, f12.8)

        end
```

```
C   MODELLING PROGRAM #4
C   Calculation of CVM statistics
C   Program to calculate CVM's from data and fitted model simulations
C   Initialization of variables
           implicit real*8(a-h,o-z)
           Real*8 rkhat(100,1000), rkbar(100,1000), rktemp, rkbartemp
           real*8 cvm(1000), rkdiff
           pi = 4*atan(1.0d0)
 C         Declare files to open
       open (unit = 1, file = "origlc2.out")
       Open (unit = 2, file = "rs321.out")
       open (unit = 10, file = "cvm321.out")
       open (unit=11,file= "cvmd321.out")
C    Read from data K into array
       Do 50 i = 1,100
         do 60 j = 1,1000
           rkhat(i,j) = 0.0d0
           rkbar(i,j) = 0.0d0
           cvm(i) = 0.0d0
  60    Continue
  50    Continue
       Do 100 i = 1,100
          read (1,10) nsim, dist, rl, rls
               rKtemp = ((rl+dist)**2)*pi
               rKhat(i,1) = rktemp
  100   Continue
  10    Format (i4, 2x, f10.5, 2x, f12.8, 2x, f12.8, 2x, f10.5)
  20    Format (i4,2x,f10.5,2x,f15.8)
C   Read in data K from models
       Do 200 i=2,1000
          Do 300 j=1,100
          Read (2,10)  nsim, dist, rl, rktemp2, rls
                       rktemp = ((rl+dist)**2)*pi
                       rKhat(j,i) = rktemp
  300     Continue
  200     Continue
         Do 400  i = 1,1000
                Cvmtemp = 0.0d0
           Do 500  j = 1,100
                 rKbartemp = 0.0d0
               Do 600  k = 1,1000
                 If (k.ne.i) then
                    rKbartemp = rKbartemp + rkhat(j,k)
                 Endif
  600     Continue
            rKbar(j,i) = rkbartemp/999d0
            rKdiff=(sqrt(rkhat(j,i))-sqrt(rkbar(j,i)))**2
            write (11, 111) i,j,rkdiff
            cvmtemp = cvmtemp+rkdiff
  500     Continue
              cvm(i) = cvmtemp/.1d0
              Write (10,30) i, cvm(i)
  400     Continue

  111   Format(i4,2x,i4,2x,f15.5)
  30    Format(i4,2x,f15.5)
          End
```

```
/* SAS Program to calculate 95% Conf.Bands for Lhat and CVMs*/

options ls=75 ps=54;

/*  Crossk */
%macro crossk (fin, fout);
/*  Read in first isim which is the data */
      data origc1;
      infile 'origlc2.out';
      input isim dist l rls;
            If isim = 1;
/*  Read in all others (simulations) and sort by distance*/
      data cross;
            infile &fin ;
            input isim dist l rk rls;
                  If isim > 1;
            proc sort;
                  by dist;
 /* For the simulations, determine 2.5% and 97.5% values for each of
    the 100 distance classes */
      data cross2;
             set cross;
             drop isim;

            proc univariate data=cross2 noprint;
                  var l;
                  by dist;
            output out = crossq pctlpre=cross pctlpts = 2.5, 97.5;
/* Combine data set with 2.5% and 97.% values and print out*/
      data two;
            merge crossq origc1;
                  by dist;
            file &fout linesize=80;
            put  dist ',' cross2_5 ',' cross97_5 ','l;

%mend crossk;

run;

%macro cvm(fin,fout);
/*  Read in all simulations and sort by distance*/

      data cvm;
      infile &fin;
      input sim dist cvm;
            if sim >1;
            proc sort;
                  by dist sim;
/* For the simulations, determine 2.5% and 97.5% values for each of
    the 100 distance classes */
            proc univariate data=cvm noprint;
                  var cvm;
                  by dist;
            output out=cvmq pctlpre=cvm pctlpts=2.5,97.5;

/*  Read in first isim which is the data */
      data cvmdata;
```

```
      infile &fin;
      input sim dist cvm;
      if sim=1;

/* Combine data set with 2.5% and 97.% values and print out*/
      data cvm2;
      merge cvmdata cvmq;
            by dist;
      file &fout linesize=80;
      put dist ' ' cvm2_5 ' ' cvm97_5 ' ' cvm;

%mend cvm;

/* List of input and output files here */
%crossk('rs31.out','rs31av.out');
%cvm('cvmd31.out','cvm31av.out');

run;
```

```
      SUBROUTINE RKHATSUB(base,bor,inbase,inneighbor,a,b,tnum,
     + totm,rl, rkhat)

C   This subroutine will calculate and return Khat and Lhat for
C        each distance class
C   area = total area, a = width (x), b = height (y)
C   u = distance between baseget plant and neighbor
C   dv = distance from baseget plant to Vertical Axis
C   dh = distance from baseget plant to Horizontal axis
C   I = number of individuals at distance t
C   it = distance class value, tnum = number of distance classes,
C   totm =   furthest distance (m)
C   inbase =# obs for base array, inneighbor = # obs in neighbor array
C         K = array of rkhat values
C         Base = input array of base species data;
C         bor = input array of neighbor species data

      implicit real*8(a-h,o-z)
      real*8 rkhat(100,2), base(10000,5), bor(10000,5)
      real*8 rl(100,2)
      area = a * b
      Pi = 4*atan(1.d0)

      Do 30 i = 1,tnum
         Do 40 j = 1,2
                rkhat(i,j) = 0d0
 40      Continue
 30      Continue

      Do 32 k = 1,tnum
         Do 42 l = 1,2
                rl(i,j) = 0d0
 42      Continue
 32      Continue

C     Calculate the value for the distance class given the total
C     distance out and the number of classes wanted; assign this
C     distance class to the t-th row, first column in the k array,
C     reset or initialize the variable ktemp

           Do 50 it = 1,tnum
                  tdist =(totm/tnum)*it
                  rkhat(it,1) = tdist
                  rl(it,1) = tdist
 50     Continue
 15      Format (f5.2, 2x, f3.1)

C        Loop for the number of base individuals.

                Do 300 i = 1,inbase
C        For the base plant, calculate the distance to the nearest
```

```
C         vertical and horizontal axes

                    dv = dmin1( base(i,2), (b - base(i,2)))
                    dh = dmin1( base(i,1), (a - base(i,1)))

C         Loop for the number of neighbor plants

                    do 400  j =1,inneighbor
C         Calculate the distance between the base and jth neighbor

          u=sqrt(((bor(j,1)-base(i,1))**2)+((bor(j,2)-base(i,2))**2))

C          Make sure u doesn't equal 0 - if it does, assign a very
C          small number

                     If (u.lt.0.001d0) u = 0.001d0

C         Calculate w one of two ways depending on whether the circle
C         with center on the base individual and radius u
C         (dist baseget - neighbor) overlaps the edge

                     If (u**2 .le. (dv**2 + dh**2)) then

           w=1-(1/(pi))*(dacos(min(dv,u)/u)+dacos(min(dh,u)/u))

                     Else

               w=0.75d0-(1.d0/(2.d0*pi))*(dacos(dh/u)+dacos(dv/u))

                     Endif
                     If (w.eq.0) write(*,*) w
C        Loop for the number of distance classes.
C        Add this w to the current sum if u < distance class
               DO 500 it = 1 , tnum
                    If (u.le.rkhat(it,1))  then
                     rkhat(it,2) = rkhat(it,2) +(1/w)
               Endif
  500          Continue
  400        Continue
  300        Continue

C      Calculate final K hat for all distance class and assign it to
C      the array
          Do 600 i = 1, tnum
               rkhat(i,2) = rkhat(i,2) * area/(inbase*inneighbor)
               rl(i,1) = rkhat(i,1)
               rl(i,2) = sqrt(rkhat(i,2)/pi) - rkhat(i,1)
  600    Continue
       Return
       end
```

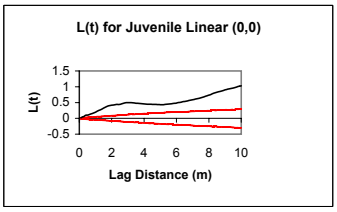
```
SUBROUTINE lambda(px, py, nlc, les,sm1,sm2,sm3)
          implicit real*8(a-h,o-z)
          Real*8 les(2000,5)

        sm1=1
        sm2=0
        sm3=0

        Do 100  j = 1,nlc
        distsij=sqrt((les(j,1)-px)**2+(les(j,2)-py)**2)
        IF (distsij.le.0.001d0) distsij = .001d0
        IF (distsij.le.2.0d0 .and. distsij.ge.(les(j,4)/200)) then
             sm1=1
             sm2=sm2+(les(j,3)/(distsij**2))
        endif
  100  Continue
             sm3 = sm2**2
        return
        end
```

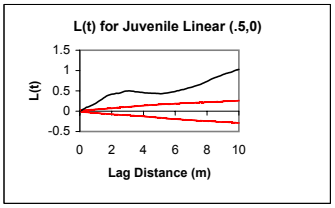
Inverse Subroutines
from (Press et al., 1992)

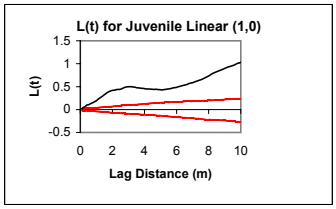
```
       SUBROUTINE inverse(a,y,np,n)
       implicit real*8(a-h,o-z)
       dimension a(np, np), y(np,np), indx(2)

       do 100 i = 1,n
         do 200 j= 1,n
           y(i,j) = 0
 200     continue
          y(i,i) = 1
 100   Continue

       Call ludcmp(a,n,np,indx,d)

       Do 300 j=1,n
          call lubksb(a,n,np,indx,y(1,j))
 300   Continue
       Return
       End

      subroutine ludcmp(a,n,np,indx,d)
      implicit real*8(a-h,o-z)
      parameter (nmax=100, tiny=1.0e-20)
      Dimension a(np,np), indx(n), vv(nmax)
      d=1
      do 100 i=1,n
         aamax=0.0d0
         do 200 j=1,n
           if (abs(a(i,j)).gt.aamax) aamax=abs(a(i,j))
 200     Continue
         if (aamax.eq.0d0) pause 'Singular matrix'
         vv(i) = 1.0d0/aamax
 100  Continue
      Do 300 j=1,n
         Do 400 i=1,j-1
            sum=a(i,j)
            Do 500 k=1,i-1
               sum = sum-a(i,k)*a(k,j)
 500        Continue
         a(i,j)=sum
 400     Continue
         aamax=0
         Do 600 i=j,n
            sum=a(i,j)
            Do 700 k=1,j-1
               sum=sum-a(i,k)*a(k,j)
 700        Continue
            a(i,j) = sum
            dum=vv(i)*abs(sum)
            if (dum.ge.aamax) then
                imax=i
                aamax=dum
            endif
 600     Continue
       If (j.ne.imax) then
          do 800 k=1,n
```

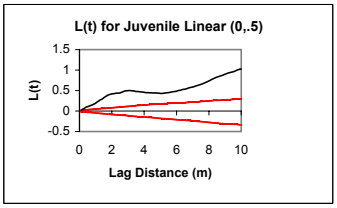
```
            dum=a(imax,k)
            a(imax,k)=a(j,k)
            a(j,k) = dum
800       Continue
          d=-d
          vv(imax) = vv(j)
        endif
        indx(j)=imax
        if(a(j,j).eq.0d0) a(j,j) = tiny
        if (j.ne.n) then
          dum=1.0d0/a(j,j)
          do 900 i=j+1,n
            a(i,j)=a(i,j)*dum
900       Continue
        endif
300     Continue

        return
        end


      SUBROUTINE LUBKSB(a,n,np,indx,b)
      implicit real*8(a-h,o-z)
      Dimension a(np,np), indx(n), b(n)
      ii=0
      do 100 i=1,n
         ll=indx(i)
         sum=b(ll)
         b(ll)=b(i)
         if (ii.ne.0) then
            do 200 j=ii,i-1
               sum=sum-a(i,j)*b(j)
200         continue
         else if (sum.ne.0) then
            ii=i
         endif
         b(i)=sum
100   Continue
      do  300 i=n,1,-1
         sum=b(i)
         do 400 j=i+1,n
            sum=sum-a(i,j)*b(j)
400      Continue
         b(i)=sum/a(i,i)
300   Continue
      Return
      End
```

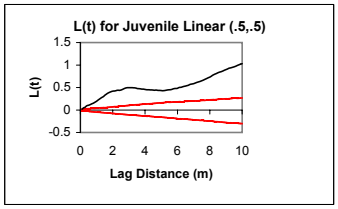
Cross L(t) Function plots for juvenile linear models
Black lines represent the data, red lines represent the 95% one-at-a-time confidence bands.

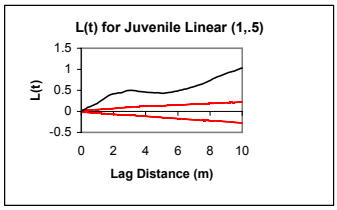


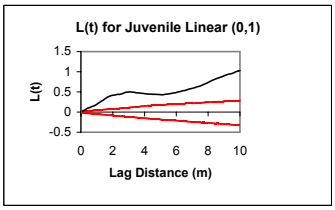


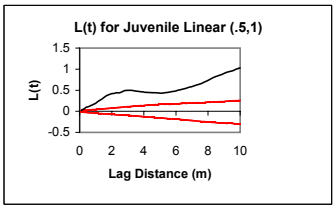


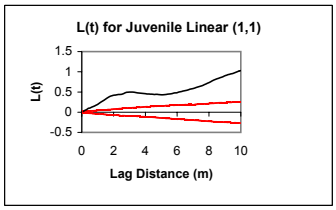


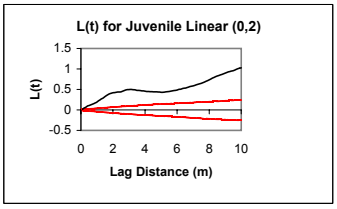




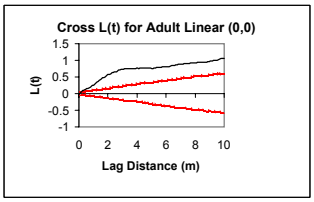


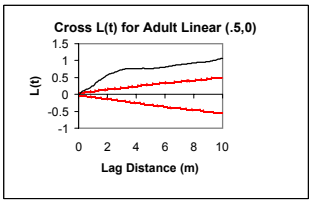


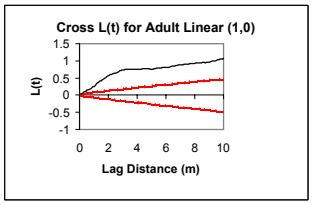


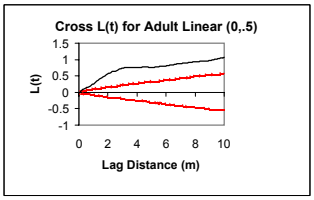


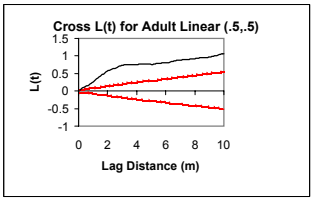
Cross L(t) Function plots for adult linear models
Black lines represent the data, red lines represent the 95% one-at-a-time confidence bands.

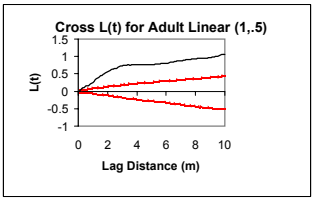


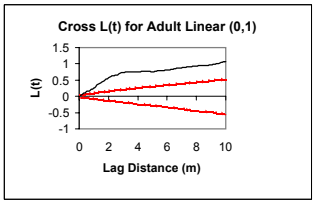


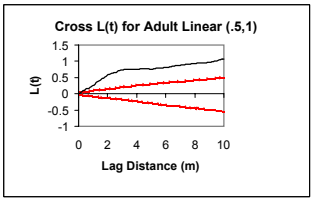


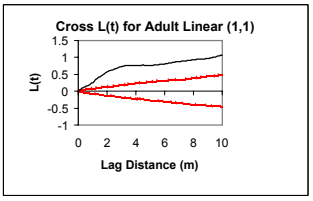


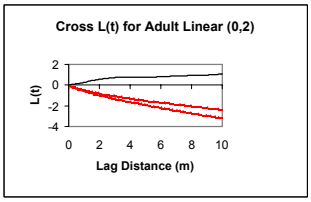




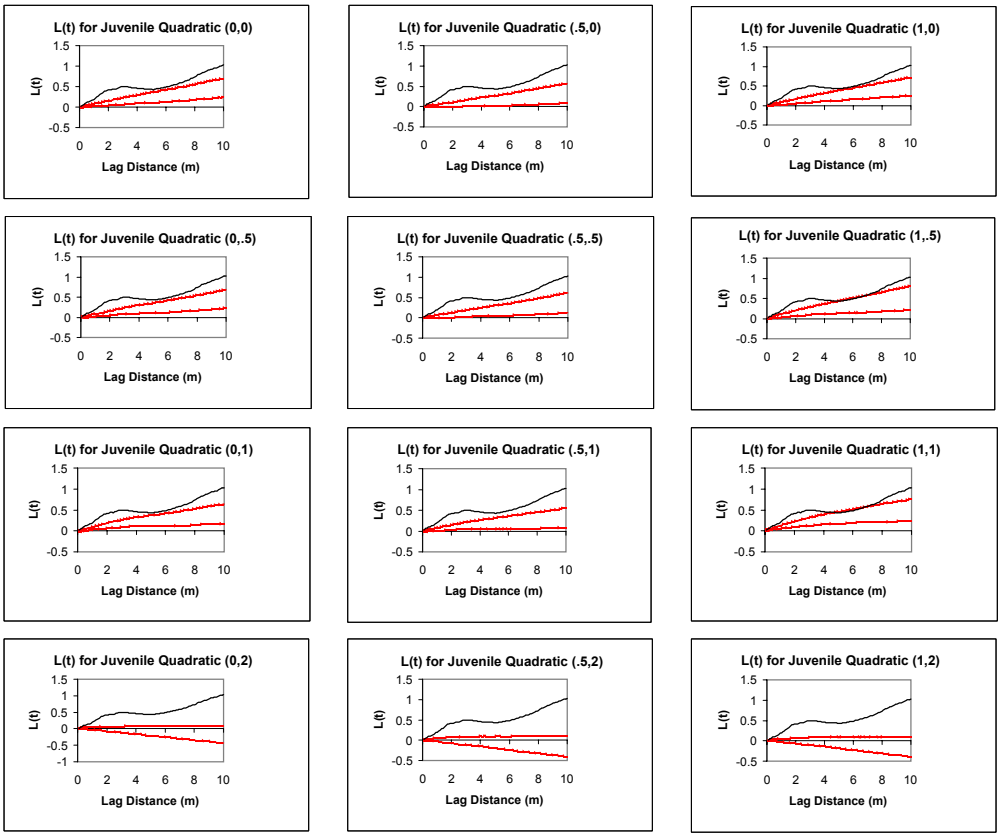








Cross L(t) Function plots for juvenile quadratic models
Black lines represent the data, red lines represent the 95% one-at-a-time confidence bands.



Cross L(t) Function plots for adult quadratic models
Black lines represent the data, red lines represent the 95% one-at-a-time confidence bands.