POPULATION ECOLOGY OF A SANDHILL ENDEMIC SHRUB, *CERATIOLA ERICOIDES* (SANDHILL ROSEMARY)

by

JOHN PAUL SCHMIDT

(Under the Direction of C. Ronald Carroll)

ABSTRACT

Ceratiola ericoides (sandhill rosemary) is a dioecious, wind-pollinated, evergreen shrub adapated to the xeric, fire-adapted communities of the Southeast. 1. Spatial pattern of males and females in *C. ericoides* was investigated. Ripley's K was used to analyze the spatial pattern of mapped populations of *C. ericoides*, and whether they exhibited spatial segregation of sexes (SSS). Results provide little evidence of SSS in this species. 2. Optimal fire frequency for *C. ericoides* was also investigated. Bayesian methods were employed to derive populations parameters from data collected in the field and from air-photos over a four-year period. Under the Bayesian approach, every parameter has a probability distribution rather than a fixed value. Results of Bayesian analyses of demographic data suggest that that increasing female distance from male significantly reduced realized female fecundity; both mortality and fecundity were higher on burned sites; shrub survivorship significantly increased with distance from longleaf pine on burned sites. These data were used to parameterize a stochastic individual-based model of *C. ericoides* population dynamics. Results suggest that a 20 year fire return cycle is optimal for *C. ericoides*, but that stochastic fire return intervals between 3 and 20 years result, on average, in population increases.

INDEX WORDS: Plant population ecology, *Ceratiola ericoides*, Sandhills, Dioecy, Individual-based model, Bayesian statistics, Fire, Stochasticity, Hierarchical models, Spatial pattern, Ripley’s K, Spatial segregation of sexes

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DEDICATION

To my wife Debbie who graciously (most of the time) endured the PhD process for a second time. To my daughter, Tamar, who has hopefully benefited in some way from witnessing my progress. To my parents who always encouraged me, and who trained me to be an observer of biological nature (Mom) and a scientific thinker (Dad). To my brothers and sisters who in their various ways (conversations, hikes, camping trips, gifts of field guides and Audubon magazine subscriptions, moral and material support during the doctorate) nurtured the development of what is now my career project.

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CHAPTER 1

INTRODUCTION

1. Xeric Sand Communities of the Southeast

General Description

Broadly, the vegetation occurring on xeric sands within the Southeast can be divided into two primary physiognomically and compositionally distinct communities (Christensen 1986): sandhill pine-oak forests and sand pine scrub--the latter restricted to Florida and the Gulf Coast. Within pine-oak sandhill forest, there is a continuum of vegetative associations. *Pinus palustris* (longleaf pine) and *Quercus laevis* (turkey oak) dominate the most xeric habitats--usually ridgetops where sands are deepest and clay content is lowest. Typically, density of pines is low and *Q. laevis* dominates the understory with occasional individuals of *Diospyros virginiana* (Ebenaceae), persimmon, and several species of low ericacious shrubs including *Lyonia mariana*, *Gaylussacia dumosa* (dwarf huckleberry), and *Vaccinium stamineum* (deerberry). Groundlayer vegetation is generally sparse and large areas of bare sand are usually present. The low shrub, *Chrysobalanus oblongifolius* (Rosaceae), gopher apple, often forms scattered clonal patches. Common and abundant herbaceous species include wiregrass (*Aristida stricta* or *Aristida beyrichiana*), *Arenaria caroliniana* and *Stipulicida setacea* (Caryophyllaceae), *Cnidoscolus stimulosus* (Euphorbiaceae), the spikemoss, *Selaginella arenicola* (Selaginallaceae) as well as N-fixing foliose lichens such as *Cladonia* ssp., and *Cladina* ssp.

Although low in vegetative diversity and cover, sandhill sites support a number of endemic species of lichen and herbaceous plants such as *Warea cunifolia* (Brassicacae) and *Polygonella gracilis* (Polygonaceae). In addition, groundlayer species such as *Opuntia ssp* (Cactaceae), *Yucca filamentosa* (Agavaceae), *Calamintha coccinea* (Lamiaceae), *Carex* ssp.(Cyperaceae) and N-fixers such as *Baptisia perfoliata* (Leguminoseae), are locally very abundant on xeric sandhills. On the lower slopes of sandhills, water tables are relatively close to the surface and coarse sands as a soil stratum are correspondingly shallow so that both groundwater and higher-nutrient clay soils are more readily accessible to the roots of woody plants, especially deeply-rooted trees. Where these less xeric conditions prevail both canopy and understory become more diverse. *Q. marilandica* (blackjack oak), *Q. margaretta* (scrub post oak), and the evergreen oaks, *Q. incana* (bluejack oak) and *Q. hemisphaerica* (laurel oak) share dominance in the canopy. Wiregrass and numerous forb species also form a more continuous ground cover on these sites and on clayey soils bracken fern (*Pteridium aquilinum*) may be abundant (Shafale and Weakley 1990, Wharton 1978).

Additional sandhill community types described (mostly for Florida but extending to adjacent Coastal Plain regions) by Monk (1968) and Abrahamson *et al.* (1984) are sandhill associations dominated by *Q. incana* and *Q. falcata* (southern red oak). In both of these communities, *Pinus palustris* (longleaf pine) forms a discontinuous canopy though it may often occur in mixed stands or be replaced by *Pinus elliottii* var. *densa* (south Florida slash pine) in central Florida. The herb layer is dominated by wiregrass; and shrubs, with the exception of *Chrysobalanus*, are scarce. Often referred to as scrubby flatwoods, the *Q.*

incana phase of the Florida sandhill community is associated with finer-textured, more fertile soils (Laessle 1942). *Q. virginiana* (live oak) is also common in the overstory, and wiregrass usually forms a dense cover (Veno 1976). The *Q. falcata* phase of the Florida sandhill community is restricted to calcareous soils.

In contrast to sandhill associations, the overstory of sand pine scrub is dominated by *Pinus clausa* (sand pine). The understory is composed of a dense and comparatively diverse assemblage of evergreen schlerophyllous shrubs. Abrahamson *et al.* (1984) differentiate two phases of the sand pine scrub community. The oak understory community is a two-layer community with a lower shrub layer of *Serenoia repens* (saw palmetto) and a mid-story of the evergreen scrub oaks *Q. geminata* (sand live oak), *Q. myrtifolia* (myrtle oak) and *Q. virginiana*. The second or rosemary phase is characteristic of the driest ridges and has a much more open pine canopy--or no pines at all--and a shrub layer dominated by even-aged stands of *Ceratiola ericoides* (sandhill rosemary). Rosemary scrub occurs on sandier, higher-pH (though still acidic), lower-nitrogen soils (Carrington and Keeley 1999) which probably reflects more xeric, less productive conditions where less organic matter has accumulated in soils. While the causes remain unclear, rosemary scrub is also restricted to xeric white sands whereas sand pine scrub occurs on both white and more iron oxide-rich yellow sands (Menges 1999). *Q. incana* may share dominance with *C. ericoides*. Because a thick canopy is absent, herbs are more abundant and diverse in this phase and include many rare and endangered species endemic to the scrubs of the Lake Wales Ridge of central Florida.

In the past, soils were considered to be a significant determinant of the development of longleaf pine-turkey oak versus sand pine scrub communities (Laessle 1958). Leaving aside the distribution of rosemary scrub, which does seem to be affected by soil properties

(Menges 1999), fire frequency appears to be the main controller of community dynamics within xeric sand vegetation communities (Kalisz and Stone 1984, Myers 1985). Natural fire return intervals for sand pine scrub range from 30-60 years, whereas the natural interval for pine-oak sandhills is estimated to be from 3-10 years. And, where fire has been suppressed on *P. palustris*-dominated sandhills, *P. clausa* has been observed to invade (Veno 1976). Within communities where *P. palustris* was historically an important component, accumulations of longleaf litter and wiregrass biomass fueled low-intensity surface fires. The effects of fire in these communities were very discontinuous because vegetated and non-vegetated areas formed an irregular patchwork.

In addition to fire, seasonal rainfall patterns appear to affect the structure of sandhill-scrub vegetation along a gradient from central Florida--exhibiting a high degree of cover--through the Fall Line sandhills. Communities within the latter geographic zone often exhibit a much more open aspect even on sites where fire has been suppressed for decades. Because summer rainfall is more restricted on the Coastal Plain with increasing latitude, summer drought conditions may become more pronounced thereby further limiting productivity on deep, xeric sands.

Effects of Fire Suppression on Xeric Sand Communities

Overlaid on the broad community outlines and seral stages presented above are the current conditions of sandhill and scrub sites. Throughout the 19th and early 20th centuries low-productivity sandhills were not cleared. However, population increases, the advent of relatively cheap fertilizers coupled with the relatively low pathogen (especially nematode) levels had lead to large areas of sandhill on the Fall Line and elsewhere being converted to loblolly or slash pine plantation, bermuda grass pasture or residential development. Much of the Lake Wales dune ridge in central Florida has been converted to citrus production or ranching. On xeric sands largely unaltered by agricultural or silvicultural development, plant communities have been modified extensively by decades of fire suppression, exacerbated by landscape fragmentation, and the harvesting of *P. palustris*.

Structure and composition of vegetation is greatly altered on long-unburned xeric sands. Menges *et al.* (1993) describe such changes on the central Florida sandhill/scrub communities which had been excluded from fire for 60 years (since the mid-1920s). Specifically, the authors investigated differences in species associations using Detrended Correspondence Analysis (DECORANA) on permanent plots sampled at 10-yr intervals from 1969-1989. Within sandhill and scrubby flatwoods vegetation types, evergreen, clonal oak species and sand pine increased in dominance, density and basal area at the expense of grasses. This leads to the development of a subcanopy increasingly similar to that of sand pine scrub. This is congruent with the fact that a 20- to 60-yr fire-free interval favors sand pine scrub and more frequent fires (3-10 yr) favor open sandhill vegetation (Parker et al. 1997).

Remarkably, despite these overall trends in the absence of fire, Menges *et al.* (1993) report that many areas changed "little or eratically", indicating a stochastic component which may be attributed to the effects of other kinds of disturbance such as windstorms and insect attacks or perhaps to a dependence on initial conditions which in turn result from an interaction of past fire frequency, intensity, and seasonality coupled with landscape position. Menges *et al.* (1993) report that classic successional patterns such as species replacement, decreases in density, and increases in basal area for a given suite of species were generally lacking. Directions of compositional vectors included divergent, opposing, and complex pattterns. Parker et al. (1997) examined population structure and spatial pattern of two coastal populations of *Pinus clausa* var. *clausa* (Ocala sand pine) which had been excluded from fire for 20 and 50 years respectively. In contrast to Menges et al. (1993), the authors concluded that in the absence of fire, little recruitment of *Pinus clausa* occurred, and that without fire or some other disturbance to remove evergreen oaks from the understory the trajectory of stands was toward an oak scrub eventually lacking pines in the overstory. Differences in findings between Parker et al. (1997) and Menges et al. (1993) may perhaps result from minor differences in site histories which may have large effects on stand development trajectories.

Community Dynamics and Fire

Within southeastern xeric sand communities there is considerable variation in the relative dominance by members of differing fire-recovery guilds. Florida scrubby flatwoods (evergreen oak scrubs) are dominated by woody species which spread clonally and resprout. The less-productive rosemary scrub is dominated by obligate reseeders. Unlike either pine-dominated sandhill or scrubby flatwoods communities, within rosemary scrub, woody plants share dominance with herbs. This pattern suggests that resprouting may be favored where productivity is relatively high and cover is dense because resprouts are competitively superior to seedlings. Where productivity is low and open spaces forming suitable microsites are abundant for many years post-fire, seeders are favored. And as a corollary, environments that favor obligate reseeders, particularly reseeding shrubs, burn less frequently than environments that favor resprouters (Menges and Kimmich 1996).

Adaptation by woody plants to xeric sand habitats is defined most prominently by the following niche axes: 1) drought-tolerance, 2) nutrient acquisition on a barren substrate, and 3) fire-tolerance/fire-recovery strategy. Adaptations to xeric conditions, for example, include investments in below-ground tissues to acquire and store water and high water use efficiency (WUE). *Q. laevis* and *P. palustris*, for example, exhibit high WUE while, in addition, adult plants are able to draw water from lower soil strata. Root systems are deep and extensive, leaves are lobed and oriented vertically (in the case of *Q. laevis*) to reduce heat load from both direct and reflected solar radiation (Donovan *et al.* 2000). In contrast, *P. clausa* and *C. ericoides* are relatively shallowly rooted species with a higher WUE but with little access to moisture deep in the soil profile.

Adaptations to fire must be considered with respect to 1) intensity, 2) frequency and 3) seasonality of burn. Considering first the effect of fire-frequency alone, *Q. laevis* and *P. palustris*, though fire-tolerant in the low stature "grass stage", reach a more fire-resistant stage within a period of approximately 10 yrs after germination from seed, whereas *P. clausa* and *C. ericoides* are extremely flammable at all stages. Depending on tree diameter and intensity of fire, *Q. laevis* is able to withstand fire or to resprout following a burn. In addition to seeds released seasonally, *P. clausa* has a "canopy seedbank" which is released from serotinous cones by stand-replacing fire. *C. ericoides* produces a soil seed-bank and germination is apparently stimulated by fire effects. A "flammability" niche could therefore be posited for *P. clausa* and *C. ericoides*. By accumulating dead wood in the canopy (*P. clausa*) and by producing volatile and highly flammable terpenes (both species), *P. clausa* and *C. ericoides* have the ability to increase the intensity of fires. By doing this, flammable species are fire-resilient clearing away competing vegetation and promote reestablishment by seed of their guild of stress-tolerating, relatively poor competitors.

Given that their life-history traits differ with respect to fire, the four characteristic species of communities occurring on southeastern xeric sands, *P. palustris*, *P. clausa*, *Q. laevis* and *C. ericoides*, should not closely coexist. Rather, they should partition the sandhill environment by zones of productivity, moisture availability, fire frequency, and behavior. Where historic fire regimes prevailed, which species dominated within a community seems to have been determined by fire frequency and intensity (Rebertus et al. 1989b). Exceptions to this pattern exist, particularly in the case of *C. ericoides* populations on the riverine and fall line sandhills of Georgia and South Carolina which grow in close association with *Q. laevis* and *P. palustris*. These riverine and fall line sandhill communities, which are more open than those of most communities of the Florida sandhill-scrub continuum, may more readily allow for cooexistence because both fire and resources (soil moisture and organic matter) are extremely patchy at the scale of tens of meters.

Rebertus *et al.* (1989a) examined differences in spatial pattern of both dominant species when long-unburned *P. palustris*-*Q. laevis* sandhills (*Q. geminata* and *Q. incana* present as sub-dominants) near Tampa, Florida were subjected to repeated growing-season fires. Using bivariate Ripley's L(t) (Ripley 1977) to interpret patterns, the authors found initial burns caused strong segregation of *P. palustris* and *Q. laevis* as a result of the higher mortality of *Q. laevis* growing in proximity to *P. palustris*. Repeated burns lead to even greater segregation between species. Similarly, Rebertus *et al.* (1989b) found *Q. laevis* crown survival was positively related to oak dbh, increased with distance to the nearest *P. palustris* and was inversely related to the dbh of the nearest *P. palustris*. Therefore, the authors concluded, increasing segregation with fire seems to be related to the higher fire temperatures associated with the well-aerated, highly combustible needle litter of *P. palustris* which can burn at temperatures 100 C hotter than those measured under oaks. Because of these factors, xeric sand communities may develop memory or landscape self-organization. This can occur whenever the spread of fire is a function of previous fires, as it is where flammability is a function of stand age or time since last fire. Under such conditions patches may be maintained over time and self-organization may evolve even in the absence of landscape heterogeneity in the form of topography or other factors (Perry 2002). Thus, differences between *P. palustris* or *P. elliotii* and oak species in adaptations to fire (resistance versus resistance/resprouting) and in life-history traits/population biology leads to a marked effect of fire frequency on community composition and structure.

The interacting effects of fire frequency and seasonality on population dynamics of tree species were examined by Glitzenstein *et al.* (1995). Through the use of controlled burning over an 8-year period, annual versus biennial frequencies and eight seasonal treatments were contrasted. Recruitment, growth, mortality, change in density, change in basal area, and change in species composition of trees were compared between longleaf-pine-dominated sandhills and more mesic flatwoods in north Florida. Surprisingly, frequency of burning had no significant effects on growth or recruitment of oaks in the sandhills. However, as a result of greater topkill among smaller size classes, the density of oaks declined significantly in biennially burned plots (by an average of >30 stems over a 7 year period), while only minor declines occurred in plots burned annually (<5 stems on average over the same time period).

Glitzenstein *et al.*'s (1995) finding that higher oak mortality results from spring burns lends support to the hypothesis that a shift from growing-season to more-easily-controlled dormant-season burning over the last several centuries (along with removal of large pines) has transformed the vegetation of many sandhills. Annecdotal evidence suggests that formerly open savannas where *P. palustris* dominated the canopy have become woodlands or scrub forests composed largely of *Q. laevis* and other hardwoods (Means and Grow 1985, Myers 1990, Platt *et al.* 1991, Gilliam *et al.* 1993). Additional results from Menges *et al.* (1993), Glitzenstein *et al.* (1995) and Rebertus *et al.* (1989a, 1989b) suggest that communities of longleaf (or slash) pines and sandhill oaks should not persist as stable mixtures.

If frequent fires occur early in the growing season—and Chen and Gerber (1990) provide data demonstrating that the environmental conditions which produce drier fuels and greater fire intensities are more prevalent early in the growing season at least in north Florida--then the relative abundance of trees can shift rapidly to one in which oaks persist only as clonal shrubs in the groundlayer. Conversely, frequent fires later in the growing season shift the relative abundance of trees toward oaks. On somewhat less xeric sites, the resulting formation of closed oak woodlands reduces longleaf pine recruitment and growth and leads to declines in the diversity of understory herbs (Lemon 1949, Vogl 1973, Streng 1979, Myers 1990). Glitzenstein *et al.* (1995) conclude that fire intensity did not affect complete kill (above- and below-ground) of oaks. Rather, oak mortality results from an interaction between fire intensity, seasonality and tree physiology. Seasonal patterns of carbohydrate storage in trees can make resprouting oaks especially vulnerable to spring fires.

Fires following initial leaf expansion in spring deplete stored reserves before they can be replenished and thus lead to greater mortality (Robbins and Myers 1992).

Interestingly, Glitzenstein *et al.* (1995) identify competition as a major factor controlling pine dynamics on sandhills and that differences in frequency, seasonality or intensity of fire regime, compared to competitive effects, have a relatively minor effect on pine dynamics. Inter- and intra-specific competition seem to particularly limit density of *P. palustris*, whereas density of sandhill oaks appears to be much less limited by competition. Therefore, were it not for variable disturbances in the form of fire, hurricanes and other storms, sandhill communities would tend toward competitive exclusion of *P. palustris* by sandhill oaks. Moreover, Glitzenstein *et al.* (1995) argue that maintaining *P. palustris* dominance on sandhills requires more frequent burning than on moist, periodically flooded, flatwoods sites. Yet, even the effects of pine harvests and fire exclusion are unlikely to result in the complete elimination of *P. palustris* because the high initial density of longleaf on most sites, the fact that unharvested trees may live several hundred years, and the likelihood of small-scale disturbances that even in the absence of fire will provide regular recruitment opportunities (Platt *et al.* 1991, Gilliam *et al.* 1993, Platt and Rathbun 1995).

Confusing this picture of early-season fire promoting relatively open pine-dominated sandhill communities, are findings that mid-summer burns promote the highest yield of viable seed in wiregrass (Outcalt 1994). Thicker wiregrass patches, in turn, fuel more continuous fire. Longterm coexistence of mature *P. palustris*, sandhill oaks and wiregrass on xeric sand habitats apparently depends on spatial patchiness and variability in frequency and seasonality of fire. The importance of variability in disturbance is further supported by data on age and stand structure in an old-growth Florida longleaf pine-sandhill oak stand where

Greenberg and Simons (1999) recorded a 123 year-old *Q. laevis* and a 230 year-old *Q. margaretta*. Though *P. palustris* appears to have dominated on these xeric sand habitats historically, oaks were able to reach canopy stature and maintain tree size within patches of varying densities within the same landscape. Medium and larger diameter *Q. laevis* trees are much less vulnerable to low-intensity ground fires thus allowing them to persist indefinitely once established even under adverse fire regimes (Rebertus *et al.* 1989b).

Fire also interacts with the physiological traits of woody species to structure sandhill-scrub communities. For example, variable response to fire among xeric-adapted oak species coupled with varying physiological tolerances results in fire-mediated shifts in the relative dominance of different oak species. *Q. laevis* has a greater ability to access soil water and a higher water use efficiency than either *Q. margaretta* or *Q. incana* and is, therefore, at a greater competitive advantage on xeric ridges (Donovan *et al.* 2000). Though it is also much more fire-tolerant than other oak species, *Q. laevis*, because of its greater drought-resistance, is able to maintain dominance on the most xeric sites without fire as a mediator of competition (Vaitus and McLeod 1995). However on more productive sites, relatively frequent fire appears necessary to promote dominance of either *P. palustris* or *Q. laevis*, which, as a species strongly adapted to low-resource conditions, exibits little plasticity in response to increased fertility or moisture availablity relative to other oaks. Therefore, fire exclusion from the lower sandhill slopes clearly favors dominance by evergreen oak species. On xeric sand ridges, fire exclusion or infrequent fire leads to greater cover or dominance by sandhill oaks such as *Q. laevis* or *Q. inopina* (Donovan *et al.* 2000).

Fire behavior can also be a product of site productivity and resultant vegetation structure. Menges and Kohfeldt (1995) compared the vegetation structure of two xeric sand communities: rosemary scrub and slash pine-oak-dominated “scrubby flatwoods”. Feedbacks between the structure of the two vegetation types and fire frequency and intensity reinforce differences in the prevalence of species with contrasting life-history strategies. Because scrubby flatwoods are more continuously vegetated (Abrahamson 1984a, Schmalzer and Hinkle 1992a, 1992b), fire is more readily spread than it is in rosemary scrub. Rosemary scrub, which is more xeric and less productive, is characterized by large open areas even within long-unburned stands (Hawkes and Menges 1995). For this reason, rosemary scrub rarely burns completely (Archbold Biological Station, unpublished data). In the case of rosemary scrub on the Lake Wales Ridge, landscape position further affects fire-return intervals. There, scrubby flatwoods act as a buffer between rosemary scrub and frequently-burned flatwoods and seasonal pond communities.

Menges and Kofeldt (1995) found that rosemary scrub is dominated by species that recover from fire by re-seeding while scrubby flatwoods are dominated by post-fire resprouters and clonal spreaders. What is interesting is that this is true even though a considerable overlap in species composition exists (Abrahamson *et al.* 1984) and these two vegetation types border one another. Because scrubby flatwoods are more productive, regrowth is more rapid and vigorous and resprouters are therefore at a competitive advantage. By contrast, recovery is slower in rosemary scrub yet open areas where seedlings can establish free from competition are frequent. Because it is a species adapted to the harshest conditions in terms of nutrient and water availability, *C. ericoides* is able to establish on barren sands. Yet, perhaps as a tradeoff, *C. ericoides* is a relatively poor competitor on more productive sites.

Community Dynamics and Productivity

The degree to which nutrient availability structures xeric sand communities is unclear. Although xeric sands exhibit low aboveground net primary productivity, the degree to which low productivity is a result of low soil moisture rather than nutrient limitation has been looked at quantitatively only recently. Wilson *et al.* (1999) found that N mineralization was highest at the xeric (longleaf-turkey oak) end of a transect across a moisture gradient within longleaf-wiregrass communities. Possible mechanisms for this finding include the much higher C:N ratio of oak litter (57) abundant on xeric sites relative to that of pine litter (126) as well as the higher soil temperatures on xeric sites which should elevate or promote N mineralization. If N availability is actually higher on oak-dominated xeric sands than on more mesic flatwoods sites, moisture availability alone would be the key determiner of productivity. Anderson and Menges (1997) offer additional, if very provisional, support for the potential importance of water over nutrients as limitation to sandhill-scrub productivity from a study of fire and nutrient availibility in Florida scrub. The flux of nutrient availibility following fire in scrub was shortlived and not significantly different from those associated with seasonal changes in rainfall. Kalisz and Stone (1984) examined chemical characteristics of sandhill and scrub soils to a depth of 500 cm. Organic matter, Ca, Mg and P concentrations (though not N) were measured. Although extractable base concentrations were low, P concentrations indicated “substantial reservoirs of this element for deep-rooted plants.”

Beyond mostly indirect interactions mediated by fire or direct interactions on more mesic lower sandhill slopes related to moisture or nutrient availability, trees, shrubs and grasses on very xeric sands may interact directly via patterns of moisture availability. Both

Q. laevis, *Pinus palustris* and to a lesser extant *Aristida stricta*, wiregrass, display the phenomenon of hydraulic lift whereby moisture from lower soil strata is transported to drier surface soil layers. Although its potential effects on community dynamics have not been studied, this process may foster both competition and facilitation within and between xeric-adapted species particularly between shallow versus deeply rooted functional groups or life-stages (Espeleta *et al.* 2004).

Fire and Vegetation of the Southeastern Coastal Plain in Recent Geologic History

Over long periods of time, cycles in the seasonality of thunderstorms and accompanying lightning-ignited fires have resulted in shifts in relative abundances of pines and oaks on the southeastern Coastal Plain. Palynological studies of peat cores by Watts (1980) and Watts and Hansen (1994) indicate dramatic changes in relative dominance by pines, oaks, shrubs and herbaceous species over the last 50,000 yrs. For example, a Florida Highlands flora in which *C. ericoides* and herbaceous species predominate with only slight evidence for the presence of either pine or oak species existed between 44,300 to 33,000 BP when the Southeast and Florida in particular were experiencing a much drier climate. From 33,000 BP, there is a decrease in *C. ericoides* and an increase in pine in the pollen record with 13,010 BP marking a peak in pine pollen and the opening of the Holocene. Whether a climatic shift favored a broad expansion of pine forests or pines increased in abundance locally, perhaps due to a reduction in fire frequency is not clear. Yet, by the early Holocene (10,410 BP), oak reached its greatest pollen frequency. Watts (1980) and Watts and Hansen (1994) attribute floristic changes since the opening of the Holocene to increased precipitation, though temperature and other climatic factors may have also played a role. If future changes in regional climate lead to drier summers and/or changes in seasonal patterns of rainfall, they are also likely to alter fire regimes (even under managed conditions), and may, therefore, alter the balance between pines, oaks, and other scrub species on the xeric sands of the southeastern Coastal Plain.

Summary: Ecology of Xeric Sand Communities of the Southeast

Coarse sandy soils are a common feature on the southeastern Coastal Plain where they exhibit both a low water-holding capacity and a low native fertility which results in extremely xeric, nutrient-poor conditions (Kalisz and Stone 1984). Deep sands known as the fall-line sandhills form a belt of rolling terrain from southern North Carolina through Georgia and eastern Alabama. Other deep sands include dune ridges that run the length of central Florida and xeric sands that cover large expanses of the Florida Panhandle and the Gulf Coast and its barrier islands. At a somewhat finer scale (from several to >100 ha), relict inland dunes formed by aoelian processes during the Pleistocene lie on floodplains and terraces along the northeast sides of streams throughout the southern Atlantic Coastal Plain. These areas often form a so-called ridge-and-swale topography, with xeric conditions and xeromorphic vegetation on the ridges and wetland features in the swales. Dune-fields associated with Carolina bays and other landscape features within the southeastern Coastal Plain have contributed to the formation of additional xeric sand habitats.

The sandhill-scrub vegetation continuum is an extremely complex community influenced by the interaction of disturbance factors and plant population biology--factors which interact, in turn, with soils, topography and hydrology—often over a scale from a few to hundreds of meters. Given complicated, non-equilibrium dynamics and the legacy of fragmentation, fire suppression and other recent human alterations of sandhill-scrub communities, defining management strategies for the maintenance of biodiversity and the conservation of rare and endemic species found on xeric sand habitats is therefore no easy task.

Maintaining xeric sand communities as more open communities promotes habitat for both threatened vertebrate species (e.g. gopher tortoise, scrub jay) and for rare and/or endemic herbaceous, plant species. Literature on conservation and restoration of sandhill/scrub communities in the Southeast has therefore focused on 1) the more theoretical issue of optimal fire regime for maintaining diversity and 2) the applied problem of reintroducing fire to sites where it has long been absent. Research over the last twenty years summarized above has provided an understanding of the historic role of fire. Fire frequency ranges have been established for sandhill versus scrub, and for sand pine versus rosemary phase scrub. However, managing for many scrub endemics continues to provide a challenge.

Reversing community shifts--e.g. from pine to oak--on long unburned sites may often require intensive management beyond simply reestablishing probable presettlement fire regimes. Indeed, returning fire to sites where biomass, woody debris and humus has accumulated over decades is a challenging project. Not only is the outcome of returning fire to a given site uncertain, but the further uncertainty of fire behavior and control makes planning and executing such burns extremely difficult for land managers. As a precursor to the reintroduction of fire, removal of biomass and herbicide application have been employed (Brockway and Outcalt 2000). However, in other respects fire is the cheapest alternative and stimulates germination of many species which do not germinate in response to the removal of woody competitors by other means (Provencher *et al.* 2001a, Provencher *et al.* 2001b).

Broadcast application of herbicides can be effective in controlling woody vegetation, but, not surprisingly, can have negative effects on herbaceous diversity and cover (Brockway and Outcalt 2000).

Although competitive effects seem to play an important role in *P. palustris* population dynamics, the overall dynamics of southeastern xeric sand communities seem to be determined primarily by the effects of fire frequency and to a lesser extent seasonality and intensity of burning. Fire regime, in turn, is a factor of latitude, climate, fire compartment size and site productivity and cover. Fire in these communities is patchy and, although likelihood of fire increases with time since fire, is also temporally variable. There is apparently no equilibrium distribution of community types and fire regimes, and fire regimes have varied both historically and over geologic time.

2. *Ceratiola ericoides* as an Indicator Species

C. ericoides is a fire sensitive species which is usually killed when exposed to fire and does not resprout, but rather must re-establish from seed. *C. ericoides* also appears to be suppressed under a thick canopy of longleaf pine and/or turkey oak on long-fire-suppressed sandhill sites. On sandhill sites, *C. ericoides* is frequently most abundant on the driest upland sites where competition from other woody vegetation is least. Given these traits, *C. ericoides* persistence on sandhill sites requires fire at some frequency. Establishing an optimal frequency for *C. ericoides* offers a guide, therefore, to the management of sandhill sites. Investigating the population dynamics of *C. ericoides* is facilitated by the fact that *C. ericoides* shrubs can be aged approximately by counting branching nodes, but is complicated by the breeding system (dioecious) of the species. As a wind-pollinated, dioecious shrub, *C.*

ericoides may exhibit spatial segregation of males and females, and pollen limitation of reproduction may result when females are isolated from males (Crawley 1997a). Survivorship of shrubs may also be strongly affected by proximity to longleaf pines. The litter of the pines carries fire and makes shrubs nearby more prone to ignition (Glitzenstein et al. 1995).

Dioecy and Spatial Pattern

Research comparing allocation patterns between genders in dioecious species indicates that female plants usually have higher resource requirements and/or reproduction imposes a greater drain on resources (Crawley, 1997). A recurring pattern observed among dioecious plant species is an increase in the ratio of males to females along an axis of decreasing site productivity. This can occur over a range of scales and with respect to broad environmental gradients or to microsite preferences. Male frequency has been shown to increase as environments become more stressful with increasing altitude (Pickering and Hill, 2002), lower moisture availability (Dawson and Ehleringer, 1993), increasing salinity (Eppley, 2001; Vitale, 1987), more anoxic conditions (Shea et al., 1993), decreasing soil fertility (Lawton and Cothran, 2000), and decreasing light levels (Nicotra, 1998; Thomas and LaFrankie, 1993). As related phenomena, higher levels of parasitism, herbivory, and disease have been detected in females (Gehring and Whitham, 1992; Krischik and Denno, 1990). Perhaps as a result of these patterns, sex ratios in dioecious plant populations are typically male-biased—often strongly so. Differential survival (Krischik and Denno, 1990), differential competitive ability (Cox, 1981; Agren, 1988) or divergent flowering phenology (Bram and Quinn, 2000; Purrington, 1993) are the specific mechanisms invoked most often to explain apparently skewed sex ratios. Only rarely have biased primary sex ratios (sex ratio among seeds or seedlings) been documented (Eppley, 2001).

In environments that are heterogeneous and/or where resources are patchily distributed, sex ratio bias at coarser scales results in spatial segregation of sexes (SSS). SSS may alleviate, at least in part, the higher reproductive cost of females if they preferentially occupy resource-rich habitats. Whereas dioecy has been found most frequently among woody plants which produce fleshy fruits, among island floras, and among plants of arid habitats, SSS is most frequent among wind-pollinated dioecious species. SSS has been shown for *Acer negundo* (box elder) (Freeman et al., 1976; Dawson and Ehleringer, 1993*), Nyssa aquatica* (water tupelo) (Shea et al., 1993) and *Juniperus virginiana* (red cedar) (Lawton and Cothran, 2000) among many other species (Vitale et al., 1987; Iglesias and Bell, 1989; Cameron and Wyatt, 1990; Sakai and Weller, 1991; Barot et al., 1999).

SSS may arise from several mechanisms: differential survival (true segregation), differential frequency of flowering (apparent segregation) or environmentally determined sex expression. Gender plasticity can also lead to temporal segregation of males and females. For serially monoecious species, such as jack-in-the-pulpit (*Ariseama triphyllum*, Araceae), where plant size (presumably an index of available resources) appears to determine sex expression (Bierzychudek, 1984), sex ratios can vary considerably from year to year. In addition, where sex is known to be environmentally determined as in the *Arisaema* genus, only plants in relatively high resource environments develop into females (Bierzychudek, 1984). The two hypotheses proposed most often to explain the evolution of dioecy from hermaphroditic ancestors in plants are 1) avoidance of inbreeding, and 2) spatiotemporal niche separation to promote reproductive efficiency. SSS and related phenomena have attracted attention, in part, because they suggest that dioecy may allow plants to optimize fecundity within an environment by efficiently partitioning reproductive roles according to underlying resource levels.

Questions

1. Does *C. ericoides* exhibit SSS? Do males and females differ in growth, survivorship, age/size at reproductive maturity?
2. *C. ericoides* demographics: how do fire and fire suppression effect rates of mortality, growth, and fecundity?
3. Given that the species is sensitive to fire, does not resprout following fire, and is slow to mature, what is an optimal fire frequency for *C. ericoides*?
4. How should an understanding the role of fire in the population dynamics of *C. ericoides* guide management of longleaf pine-turkey oak sandhills?

CHAPTER 2

DIOECY AND SPATIAL PATTERN IN THE DIOECIOUS SANDHILL SHRUB, *CERATIOLA ERICOIDES* (EMPETRACEAE)

Introduction

Research comparing allocation patterns between genders in dioecious species indicates that female plants usually have higher resource requirements and/or reproduction imposes a greater drain on resources (Crawley 1997a). A recurring pattern observed among dioecious plant species is an increase in the ratio of males to females along an axis of decreasing site productivity. This can occur over a range of scales and with respect to broad environmental gradients or to microsite preferences. Male frequency has been shown to increase as environments become more stressful with increasing altitude (Pickering and Hill 2002), lower moisture availability (Dawson and Ehleringer 1993), increasing salinity (Eppley 2001, Vitale 1987), more anoxic conditions (Shea et al. 1993), decreasing soil fertility (Lawton and Cothran 2000), and decreasing light levels (Nicotra 1998, Thomas and LaFrankie 1993). As related phenomena, higher levels of parasitism, herbivory, and disease have been detected in females (Gehring and Whitham 1992, Krischik and Denno 1990). Perhaps as a result of these patterns, sex ratios in dioecious plant populations are typically male-biased—often strongly so. Differential survival (Krischik and Denno 1990), differential competitive ability (Cox 1981, Agren 1988) or divergent flowering phenology

(Bram and Quinn 2000, Purrington 1993) are the specific mechanisms invoked most often to explain apparently skewed sex ratios. Only rarely have biased primary sex ratios (sex ratio among seeds or seedlings) been documented (Eppley 2001).

In environments that are heterogeneous and/or where resources are patchily distributed, sex ratio bias at coarser scales results in spatial segregation of sexes (SSS). SSS may alleviate, at least in part, the higher reproductive cost of females if they preferentially occupy resource-rich habitats. Whereas dioecy has been found most frequently among woody plants which produce fleshy fruits, among island floras, and among plants of arid habitats, SSS is most frequent among wind-pollinated dioecious species. SSS has been shown for *Acer negundo* (box elder) (Freeman et al. 1976, Dawson and Ehleringer 1993*), Nyssa aquatica* (water tupelo) (Shea et al. 1993) and *Juniperus virginiana* (red cedar) (Lawton and Cothran 2000) among many other species (Vitale et al. 1987, Iglesias and Bell 1989, Cameron and Wyatt 1990, Sakai and Weller 1991, Barot et al. 1999).

SSS may arise from several mechanisms: differential survival (true segregation), differential frequency of flowering (apparent segregation) or environmentally determined sex expression. Gender plasticity can also lead to temporal segregation of males and females. For serially monoecious species, such as jack-in-the-pulpit (*Ariseama triphyllum*, Araceae), where plant size (presumably an index of available resources) appears to determine sex expression (Bierzychudek 1984), sex ratios can vary considerably from year to year. In addition, where sex is known to be environmentally determined as in the *Arisaema* genus, only plants in relatively high resource environments develop into females (Bierzychudek 1984). The two hypotheses proposed most often to explain the evolution of dioecy from hermaphroditic ancestors in plants are 1) avoidance of inbreeding, and 2) spatiotemporal niche separation to promote reproductive efficiency. SSS and related phenomena have attracted attention, in part, because they suggest that dioecy may allow plants to optimize fecundity within an environment by efficiently partitioning reproductive roles according to underlying resource levels.

Study species—*Ceratiola ericoides* (Empetraceae) Michx. is the sole member of its genus. The Empetraceae (crowberry family) is comprised of 3 genera and 6 species, all but 2 of which are dioecious. Monoecy appears to be a derived condition in the Empetraceae (Heywood 1993). *C. ericoides* is wind-pollinated, blooms September-October, and produces 3 mm diameter fleshy fruits which ripen January-April. In mature plants, a flower is borne in each leaf axil of the previous year's growth. *Ceratiola ericoides* has a whorled branching pattern with the main unshaded branches producing new shoots once a year, therefore shrubs can be aged nondestructively by counting the nodes on the main branches. The fruits of *C. ericoides* are apparently dispersed by vertebrates and birds such as towhees are known to consume them. Harvester ants have also been observed to collect and consume the fruits of *C. ericoides* (Johnson 1980). *C. ericoides* (Florida or sandhill rosemary) is an aromatic, needle-leaved, evergreen, dioecious shrub which grows to 2 m in height and is found on dry, sandy soils on both coastal and inland sites in the southeastern United States.

In central Florida where it occurs most abundantly, *C. ericoides* is typically dominant only on xeric, deep sands on the uplands of old dune ridges. However, on many sites north of the Lake Wales Ridge in Florida, *C. ericoides* grows in close association with *Quercus laevis* (turkey oak) and *Pinus palustris* (longleaf pine). Many populations of *C. ericoides* occuring in Georiga or South Carolina appear to be suppressed by *Q. laevis* which has encroached probably as a result of fire exclusion. Periodic fire--by removing smaller diameter *Q. laevis* stems--may prevent *Q. laevis* from spreading vegetatively into the driest portions of the dunes and overshading or otherwise out-competing *C. ericoides*. My objective was to investigate sex ratios and their spatial distribution 1) to assess overall sex ratios 2) along a gradient from xeric upper dune to more mesic slopes or toe-slopes and 3) in relation to competing vegetation--hypothesizing that, as a result of differential mortality, females would be 1) less abundant on the most xeric micro-environments and 2) less frequent in close proximity to *Q. laevis* and *Pinus palustris*. A second objective was to investigate potential differences in growth rate and age at first reproduction of males and females.

Materials and Methods

Study sites--The study was carried out in Georgia and South Carolina (U.S.A.). Individual study sites were located in the Coastal Plain physiographic province of both states, sandhill habitats occurring in distinct sub-provinces (Figure1). Populations mapped at Fort Gordon and in Burke County, Georgia and Aiken County, South Carolina are located within the Fall Line sandhills, a formation of remnant dunes which marked the Atlantic shoreline during the Miocene epoch (Ivester and Leigh 2003). Three other populations (at the state-owned Ohoopee Dunes Natural Area and at 2 sites near Cobbtown, Georgia) were mapped on riverine sandhills located along the Ohoopee River in southeastern Georgia. A second contrast, and one likely to be more important in determining the structure of vegetation at sites is the frequency of fire and time since last burn. Sites at Fort Gordon are burned annually whereas most other sites have not burned within the last 10 years, though detailed fire histories prior to 1990 are not known for any sites other than Fort Gordon. A third contrast between sites is soil substrate: some sites at Fort Gordon and in Aiken County occur on kaolin (highly leached clay) rather than on deep sandy soils (Table 1). Of the populations mapped, Ohoopee Dunes site was the largest population completely mapped and the only population available for study which spanned a topographic gradient from floodplain to upper dune.

Field mapping--1583 shrubs from 7 populations from 3 habitat variants were mapped (Table 1) using a Trimble GeoExplorer 3 GPS unit (and associated Trimble Pathfinder software to perform differential correction from base-station files). Trimble advertises 1-5 m accuracy. Comparing deviation of coordinates of GPS-mapped landmarks (roads, large trees) with their locations on rectified aerial photos (DOQQs), I estimate an accuracy of 1-2 m. GPS mapping was facilitated by the open terrain and the low, open canopy of sandhill vegetation. For all populations except Cobbtown 2, the entire population was mapped with transects established to find all plants. For Cobbtown 2, plots were arbitrarily established to include a sample of 300-400 plants. In addition, for Cobbtown 2 and Ohoopee Dunes populations, sex, stage (juvenile or adult), size (height and diameter), age (estimated by node counts), and distance, dbh and species for all trees within a 3 m radius were recorded for each mapped shrub.

Spatial pattern and comparison of growth and flowering between sexes--Spatial segregaton between males and females was assessed in two ways. First, a chi-square test was used to compare the sex ratios between contrasting sandhill cover classes: open sand versus canopy overstory. As they were mapped, each *C. ericoides* shrub was classed as growing in the open or under a canopy of *Q. laevis* or *P. palustris*. Sex ratio was also examined along a moisture gradient by comparing ratios on xeric upper dunes to those on dune slopes and on bottomlands adjacent to dune swales. A chi-square test of equal proportions in a 2x2 contingency table was used to determine whether the proportion of males on the upper dune significantly differs from the proportion of males on dune slopes and bottoms. Topographic analysis was possible only at the Ohoopee Dunes, the only site where a population could be mapped along a full topographic gradient.

Second, for the five populations larger than 100 individuals, spatial pattern was tested using Ripley's K-function (1977) analysis of spatial pattern. Ripley's K is a second-order statistic based on the distribution of distances of pairs of points. Ripley's K and other second-order statistics describe the spatial correlation of the point pattern. Bivariate Ripley's K-function was used to assess patterns of male and female *C. ericoides* shrubs in relation to one another. In order to remove scale-dependence and stabilize the variance, a square root transformation of K, called the L-function, is used instead:

$$L_{12}(r) = \left(\sqrt{\frac{K_{12}(r)}{\pi}} - r \right)$$

where r = distance. $L_{12}(r)$ are determined from the number of males within a distance t of an arbitrary female, and $L_{21}(r)$ is determined by the number of females within distance t of an arbitrary male (Diggle 1983).

In bivariate point pattern analyses, the choice of null hypotheses is between independence and random labelling. To test the first case, simulations are performed that involve random shifts of the whole of one component pattern relative to the other. To test against a null hypothesis of random labelling, labels (1 or 2) are assigned to points whose locations are fixed. The null hypothesis of random labelling is applied not to questions about the interaction between two processes, but rather about the process that assigns labels to points (Wiegand and Moloney 2004). Random labelling is appropriate when the "locations of type 1 and 2 points result from a completely random process affecting *a posteriori* a single spatial pattern (Goreaud and Pelissier 2003)." Therefore, random labelling is the appropriate null model in testing for spatial segregation of male and female shrubs. The specific test for bivariate random labelling used here corresponds to that proposed by Goreaud and Pelissier (2003): $L_{12}(r)=L(r)$. Values of $L_{12}(r)>0$ indicates that there are on average more points of pattern 2 within distance r of pattern 1 than expected under the null hypothesis. Conversely, $L_{12}<0$ indicates repulsion between the two patterns up to distance r. Analyses were performed using Programita (http://www.oesa.ufz.de/towi/towi_programita.html), a software progam written by Wiegand and Moloney (2004). $L_{12}(r)$ was calculated over an area corresponding to the minimum bounding box of each population

GLIM Model--To assess potential differences in size (estimated as relative diameter/age) for adult shrubs in the Cobbtown2 and Ohoopee Dunes populations, a Generalized Linear Model was constructed using R statistical software as follows:

$$diameter = nodes + nodes^2 + sex + nbor1 + nbor2 + nbor3 + site + interaction\ terms + \varepsilon_{ij}.$$

Because the variance of the data is inhomogeneous, a gamma distribution was chosen as the best-fitting model. Maximum likelihood estimation using Alkaike's Information Criterion (AIC) was used to evaluate the significance of terms within the model. *Nodes* is the node count of each mapped shrub used as an estimate of age; *diameter* is the basal width of each shrub at its broadest dimension. *Ceratiola ericoides* shrubs have a sprawling mound-shaped form except in shaded or closely crowded conditions. Typical of plants adapted to high-light conditions, *C. ericoides* shrubs when shaded exhibit a more vertical, open growth form. Measures of shrub volume do not take into account relative density of foliage. *Diameter* (m) therefore serves as the dimension most sensitive to degree of suppression by shading and, in addition, to the relative success of an individual shrub in intraspecific competition. *Nbor1*, *nbor2* and *nbor3* are indices of relative competition from neighboring trees and conspecific shrubs:

$$nbor1=\sum_{j} 1/r_j$$

$$nbor2=\sum_{j} d_j/r_j$$

$$nbor3=\sum_{j} d_j/r_j \,.$$

Nbor1 is the sum of the inverse distance (m) *r* for all trees *i-j* within 3 m of a focal *C. ericoides* shrub. *Nbor2* is the sum of tree diameter *d* divided by distance *r* for all trees *i-j* within 3 m of a focal *C. ericoides* shrub. Similarly, although derived from mapped data, *Nbor3* is the sum of shrub canopy diameter *d* divided by distance *r* for all trees *i-j* within 3 m of a focal *C. ericoides* shrub.

Results

Sex ratio—Only at the Ohoopee Dunes site did sex ratios differ significantly from 1:1 for any age class (Table 2). The female-biased Ohoopee Dunes population also exhibited a greater bias toward females along a gradient from xeric upper dune to more mesic lower slopes (Figure 2, Table 3). However, this difference was not statistically significant. Though no differences appear between males and females or between adult and juvenile life stages, most plants grew in close association to canopy trees (*Q. laevis* and *P. palustris*) on those sites where there is no documented recent history of burning (Table 4). Fort Gordon and Burke County populations contain very few plants growing in close association with canopy trees.

Spatial segregation of sexes—Maps (Figure 2) of the five largest populations depict a highly clumped spatial pattern of individuals within each population. Bivariate Ripley's K comparisons of the spatial distribution of males and females revealed them to be closely associated--rather than segregated--across the scales at which populations were mapped (Figure 3) for all populations except Cobbtown 2. The exception, however, is quite striking. A pattern of segregation at Cobbtown 2 is quite strong over a sizeable distance range. Therefore, a pronounced spatial differentiation in the occurrence of males and females along microenvironmental factors such as proximity to competing woody vegetation or small-scale topographic or edaphic features may be occurring at one of the five sites athough there is no obvious causal factor for the apparent SSS. At Ohoopee Dunes, the only population for which differentiation in occupation along a broad moisture gradient could be tested, males and females were significantly aggregated up to 720 m. At larger distances, association between sexes was random. The fact that sex ratios were increasingly female-biased along a topographic gradient at Ohoopee Dunes apparently had little influence on overall patterns of association since most plants occurred on the upper dunes.

Generalized Linear Model of effects of sex and shade on shrub size—Means of shrub age (node counts) varied little between sexes at any site (Table 4) nor did age distribution differ (Figure 4) significantly (using the Wilcoxon-Mann-Whitney two-sample test) by sex at any site. While shrub size is, not surprisingly, closely correlated with age as estimated by node counts, GLIM analyses showed no significant effect of gender on size. Aside from age (nodes) and a second-order nodes term, only *Nbor2*, an index of distance to turkey oaks and their size *Nbor3*, a measure of intraspecific competition, appear to have a significant effect on shrub diameter (Table 5). However, the effects of *nbor2* and *nbor3* were apparent only on the more xeric Cobbtown site. Moreover, the effects of neighboring trees and shrubs, though slight, are positive—perhaps indicating a facilitative rather than competitive effect—or merely a similar habitat requirement.

Discussion

Based on the results of this study, there appears to be little differentiation between sexes in *C. ericoides* in either growth rate (estimated as size/nodes), age and size at first reproduction, longevity, or growth or survivorship in proximity to woody species. *C. ericoides* was expected to demonstrate some form of segregation as a strictly dioecious, fleshy-fruited, wind-pollinated species growing in a stressful environment where resources appear to be both patchy and distributed along a gradient. In this study, there was strong evidence of SSS in only one population (Cobbtown 2), and what underlying resource or disturbance factor that segregation may be a response to is unclear. From an evolutionary standpoint there are also many reasons to predict this tentative finding of little segregation. Selection can be expected to minimize differences in reproductive costs between the sexes. Differences between the sexes in reproductive costs, if they exist at all, may be very slight given the large volume of pollen produced by males (Pedro Quintana-Ascencio pers comm.) and the variability in fruit production by females. Female reproductive investment may exceed the average outlay of resources by males in some years, but fall well short in other years, averaging to a similar or lesser value.

Moreover, measuring total cost of reproduction is a difficult proposition. Carbon invested to fruit biomass, for example, may not always represent a limiting resource. Some reproductive structures may yield a significant photosynthetic return and nutrients expended in reproductive structures may be resorbed (Ashman 1994). Yet reproductive costs may be inferred from lower growth, survival, and/or frequency of flowering often reported for females, and/or by a more variable reproductive effort through time (Popp and Reinartz 1988, Obeso et al. 1998, Antos and Allen 1999, Nicotra 1999). Allen and Antos (1988), Cipollini and Stiles (1991), Guitian et al. (1997), Nicotra (1999), and Rocheleau and Houle (2001) demonstrate larger investments in reproduction by females. Where reproductive costs have been quantified in terms of differential allocation patterns to flowers and fruits, males frequently invest more in reproduction at time of flowering (Rocheleau and Houle 2001, Guitian et al. 1997, Cipollini and Whigham 1994, Thompson and Edwards 2001). However, total reproductive investments in biomass (Thompson and Edwards 2001, Cipollini and Stiles 1991), N (Cipollini and Whigham 1994) and Mg and Ca (Rocheleau and Houle 2001) were higher for females than males—as a result of fruit production.

Determining real reproductive costs in *C. ericoides*, a highly aromatic (terpene-releasing) shrub which grows in an environment where light is generally not limiting, is difficult since carbon compounds probably do not represent a significant expense. For many plants of arid or low-productivity environments, growth and reproduction may be limited by the availability of limiting nutrients, yet C-based compounds produced through photosynthesis are in surplus (Crawley 1997b). The relatively minor effect of local density of *Q laevis* and *P. palustris* on rosemary diameter despite the frequently apparent suppression of individual *C. ericoides* shrubs suggests that indices of neighborhood density do not capture the (highly variable) degree of shade cast by nearby trees. An equally important competitive effect may be the result of competition from neighboring trees and shrubs for limiting nutrients such as N and P. On xeric dunes, nutrient availability is likely to be highly variable in space as a result of patchiness in litter deposition and differences in clay content of soil. The degree of belowground competition, therefore, may also be highly variable. Given this, interactions with woody species probably occur along a continuum from competition to facilitation. In fact, in the absence of fire, juveniles appear to establish most readily within 2 m of canopy trees. This may be due to greater soil organic matter providing more available nutrients, to shading which may reduce the heat load on recruits and juveniles, to improved moisture relations as a result of hydraulic lift from longleaf pines and turkey oaks (Espeleta et al. 2004) or perhaps as a result of patterns of seed dispersal by frugivores.

More female-biased sex ratios moving from xeric to mesic along a soil moisture gradient are similar to patterns found in box elder (*Acer negundo*) in Utah. However, it is not clear whether the pattern at the Ohoopee Dunes can be generalized to other sandhill populations of *C. ericoides*. Moreover, while the female:male ratio in box elder is higher in stream bottoms than on xeric slopes because female mortality is lower along streams, it is unclear what mechanism would promote the low female:male ratios of *C. ericoides* on mesic sites. Furthermore, the mesic end of the sandhill continuum seems to form secondary rather than prime habitat for *C. ericoides*: a relatively small proportion of the Ohoopee Dunes population is found there. Interactive effects of neighborhood by sex did not significantly improve the GLM model even for the Cobbtown2 population which is located on more xeric Kershaw sands—a deeper dune formation.

If reproductive costs for *C. ericoides* in either nutrients or carbon are higher for females as has often been reported for dioecious species of similarly stressful habitats, then females may be compensating via greater allocation of photosynthate to roots or mycorrhizae. Such a difference in allocation might not be apparent in intersexual growth differences in most environments if males are volatilizing more aromatic compounds and/or expending more photosynthate during flowering through pollen and flower production. However, where a combination of stressors exists, compensation by females may not be possible. Gehring and Whitham (1992), for example, found that mistletoe-infested females *Juniperus monosperma* trees showed lower rates of root mycorrhizal infection.

Evolutionary drivers of dioecy in plants--The two hypotheses proposed most often to explain the evolution of dioecy from hermaphroditic ancestors in plants are 1) avoidance of inbreeding, and 2) spatiotemporal niche separation to promote reproductive efficiency. Among plants in which gender expression is labile, the niche separation hypothesis is seemingly supported by environmental induction of flowering in either the male or female phase or the frequently observed relationship of gender to size or level of accumulated resources. Similarly, segregation resulting from differential rates of flowering or differential survivorship between contrasting microsites or across gradients seems to support this hypothesis. Examples of either spatial or temporal segregation of male and female function among dioecious species with fixed or labile sex determination are apparent instances of niche separation. However, the well-documented prevalence of such phenomena does not necessarily preclude avoidance of inbreeding as the primary evolutionary driver.

Finding support for niche partitioning as a causal factor in the evolution (or maintenance) of dioecy is quite difficult. Once a form of dioecy in which sex expression is genetically controlled has evolved, divergent physiological and phenological traits may evolve in parallel and segregation along a niche axis or set of environmental optima may develop. This seems to have happened most frequently in wind-pollinated species. As a rule, females occur in greater numbers on more productive sites and males occur more frequently on less productive sites or sites that seem to confer a fitness advantage by, for example, promoting pollen dispersal (e.g. box elder in Utah, Dawson and Ehleringer 1993).

Freeman et al. (1997) argue that, whether the apparent cause is differential flowering, differential mortality or sexual lability, SSS should be selected for when "at some consistent time in the organism's life-cycle, or in some consistent places in the environment, individuals that reproduce primarily through one sexual function will be more successful than individuals that reproduce primarily through the other sexual function." The same authors present tentative data to support the argument that, for many wind-pollinated dioecious plants, dioecy evolved primarily from selection for sexual specialization. Freeman et al. (1997) do this by comparing prevalance of intrafloral dichogamy (breeding systems in which male and female functions of an individual plant are asynchronous--presumably evolved as a means of preventing self-pollination) to SSS, a proxy for sexual specialization, within plant families. The authors then find a significant relationship between SSS (compiled from Bierzychudek and Eckhart 1988) and the presence of some form of protogyny (data from Bertin and Newman 1993) within families. Families with species exhibiting SSS were five times more likely to contain species exhibiting protogyny than those that did not contain species displaying SSS. Still, strong conclusions are not possible since both the literature on niche partitioning among the sexes in dioecious plants and the literature on self-incompatibility are fragmentary.

Freeman et al. (1997) go further to propose a comprehensive scheme for the evolutionary development of dioecy from hermaphroditic ancestors: 1) dioecy evolved from hermaphrodism via monoecy as a result of selection for sexual specialization; 2) dioecy evolved from hermaphrodism via gynodioecy (females and hermaphrodites) as an inbreeding avoidance (IA) adaptation. The evolution of dioecy from gynodioecy seems to be restricted to animal-pollinated species and families dominated by them. Among these dioecious species there may be some sexual specialization, but the need to attract the same pollinators limits the degree of differentiation possible between the sexes. Species that evolve dioecy from monoecy, by contrast, frequently show sexual specialization. In particular, the features of plant architecture associated with monoecious wind-pollinated plants--such as the concentration of anther-bearing flowers in upper branches and pistillate flowers in lower branches--lend themselves to the further specialization of male and female functions in separate plants.

C. ericoides is a species within a small family of wind-pollinated, mostly dioecious shrubs. It is therefore difficult to determine whether the species is derived from ancestors which were monoecious or hermaphoditic. Certainly members of the Ericaceae, a large family allied to the Empetraceae, are known to be mostly hermaphroditic and to frequently possess self-incompatibility mechanisms. Yet there is little evidence in the case of *C. ericoides* that the dioecious habit operates to allow reproductive niche partitioning. A similar study of *Corema conradii* (Rocheleau and Houle 2001), an Empetraceous shrub of the coastal dune heathlands of northeastern North America, found no spatial segregation between males and females although males were significantly larger. Still, females did not begin reproduction at a later age or exhibit shorter lifespans.

The prevalance of dioecy among remote island floras has also been related (Givnish 1980) to a dearth of pollinators and to selection for outcrossing. Many of these dioecious species also possess small, wind-pollinated flowers. The floral traits of *C. ericoides* and *C. conradii*, small wind-pollinated flowers, may well have evolved to promote outcrossing within an environment where pollinators may be in short supply and/or inhibited from travelling the distances between populations. The lack of differentiation between sexes in *C. ericoides* together with the habitat affinities and floral features of the species provide only very ambiguous support for any of the prevailing theories for the evolution of dioecy. Even provisional validation of these theories awaits a much larger accumulation of data on the biogeography of dioecy and on breeding systems across plant families and genera.

Table 1.1. Site summary showing ecoregion, fire regime, and soil type for each population.

Population	Region	Fire regime	Soil
Fort Gordon1	Fall Line	annually burned	sandy
Fort Gordon2	Fall Line	annually burned	clay
Burke County	Fall Line	< 10 years	sandy
Aiken County	Fall Line	> 10 years	clay
Ohoopee Dunes	Coastal Plain	> 15 years	sandy
Cobbtown1	Coastal Plain	? > 15 years	deep sands
Cobbtown2	Coastal Plain	? >15 years	deep sands

Table 1.2. Sex ratios for each mapped population.

Population	Total	Male	Fem.	Juv.
Fort Gordon1	57	18	17	22
Fort Gordon2	490	73	77	340
Burke County	124	45	46	32
Aiken County	66	14	14	38
Ohoopee Dunes*	583	193	258	123
Cobbtown1	115	62	53	0
Cobbtown2	219	68	73	78
Total	1654	473	538	633

* Sex ratio significantly female-biased ($\chi^2 = 9.39$, df=1, p= 0.002).

Table 1.3. Sex ratios a) along a topographic gradient at Ohoopee Dunes, and b) by neighborhood: < 2 m from canopy tree (canopy), > 2 m from nearest canopy tree (open) for Ohoopee Dunes, Cobbtown1 and Cobbtown2.

a)	males	females
Upper Dune	111	137
Dune Slope and Bottom	82	121

b)	males	females	juveniles
open	65	72	58
canopy	211	238	143

Table 1.4. Mean age (nodes) by sex.

	males	females
Aiken County	9.4	8.1
Burke County	12.6	12.6
Cobbtown1	15.5	13.5
Cobbtown2	12.2	12.2
Gordon1	9.5	11.4
Gordon2	10.2	7.1
Ohoopee Dunes	17.4	18.8

Table 1.5. Results of generalized linear model using AIC to select the best-fitting model.

	Cobbtown2		Ohoopee Dunes	
	parameter	AIC	parameter	AIC
intercept	2.018		2.2016	
nodes	-0.157	529	-0.186	858
nodes^2	0.0035	450	0.0044	800
nbor2	0.044	337.88		
nbor3	0.0667	337.25		

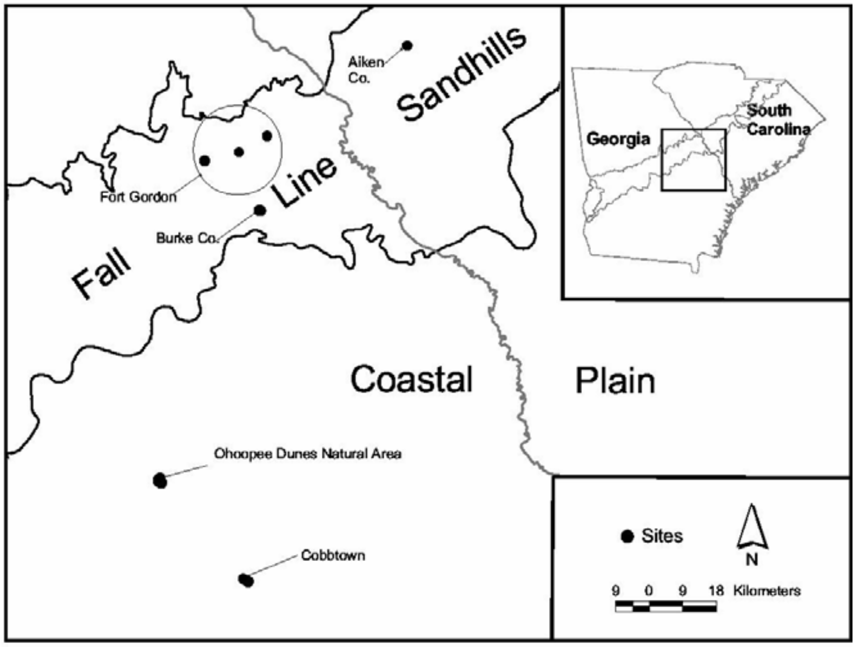
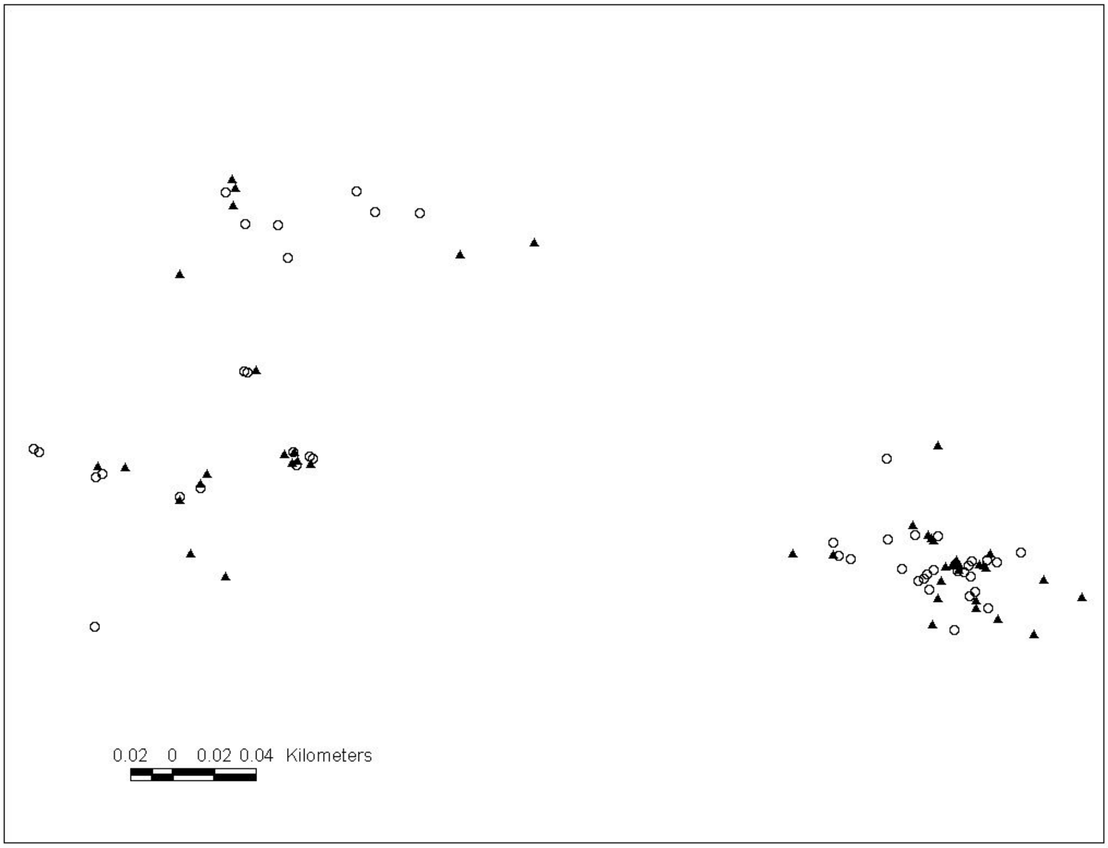
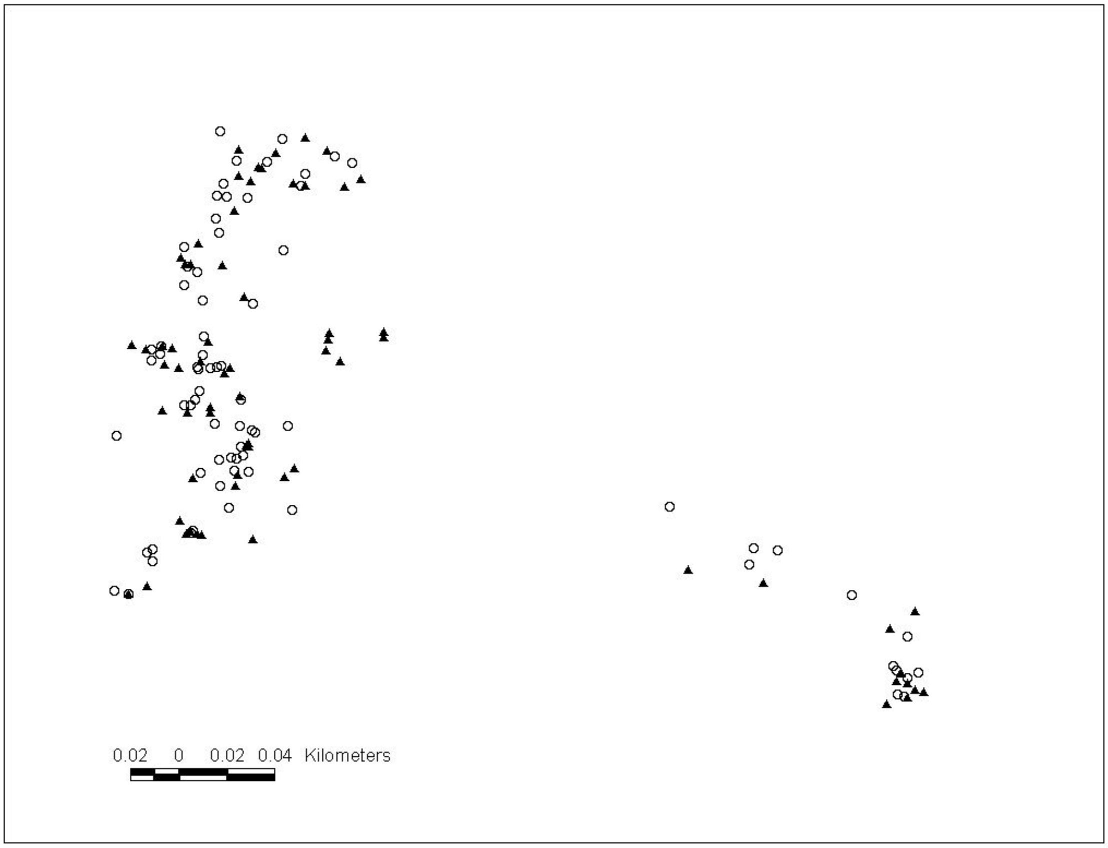


Figure 1.1. Map of sites.

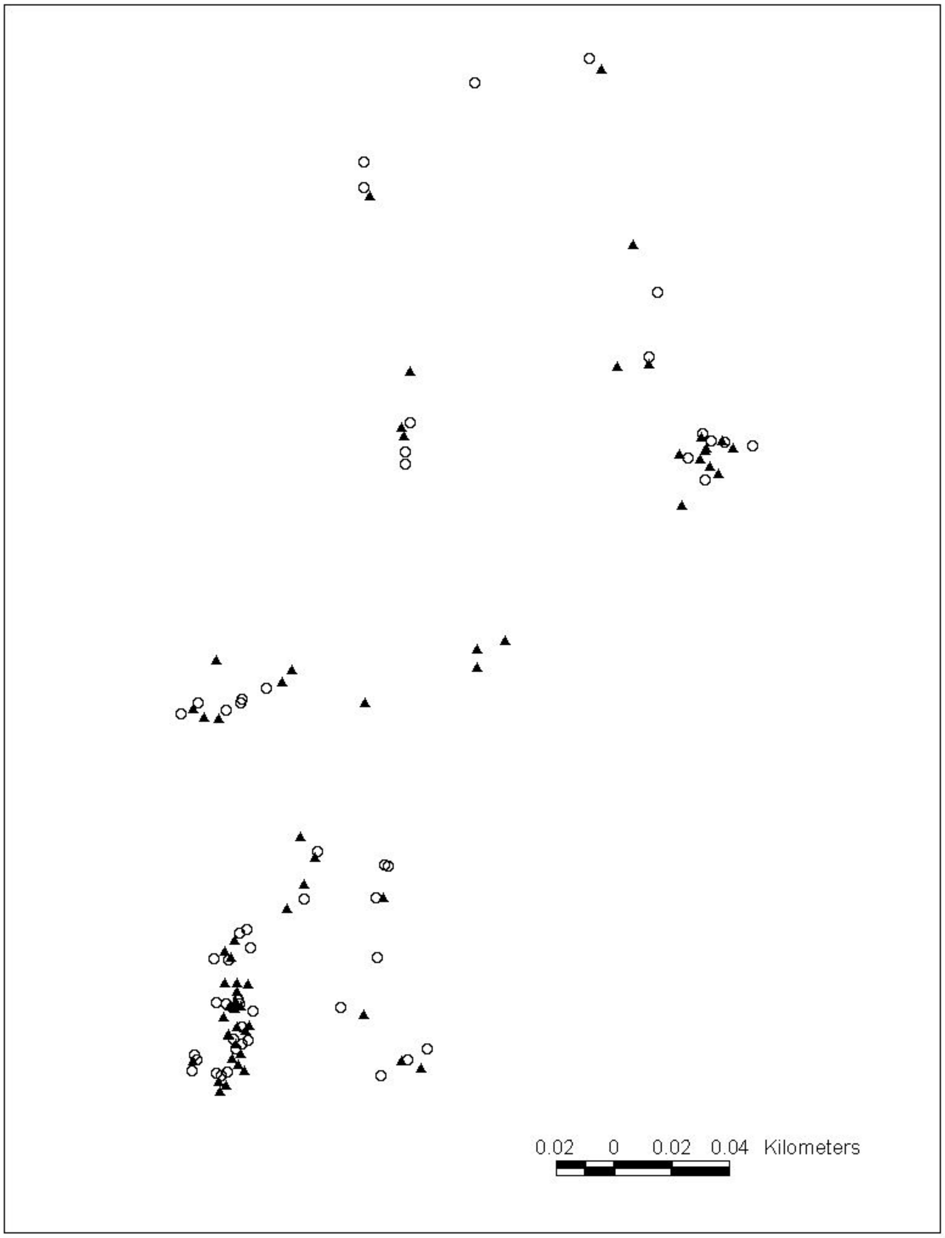
Figure 1.2. Mapped adult shrubs, males (Δ) and females (O), by site.



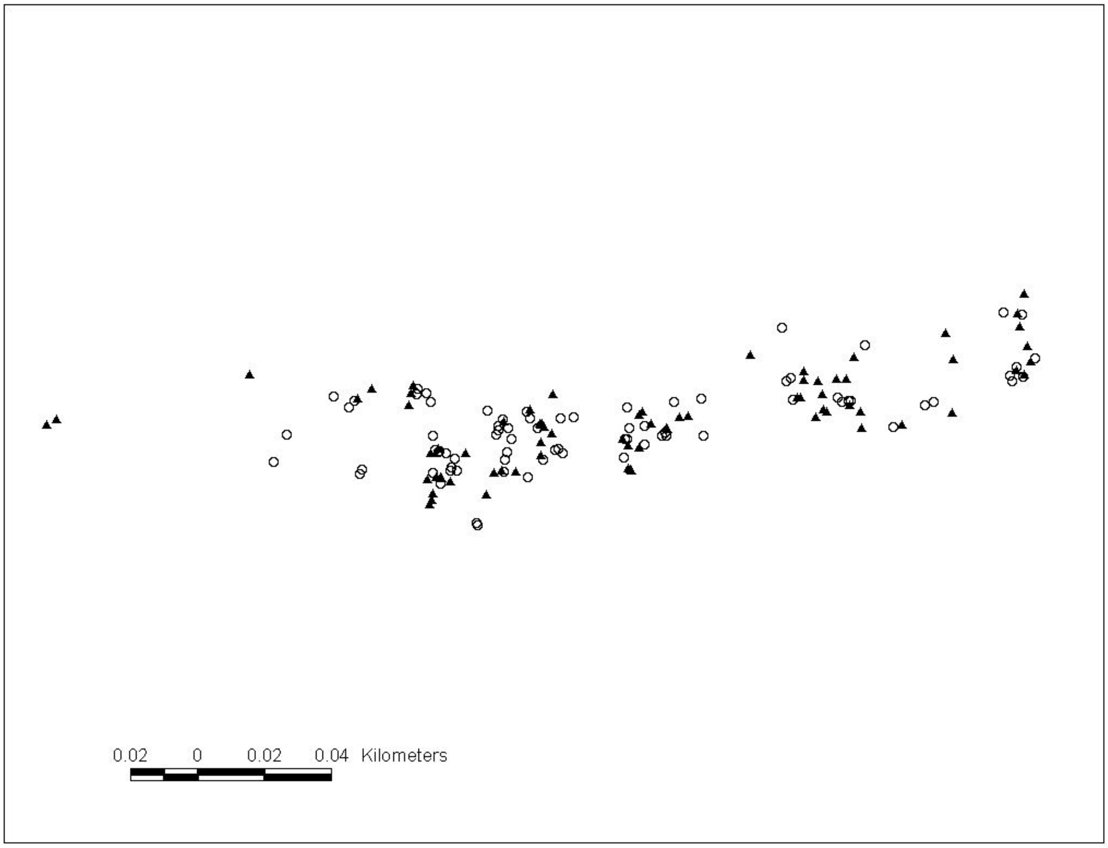
Burke County



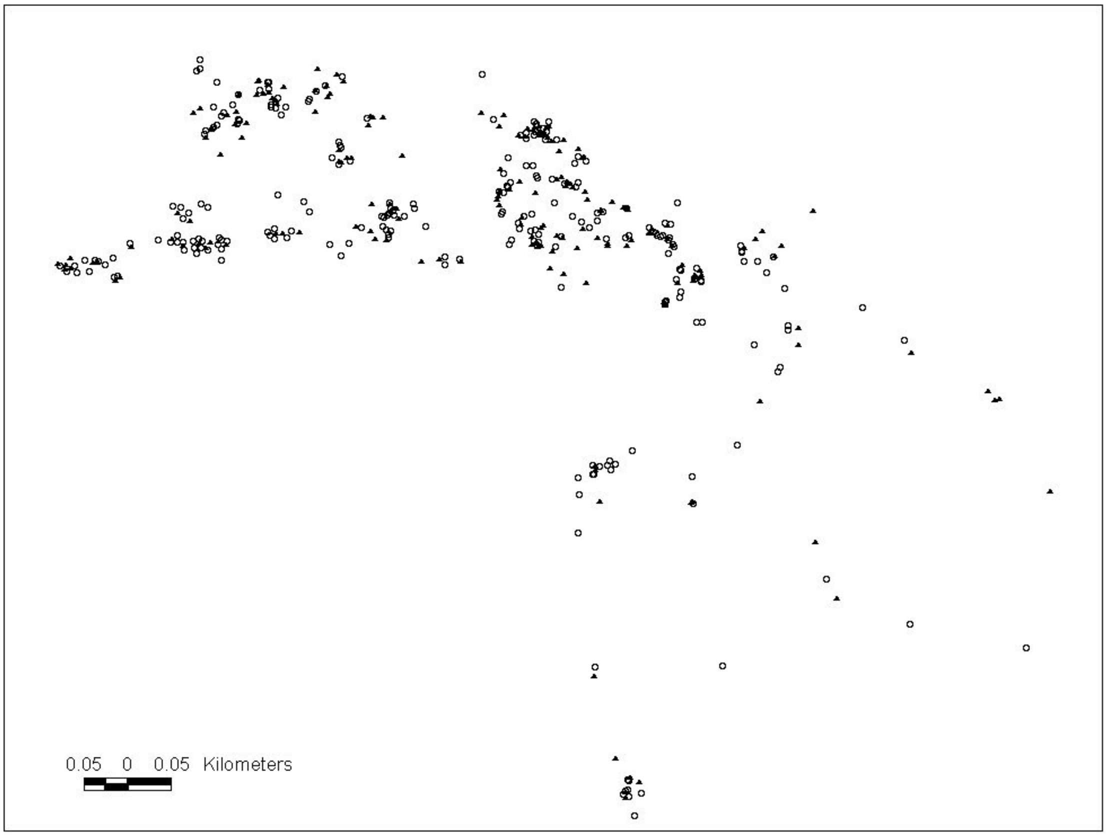
Cobbtown 1



Cobbtown 2

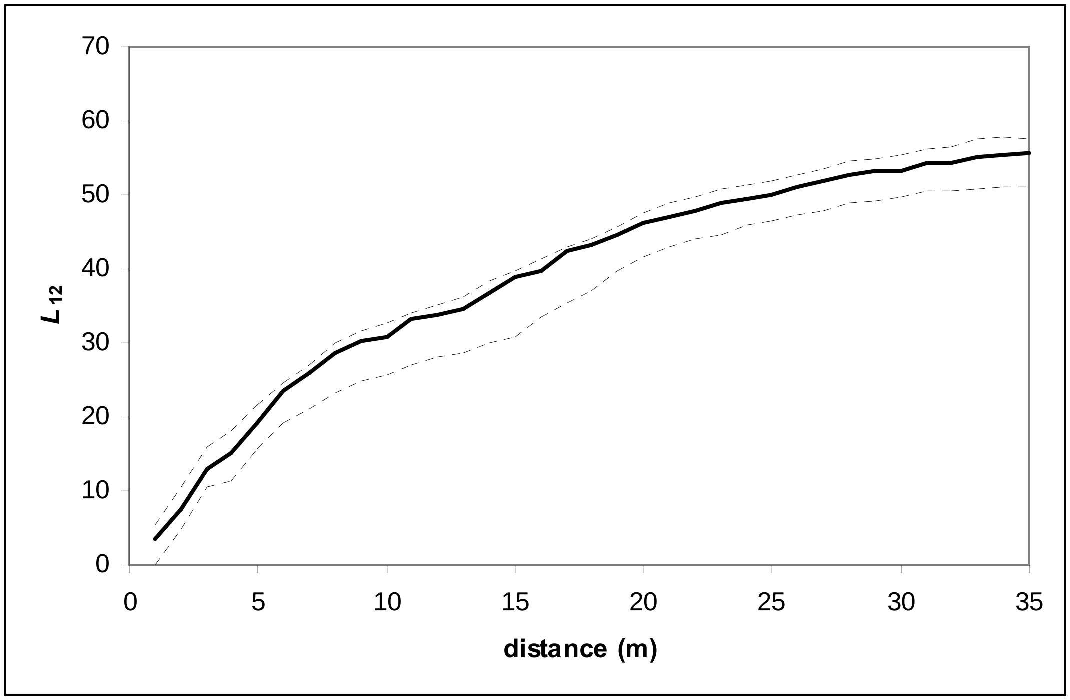


Fort Gordon 1

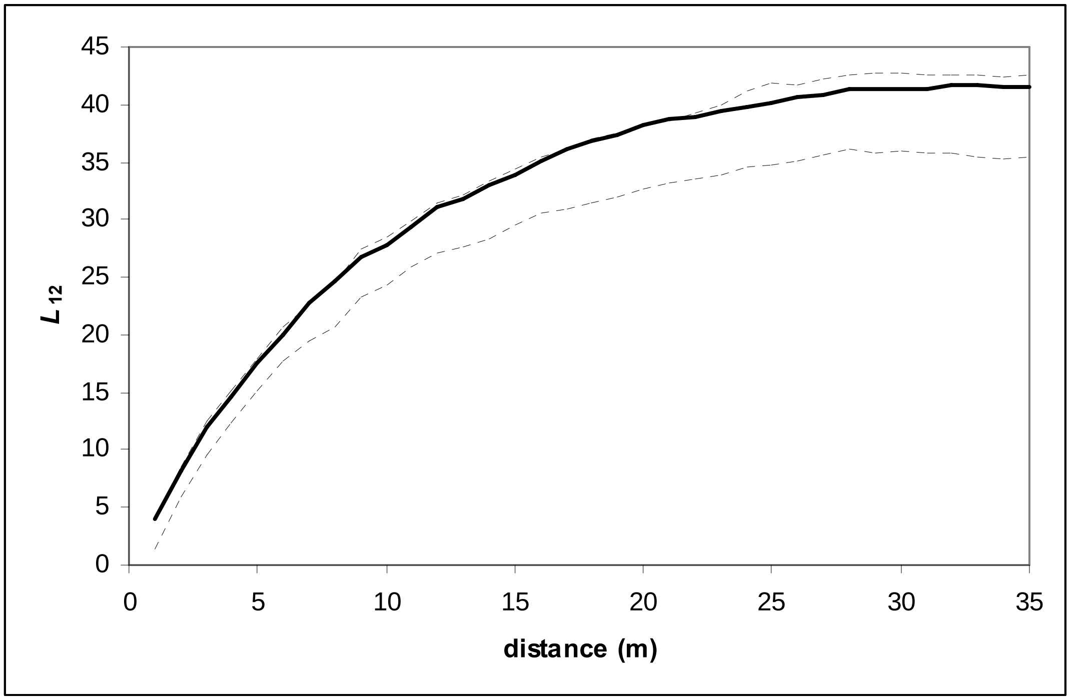


Ohoopee Dunes Natural Area

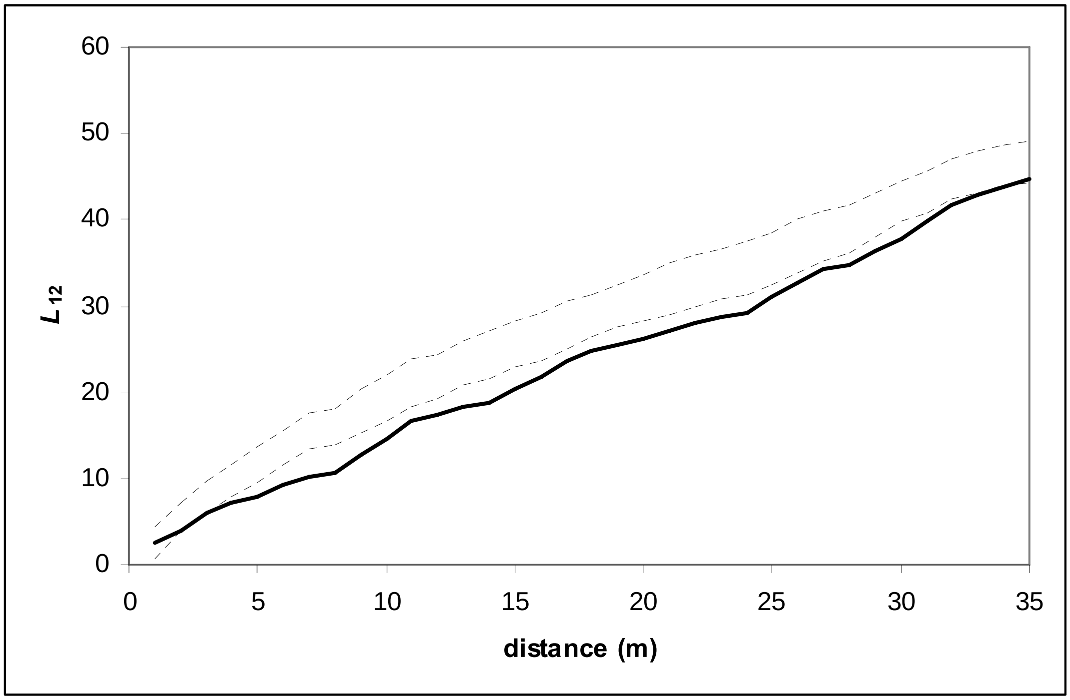
Figure 1.3. Observed *L(t)* values for unvariate Ripley analysis of all adults *C. ericoides* shrubs (on left side) paired by site with *L(t)* values for bivariate Ripley analysis of male and female shrubs. *L(t)* values are represented by solid lines. Dashed lines represent 5% highest and lowest values generated from 1000 Monte Carlo simulations of a randomly distributed population. *L(t) > 0* indicates aggregation; *L(t) <0* indicates hyper-dispersion.



Burke County



Cobbtown 1



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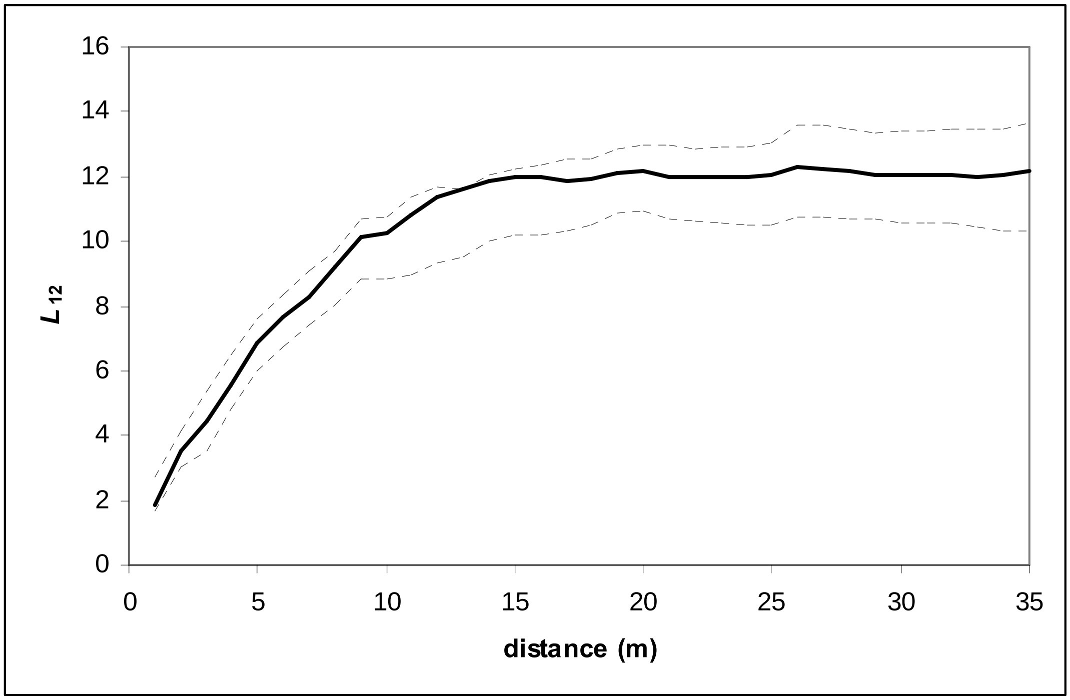
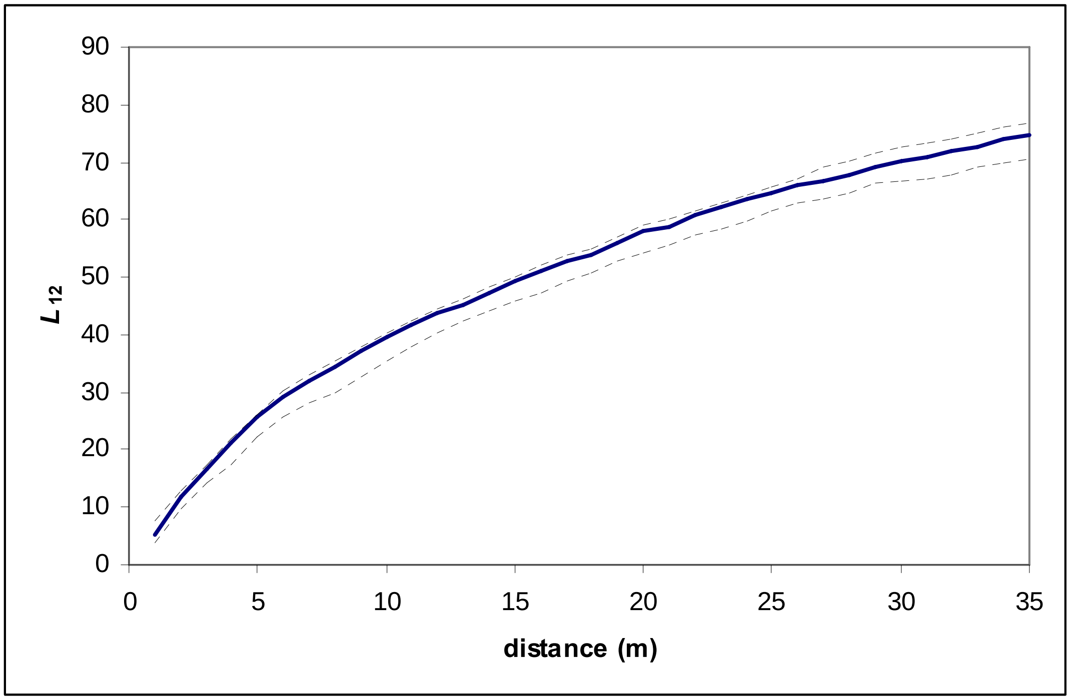
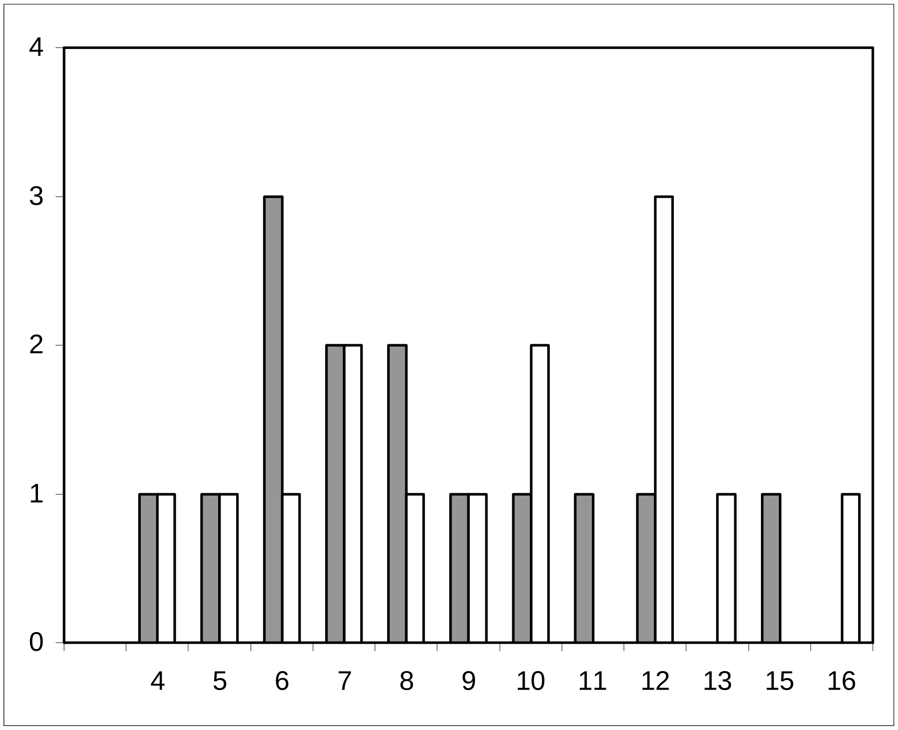


Fort Gordon 1

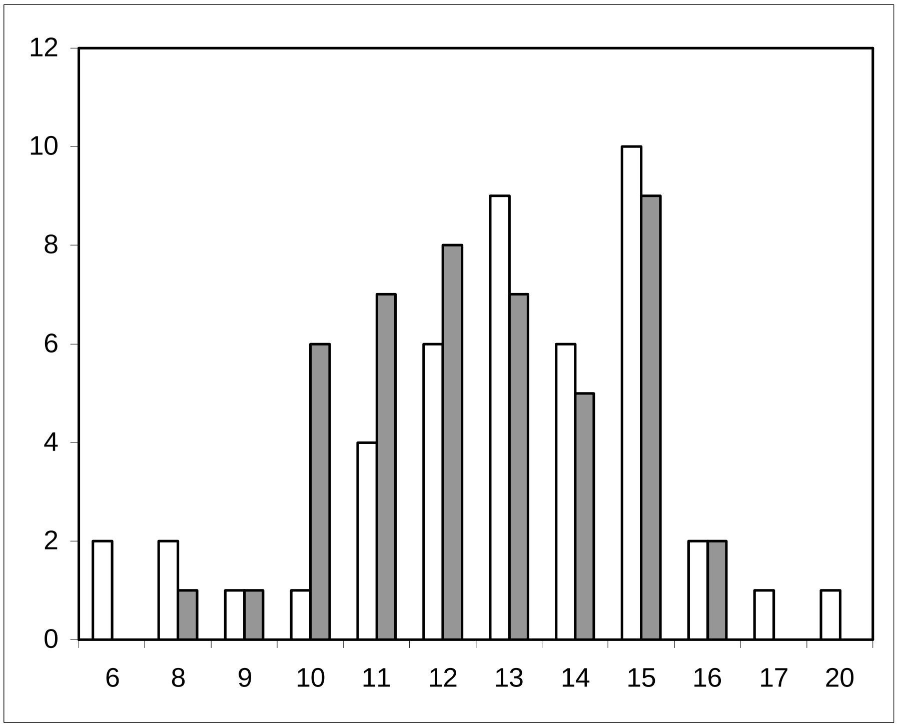


Ohoopee Dunes Natural Area

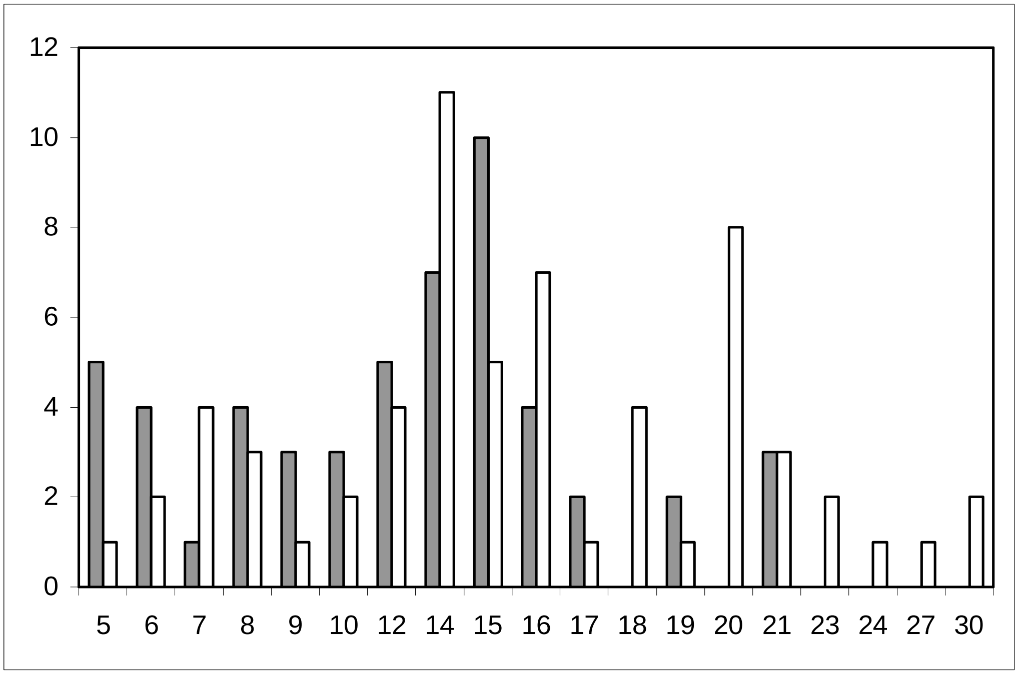
Figure 1.4. Age distribution (nodes) of males and females by site.



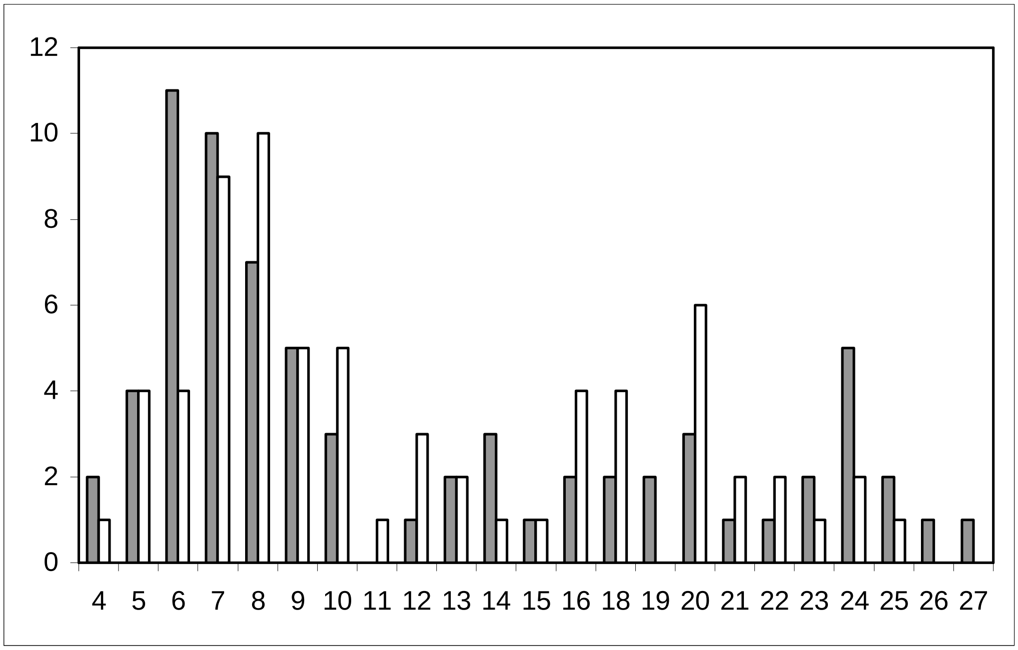
Aiken County



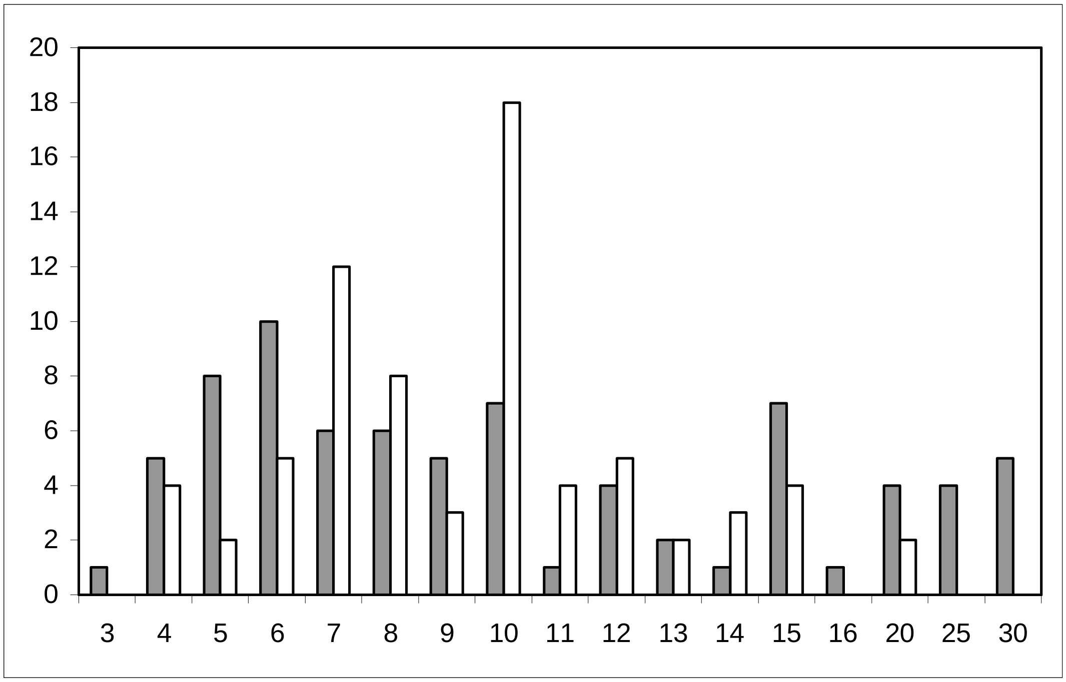
Burke County



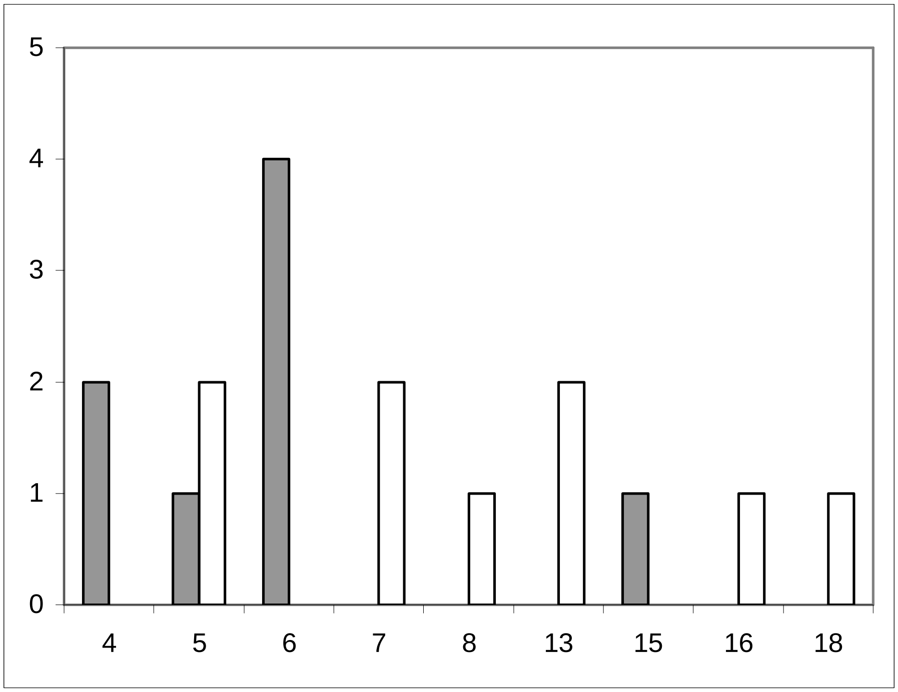
Cobbtown1



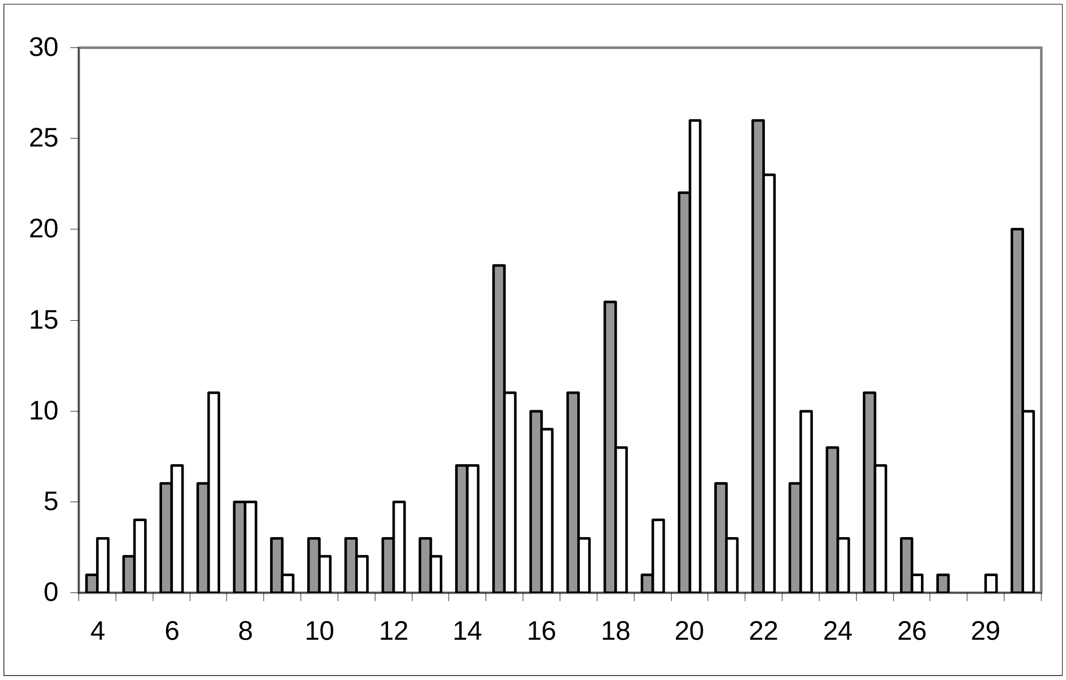
Cobbtown2



Gordon1



Gordon2



Ohoopee Dunes

CHAPTER 3

POPULATION PARAMETERS FOR AN INDIVIDUAL-BASED MODEL OF POPULATION DYNAMICS OF A SANDHILL ENDEMIC SHRUB, *CERATIOLA ERICOIDES*

Introduction

Xeric sand environments of the southeastern U.S. support a suite of rare and endemic plants and animals, yet an understanding of the long-term management needed to conserve biodiversity on these sites is not well-established. The effects of various disturbance regimes, particularly fire-return cycles, on long-term population dynamics of sandhill species or on community dynamics are incompletely understood. Establishing management guidelines is further complicated by a recent history of fire suppression at many sites (Reinhart and Menges 2004, Heuberger and Putz 2003, Glitzenstein et al. 1995, Rebertus et al. 1989a, Myers and White 1987).

In this paper I present the results of a set of analytical methods used to develop demographic parameters for a dioecious shrub, *Ceratiola ericoides* (sandhill rosemary), endemic to xeric sand environments within the Southeast characterized by sterile soils, drought, and, historically, by periodic fire. *C. ericoides*, a shrub that lives to 40+ years, which commonly occurs on sandhill sites, is not resistant to fire and, following fire, reestablishes only by seed (Johnson 1982). However, fire also seems to stimulate germination in *C. ericoides* (Gibson and Menges 1994). Because *C. ericoides* demography is sensitive to fire frequency, a fire regime that promotes long-term persistence of *C. ericoides* is assumed to be beneficial to many other sandhill endemics. Therefore, my larger goal is to develop from demographic parameters a model of population dynamics at varying fire-frequencies in order to guide a management regime of controlled burning.

In this demographic study, I employ both short-term data collection (censuses for 3 years) and long-term growth estimates based on age-size relationships to estimate population parameters for subsequent demographic modelling. I also incorporate Geographic Information Systems (GIS) approaches in order to map and quantify neighborhood effects. In a companion study, I incorporate parameters developed from these analyses into a spatially explicit individual-based simulation model to explore the effects of fire-frequency on population dynamics of *C. ericoides*.

Size of individual plant is often reported as a key correlate of plant survivorship and fecundity (Hutchings 1997). Size often strongly predicts reproductive status (juvenile or adult), fecundity, and likelihood of survival. In addition, factors influencing demographic processes in plants include not only temporal variability in climate and rainfall, but also the effects of spatial variability. Spatial effects can result from intra- and interspecific competition as well as facilitation by neighboring plants. As an additional spatial effect, pollen limitation can introduce positive density dependence or Allee effects (Davis et al. 2004, Koenig and Ashley 2003). Both pollen and seed dispersal limitation have the ability to slow colonization and population growth. For these reasons, realistic demographic models for long-lived woody plants often require that the effects of dispersal, density and perhaps other spatial variables on mortality and fecundity be considered.

Many state variables extrinsic to the individual plant such as intraspecific density, proximity of interspecific neighbors, and impact of disturbance and climatic patterns may have strong effects on individual plant survivorship, growth, and fecundity. In the *Ceratiola*/sandhill system, *Pinus palustris* (longleaf pine) produces a highly combustible litter which promotes fire (Glitzenstein et al. 1995). Therefore, distance from individual shrub to nearest *P. palustris* is a state variable of potential importance in predicting survivorship of *C. ericoides* shrubs on burned sites, as is intraspecific density. The effect of proximity to nearest male, hypothesized to be a factor limiting realized female fecundity in this wind-pollinated dioecious species (Davis et al. 2004, Koenig and Ashley 2003) also has the potential to influence population dynamics.

Size of shrub, distance from neighbourhood indices and rainfall were used to predict survivorship in fire and non-fire years. Size of shrub, distance from nearest male, and rainfall were used to predict the probability of a female having any recruits in a given year. These same predictors were used to model the number of recruits for females with at least one recruit. In addition to the demography of living plants, seed bank longevity of dead females was investigated at burned and unburned sites. Because in all cases the data consist of repeated measures of individual shrubs, individual shrub was used as the unit of observation to model the effect of size and spatial/environmental variables on fecundity and mortality. To account for random effect of individual shrub and site plus the fixed effects of state variables (diameter, distance from nearest male, distance from nearest *P. palustris*, rainfall), Bayesian and hierarchical Bayesian statistical modelling approaches were employed.

Methods

Study species--*Ceratiola ericoides* (Empetraceae) Michx. is a wind-pollinated, evergreen shrub. In mature plants, a flower is borne in each leaf axil of the previous year's growth. *C. ericoides* has a whorled branching pattern with the main unshaded branches producing new shoots once a year, therefore shrubs can be aged nondestructively by counting the nodes on the main branches. The fruits of *C. ericoides* are apparently dispersed by vertebrates but some birds, such as the towhee (*Pipilo erythrophthalmus*), are known to consume and destroy them. Ants (*Pogonmyrmex* spp.) have also been observed to collect and consume the fruits of *C. ericoides* (Johnson 1982). *C. ericoides* is atypical of woody species adapated to xeric environments of the Southeast in being a flammable, highly aromatic, obligate reseeder. *C. ericoides* forms a persistent seed bank. Seeds have been reported to germinate from seed banks formed beneath female shrubs up to 8 years after parent plants have been destroyed by fire (Ken Boyd, Environmental Officer, Fort Gordon, pers. comm.). *C. ericoides* occurs within sandy habitats throughout Florida, west to Mississippi, and north to South Carolina.

Study sites--The study was carried out in Georgia (U.S.A.). Individual study sites were located in the Coastal Plain physiographic province in sandhill habitats occurring within two distinct sub-provinces (Fig.1). One population was mapped at Fort Gordon which is located within the Fall Line sandhills, a formation of remnant dunes which marked the Atlantic shoreline during the Miocene epoch (Ivester and Leigh 2003). The two other populations mapped were at the state of Georgia-owned Ohoopee Dunes Natural Area and on private land near Cobbtown. Both populations were located on riverine sandhills along the Ohoopee River in southeastern Georgia. A central contrast between sites is the frequency of fire and time since last burn (Table 1). Both factors are expected to strongly influence *C. ericoides* population dynamics. Sandhills at Fort Gordon have been burned annually since 1970—with fire estimated by site managers to reach the study population approximately every 3 years. Tree ring records from fire-scarred *Quercus laevis* (turkey oak) indicate the most recent fires at the Ohoopee Dunes Natural Area have occurred 16-20 years ago. The fire history of the Cobbtown site is unclear. Based on tree ring data and evidence of recent fires, the site seems to have experienced small-scale fires at short intervals within the last decade. Of the populations mapped, the Ohoopee Dunes population was the largest population mapped completely and the only population available for study which spanned a topographic gradient from floodplain to upper dune.

Field mapping--During the summer of 2002 (Ohoopee Dunes and Cobbtown) and winter of 2003 (Fort Gordon), 1330 shrubs from 3 populations (Table 1) were mapped using a Trimble GeoExplorer 3 GPS (Global Positioning System), and tagged with numeric labels. Subsequently, Trimble Pathfinder software (incorporating data from base-station files) was used to perform differential correction to improve the accuracy of point locations. Trimble advertises 1 m accuracy for differentially corrected data. Comparing deviation of coordinates of GPS-mapped landmarks (roads, large trees) with their locations on rectified aerial photos, digital ortho-quarterquads (DOQQs), I estimate an accuracy of 0.5-1.5 m for shrub locations. GPS mapping was facilitated by the relatively level terrain and the low, open canopy of sandhill vegetation. For the Fort Gordon and Ohoopee Dunes populations, the entire population was mapped with transects placed to include all plants. For Cobbtown, plots were established to roughly encompass several subpopulations. For each population, sex, age, size (height and diameter), age (estimated by node counts), and distance, dbh and species for all trees within a 3 m radius were recorded for each mapped shrub.

Survivorship—Populations at Ohoopee Dunes Natural Area and Cobbtown were originally mapped in the summer of 2002 and recensused during the summers of 2003 and 2004. The Fort Gordon population was originally mapped during the winter of 2003 and recensused during the winters of 2004 and 2005. At Fort Gordon, controlled burns are done every winter across the entire sandhill portion of the installation, yet fuels and, therefore, fires are patchy and discontinuous. The 2003 mapping at Fort Gordon was done after controlled burns had been conducted, yet no evidence of recent burn effects was apparent during the mapping—indicating that fire did not reach the mapped population during that season. Controlled burns carried out in 2004 did reach the Fort Gordon population, and survivorship over the 2003-2004 interval, therefore, reflects increased mortality due to fire. There was no evidence that fire had recently burned through the population during recensus visits in the winter of 2005. Survivorship was modelled using diameter, a second order diameter term (diameter^2), distance to nearest conspecific neighbor, site, and year as dependent variables.

Neighborhood effects on survivorship—Because *Pinus palustris* (longleaf pine) is known to promote the spread of fire on sandhills (Rebertus 1989a and 1989b, Glitzenstein 1995), distance to nearest longleaf pine was also included as a covariate. *C. ericoides* and *P. palustris*. *P. palustris* locations were captured from 1999 DOQQs--orthorectified color infrared aerial NAPP photography which has a 1 meter spatial resolution. As no other species of pine were observed on sandhill sites during fieldwork, all pines evident on air photos were assumed to be *P. palustris*. The evergreen canopies of individual trees, clearly visible on sandhill sites, were digitized as points using Arcview GIS software. Once digitized, *P. palustris* coordinates were compared to *C. ericoides* points at each site to estimate minimum distances from *C. ericoides* to nearest mature *P. palustris*.

Fecundity and recruitment—Because the number of recruits per year was very low on unburned sites, data used to estimate annual fecundity were gathered from several sources. Direct counts of seedlings from recensus data were combined with data inferred from the spatial relationships and age structure of the original mapped data using Arcview GIS software (ESRI 2005). For Ohoopee Dunes and Cobbtown, the nearest neighbor female was found for each juvenile—operationally defined as shrubs with 4 or fewer nodes. Juveniles were assigned to the nearest neighbor female and to a recruitment year (2000-2004) based on age estimates (nodes). Mapped data from Fort Gordon were analyzed in the same way, but restricted to only three recruitment years (2001-2003), because seedling and juvenile plants were much more abundant and potentially high mortality due to fire could confound estimates. For statistical analyses, size (diameter, diameter^2), site, total rainfall in year of recruitment, total rainfall in year previous to recruitment, distance from nearest male, and distance from nearest female were included as explanatory variables during model selection. Reproductive maturity was also modelled by comparing reproductive status (male, female, juvenile) to diameter across all sites.

Recruitment experiments—In order to determine cues to germination in *C. ericoides*, a simple experiment was performed. Ripe fruits were gathered and seeds extracted in September and October 2004. All seeds were scarified using fine sandpaper following the protocol of Ann Johnson at the Florida Natural Heritage Program. Because both smoke and heat are known to stimulate germination in species from pyric communities (Brown and

Botha 2004, Tang et al. 2003, Morris 2000), half of the seeds were soaked in Liquid Smoke, a commercial preparation used in cooking. Liquid Smoke is prepared from a solution of wood smoke combustates, and was, therefore, used to simulate exposure to smoke. The two germination treatments were sown in flats containing a sandy medium, placed in a greenhouse, and watered twice a week.

Seed bank recruitment—To obtain estimates of recruitment from the persistent seed banks beneath dead females at burned sites, data were collected at Fort Gordon (though not within the mapped population where dispersal from living females could confound estimates of recruitment from seedbanks), and a second nearby site where all adults were killed as a result of past controlled burns.

At each site, dead shrubs were identified, and those without recruits assumed to be male. Juveniles within a 3 m radius from the center of each dead shrub were counted and aged by counting nodes. Using these methods, the number of recruits per year following fire was recorded, and size of shrub at time of death was estimated from the radius of the debris shadow. Seed banks were estimated from a small sample (n=25) of dead females. Seedlings were censused 2003-2005.

In order to estimate the contribution of persistent seed banks at unburned sites, a similar census of seedlings and young shrubs was done within a 3 meter radius of dead shrubs (n=50) within a large patch of dead and senescent shrubs at Ohoopee Dunes.

Growth—Annual growth was estimated by analyzing the relationship of diameter in meters (as a measure of size) to node counts for all mapped shrubs. The effects of neighboring shrubs and interspecific neighborhood on growth were investigated in Chapter 2. No significant effect of either intra- or interspecific neighborhood was found.

Dispersal—Dispersal distance was estimated by the simplest model: from a frequency distribution of distances between juveniles and canopy edge of nearest neighbor adult female for mapped data from all three sites. A gamma probability density distribution was fitted to these data.

Rainfall and survivorship/recruitment—Annual rainfall data obtained from National Weather Service climate data stations closest to each study site were included in predictive models for recruitment and survivorship (Table 8).

Statistical analyses

***Bayesian Hierarchical Models.* —** Hierarchical Bayesian methods were employed to perform logistic (probability of survivorship, probability of recruits) and Poisson (number of recruits) GLMs. A central feature of the Bayesian approach is that there are no fixed parameters, but rather every parameter has a probability distribution. The goal of Bayesian statistical analysis is therefore to estimate the probability distributions of the parameters, called posterior distributions. To derive the posterior probability distribution for each parameter of the logistic and Poisson GLMs, a normally distributed prior distribution (which is uninformative since I have no previous results to inform the analyses), and the results of data analysis are combined. In the case of hierarchical models, data from (in this case) different years and sites are used to inform one another.

Because survivorship and recruitment data were gathered for the same plants over multiple years, the data consist of repeated measures so that observations made for the same individual shrubs in different years cannot be assumed to be independent. Repeated measures can be handled by hierarchical Bayesian models which allow the derivation of an aggregate distribution of survivorship or recruitment probabilities and mean number of recruits across sites and years and also allow information from one site and year to help inform estimates at others. The models estimate the background probabilities and means at each site and for each year, but assume that these rates are sampled from a "parent" aggregate distribution.

Survivorship model—Probability of survival of the *i*th female shrub at site *j* in year *k* is denoted by p_{ijk} and modeled as

$$\operatorname{logit} p_{ijk} = \beta_{0jk} + \beta_1 D + \beta_2 D^2 + \beta_3 DLP\text{*fire} + \beta_4 DNC,$$

where β_{0jk} is a random intercept reflecting site by year effects on survivorship, D and D^2 are diameter and diameter^2 (m), $\beta_3 DLP$*fire interaction of site and distance from *P. palustris*, and DNC = distance to nearest conspecific. Rainfall effects were estimated at the site/year level so that β_{0jk} was estimated as a function rainfall (mm) during the year prior to each census.

Recruitment models—Because recruitment data were overdispersed, data was analyzed in a two-step process. First a logistic regression model was used to analyze probability of recruits (presence/absence) for each female. For those females with a least one recruit, number of recruits per female was analyzed using a Poisson regression model.

Recruitment probability of the *i*th female shrub at site *j* in year *k* is denoted by p_{ijk} and modeled as

$$\operatorname{logit} p_{ijk} = \beta_{0jk} + \beta_1 D_{\mathrm{ijk}} + \beta_2 D^2_{\mathrm{ijk}} + \beta_3 DM_{\mathrm{ijk}} + \beta_4 DF_{\mathrm{ijk}},$$

where β_{0jk} is a random intercept reflecting site by rain/year effects on survivorship, D and D^2 are diameter and diameter^2 (m), DM = distance from nearest neighboring male > 1 m in diameter, and DF = distance from nearest neighboring female. Mean number of recruits per female with recruits, μ_{ijk}, was modeled as a Poisson-distributed variable:

$$\ln(\mu_{ijk}) = \beta_{0jk} + \beta_1 D_{\mathrm{ijk}} + \beta_2 D^2_{\mathrm{ijk}} + \beta_3 DM_{\mathrm{ijk}} + \beta_4 DF_{\mathrm{ijk}},$$

For both models rainfall and fire effects were estimated at the site/year level so that β_{0jk} was estimated as a function of rainfall (mm) in the year of recruitment and in the previous year.

Seed germination experiment—Two experiments were performed to test the possible effects of fire and scarification by sand on germination in *C. ericoides*. Fruits were collected in August 2004 and seeds removed from them mechanically. All seeds were then roughed with fine sandpaper (scarified). Half of the scarified seeds were then soaked in Liquid Smoke—a commercial flavoring produced from wood-smoke. Seeds from both treatments were then sown onto flats filled with a sandy medium and watered twice weekly.

Seed bank recruitment—For burned sites, seed bank recruitment beneath dead females was modeled similarly to that of living females with a logistic model of recruitment probability and a Poisson model of mean number of recruits per dead female. Recruitment probability of the *i*th female shrub denoted by p_i and modeled as

$$\operatorname{logit} p_{ij} = \beta_0(i) + \beta_1 Y + \beta_2 D,$$

where $\beta_0(i)$ is the effect of random dead female i, Y is years since death, and D is the diameter (m) or the debris shadow of the dead female. The Poisson model is

$$\log \mu_{ij} = \beta_0(i) + \beta_1 Y + \beta_2 D.$$

Bayesian Growth Model—To model growth, diameter and node data were fitted to a 3 parameter Gompertz curve--an asymptotic growth curve similar to the 2 parameter logistic (Zeger and Harlow 1987). Whereas the logistic curve is constrained to be symmetrical about the point of inflexion, the Gompertz curve is more flexible. The Gompertz equation can also be modified to constrain the lower asymptote to 0 by setting parameter c of the equation to 0.

$$y = c + a(exp(-exp(-b(x - m)))$$

where $a + c$ = upper asymptote, c = lower asymptote, m = point of inflection, b = slope parameter, and x = age (nodes). Because no environmental parameters (neighborhood density of conspecifics or trees) were significant predictors of the relationship between nodes (age) and diameter (Chapter 2), Bayesian analysis was used to estimate distributions for growth parameters without the inclusion of individual shrub neighborhood. Because relatively few large adults exist within the Fort Gordon population, and the Ohoopee Dunes and Cobbtown populations did not significantly differ in node/size relationships, data from all three populations were combined for this analysis.

Parameter estimation using Markov Chain Monte Carlo—Markov Chain Monte Carlo (MCMC) is a simulation procedure that provides a very flexible methodology for statistical modeling. It involves Monte Carlo integration through the generation of a sequence of dependent (Markov chain) samples. The sampled points characterize the joint posterior distribution of the uncertain model parameters, and these points can be analyzed to obtain point estimates (e.g., the mean, median, or mode of the parameter distribution), and to characterize the uncertainty in the estimated parameters (e.g., using the standard deviation of the distribution, or 95% "credible intervals"). The MCMC estimation is implemented in this study using the BUGS (Bayesian inference using Gibbs sampling) software system (Spiegelhalter et al. 2003), with the Metropolis-Hastings or Gibbs sampling method.

Model selection--The model was fit using WinBUGS (Spiegelhalter et al., 1996) version 1.4 and inference based on 50,000 samples after the first 5000 were discarded as burn-in. Convergence of the model on a probability distribution for a given parameter was assessed using trace plots and by running multiple (MCMC) chains from dispersed starting values (Gelman and Rubin 1992). For each coefficient, a posterior probability distribution was determined and a 95% credible interval calculated. For the purposes of model selection, model variables were accepted as significant predictors if variable parameter distributions did not overlap zero.

Results

Summary of* Ceratiola ericoides *demography—*C. ericoides* populations show much higher recruitment and mortality at the frequently burned site (Fort Gordon) than at either of the unburned sites. Whereas shrubs are associated with *P. palustris* on unburned sites, mortality risk is much higher near *P. palustris* when burning occurs. Maximum growth rates and reproductive output for *C. ericoides* occur when individuals are ~3 m in diameter (~15-20 years). Distance from nearest male is an important predictor of female fecundity. Seed banks may persist for more than 10 years. Dispersal—based on distance to nearest female--is highly leptokurtic and short-distance with the bulk of seeds deposited within 10 m from mother plant. Rainfall effects on either mortality or fecundity in *C. ericoides* could not be determined from this short-term data set.

Parameter distributions—Figures accompanying these results provide a graphical representation of the distribution of posterior probability distributions for parameters of each model. The mean and 95 % confidence intervals are provided for all parameters. Excluding random year-site intercept parameters, parameters which overlap zero have not been included in the final models.

Survivorship—In the absence of fire, mortality is low (<5%) in most years, though highest during establishment (< ~10 years, < 1 m diameter) and senescent (> ~ 25 years, 4 m diameter) phases. By contrast, mortality at Fort Gordon following a burn reached 40%. Apparently because fires have been frequent at Fort Gordon, few shrubs exceeded 3.5 m in diameter or ~20 years in age.

The Ohoopee Dunes NA population showed the highest survivorship with greater than 95% survivorship in all census periods. The relatively high mortality of the Cobbtown population during the 2002-2003 census period may be attributable to drought over that period. The much higher mortality at Fort Gordon during the 2003-2004 census period is largely the result of fire from controlled burns set during the winter of 2004 when fires reached this population. Although controlled burning is carried out every year, fires did not reach the Fort Gordon population during 2005 winter burns (Table 3, Figures 2 and 3).

Survivorship increased with distance from *P. palustris* for the Fort Gordon population during a year in which fire reached the population, but showed no significant trend in non-fire years/sites. Distributions with 95% confidence intervals are presented in Table 3 and the parameters of the full model in Table 4a. The effect of intraspecific density was not included in the Bayesian statistical model, because preliminary statistical analyses indicated no relationship between various neighborhood density indices and shrub mortality. Furthermore, a related study (Chapter 2) investigating spatial patterns in *C. ericoides* showed no significant effect of conspecific neighborhood density indices on shrub age-size relationships.

Rainfall effects on survivorship--From existing data, the relationship between survivorship and rainfall could not be determined from this relatively brief temporal data set. Although, the greatest mortality (Cobbtown 2002) coincides with lower than normal rainfall, there is no consistent pattern across sites (Table 3).

Neighborhood effects on survivorship—While survivorship showed a positive relationship with distance from nearest longleaf pine at regularly-burned Fort Gordon, survivorship showed a weaker positive effect at Ohoopee Dunes, and was negatively related to distance at Cobbtown (Table 3). The effect of proximity to longleaf pine on *C. ericoides* mortality was particularly striking at Fort Gordon following a burn in early 2004 (Fig. 4).

Fecundity and recruitment— Over half of plants are reproductive at 0.4 m diameter (Fig. 5). Mean fecundity (recruitment likelihood) increases with size (diameter) up to ~4 meters and then declines thereafter (Table 4a, Fig. 6, Fig. 7). Large females (> 6 m) appear to have relatively low reproductive value. Recruitment likelihood decreased with distance from male shrubs at all sites (Table 4, Fig. 7). A significant site effect was found for recruitment likelihood. Annual recruitment likelihood for females is strikingly higher at Fort Gordon (Fig. 7), probably as a result of fire effects on germination, than at Cobbtown or Ohoopee Dunes. Distance to nearest female was rejected as a significant effect in the logistic model of recruitment likelihood.

Sites show much less differentiation in the number of offspring per recruiting female (Table 4b, Figures 8 and 9) except at Fort Gordon 2001 where much higher recruitment was probably stimulated by burning during the previous year. Temporal variation in recruitment also showed a relatively limited range of variation. Distance to nearest male and female were significant predictors of the mean number of recruits per females with recruits (Fig. 7, Fig. 9). A weaker effect, distance to nearest female had a negative effect on mean number of recruits. Decreasing fecundity with proximity to other females is likely an artefact of the nearest neighbor methods used to calculate fecundity. Because offspring are assigned to the nearest neighboring female, females growing in dense clusters compete for offspring.

Rainfall effects on recruitment--Rainfall, in either year of recruitment or in the year previous, does not appear to be a predictor either of recruitment likelihood or number or recruits given that a female has recruits. Posterior probability distributions of the value of the rainfall effect parameter broadly straddle zero (Table 5a, Figures 6c and 8c)—indicating no significant effect of rainfall on recruitment. Yearly variation in rainfall may account for some of the temporal variation across sites in both recruitment probability and mean number of recruits (Figures 6a and 8a), however a long term data set is needed to establish clear trends. Analyses of the available data suggest that rainfall is far less important in stimulating germination than fire, and that seeds germinate and seedlings establish during most years.

Seed germination experiment—In February 2006, seventeen months after seeds were sown, the smoke-treated seeds had germinated in large numbers in greenhouse flats. By contrast, none of the scarified, but not smoke-treated, seeds had germinated. Smoke and, secondarily, day-length—promoting late winter/early spring emergence--appear to cue germination in *C. ericoides*.

Seed bank recruitment— Both dead female diameter and years since death appear to be predictors of both likelihood of recruitment from seed bank and mean number of recruits from seed bank annually. For recruitment from seed banks at burned sites, parameter estimates for logistic and Poisson recruitment parameters are broad reflecting the paucity and variation with the available data (Table 6 and Figures 10 and 11). Predicted values (Fig. 11) of both recruitment likelihood and number of recruits are much higher for seed banks than for living females of similar size.

Recruitment from seed banks at Cobbtown and Ohoopee Dunes, where major fires have been absent for at least a decade, is negligible. Only one of 63 dead shrubs (sex and time since shrub death unknown) located and surveyed for seedlings had a seedling or juvenile within a 3 m potential seed shadow.

Growth— Mean diameter value for upper growth asymptote across all sites was 4.41 m (Fig. 12, Table 7), and average growth rates were highest in shrubs ~2 m in diameter. A Gompertz curve fitted to age/size (nodes/diameter) data shows a point of inflection (where growth rates are maximal) at age 10 (Fig. 13). Distributions (point estimates and 95 % confidence intervals) for Bayesian estimation of Gompertz growth parameters from node-diameter data are constrained within relatively narrow limits (Fig. 12).

Dispersal—Dispersal distance was estimated from a frequency distribution of distances between juveniles and canopy edge of nearest neighbor adult female for mapped data from all three sites. A gamma probability density distribution was fit to these data (Fig. 14). This model suggests a highly leptokurtic dispersal kernel. Most dispersal is short-distance (< 10 m).

Discussion

***Survivorship and neighborhood effects*--**At infrequently burned sites (Cobbtown and Ohoopee Dunes), individual *C. ericoides* shrubs are associated with *P. palustris* trees, and *C. ericoides* mortality increases with minimum distance from *P. palustris* tree. (Because it straddles zero and has a very broad probability distribution, the estimate of the effect of *P. palustris* on *C. ericoides* mortality at unburned sites and non-burn years at Fort Gordon (Fig. 3c) cannot be interpreted as significantly positive or negative. Unlike either Fort Gordon or Cobbtown, mortality at Ohoopee Dunes was extremely low in both years surveyed.) At Fort Gordon, mortality of *C. ericoides* decreases with distance from *P. palustris* due to the flammable nature of *P. palustris* litter reported by Rebertus (1989a, 1989b) and Glitzenstein (1995).

Although density-dependent effects on growth and mortality are frequently reported for plant populations and populations of sessile organisms generally, analyses of these data did not reveal any significant effect of density on either growth or survivorship in *C. ericoides*. Although clumped in their distribution, *C. ericoides* shrubs occur at a low enough density that growth and survivorship do not appear to be significantly constrained by density-dependent effects. The lack of density-dependent effects on mortality follows from the relatively low densities of the shrubs, and from high seedling mortality during the establishment phase. Seedling mortality is high in some years, but does not appear to be strongly density dependent. The data suggests that younger plants experienced higher mortality at Fort Gordon, in part, because they were more likely to be growing in more fire-prone zones near *P. palustris*.

***Fecundity, recruitment: Allee effects and fire*—**The relationship between realized female fecundity and size—likelihood of recruits increases with size up to 3 m in diameter then declines--suggests that reproductive value of female shrubs > 3 m declines steadily with age. A diameter of 3 m corresponds to an average age of 18 years (Fig. 13) when shrubs begin to senesce consistent with the life-history strategy of a fire-sensitive, woody species of the pyric sandhill community (Menges and Kohfeldt 1995).

Recruitment likelihood also increases with proximity of female shrubs to males. Although wind-pollinated plants have in the past been considered less subject to pollen limitation, recent studies have demonstrated that even bisexual, wind-pollinated tree species are frequently limited in their fecundity by pollen availability (Koenig and Ashley 2003, Davis et al. 2004). Concordant with these findings, *C. ericoides* fecundity appears to be pollen-limited at all sites. Mean likelihood of producing recruits decreases by half for females isolated by 50 m from the nearest male.

Evidence from experiments I conducted suggests that *C. ericoides* seeds germinate in response to smoke as a trigger. The very large difference in fecundity between Fort Gordon and the other sites, therefore, reflects the effect of fire on seed germination. Fire-stimulated seed germination has been reported for a variety of fire-adapted South African fynbos species, and species in the Asteraceae, Ericaceae, Proteaceae and Restionaceae have all shown a germination response to smoke and/or aqueous smoke extracts (Brown and Botha 2004). Smoke treatment increased seed germination of seven Australian species of *Grevillea* (Proteaceae) (Morris 2000). Brown et al. (1994) report increases in seed germination following smoke treatment in species of the South African Restoniaceae family of 147-25300%.

Despite the importance of fire in stimulating germination in *C. ericoides*, some germination is clearly possible in the absence of fire given the low, but continuous recruitment recorded at long-unburned sites. Interannual variation in recruitment may also be related to increased fruit production or higher seedling survivorship as a result of increased rainfall in spring and summer of the survey year and/or the year preceeding, however, no trend could be detected from this data set which spans only 6 seasons.

Seed bank recruitment—Results concur with estimates of seed bank longevity reported by researchers in Florida (Gibson and Menges 1994, Johnson 1982) who estimate that for inland populations of *C. ericoides* (which experienced stand-replacing fires historically unlike Florida coastal dune populations) most recruitment occurs within 10 years following a major fire. Smoke as an environmental trigger to germination synchronizes seedling emergence with post-fire conditions--a more open canopy and greater nutrient availability (Anderson and Menges 1997)—thus optimizing seedling establishment.

At unburned sites where recruitment levels are low generally, seedling recruitment from persistent seed banks appears to be negligible. Even though the data suggest that persistent seed banks are present beneath dead females at unburned sites, apparently the absence of a strong environmental trigger to germination from smoke results in extremely low rates of germination as the viability of seeds within these seed banks decays over time.

Seed bank recruitment was estimated from a small sample (n = 25) of females which had been killed by fire. As estimates of overall rates of recruitment, these values may be inflated for several reasons: 1) female shrubs were identified only after the burn; 2) debris shadows with no recruits were assumed to be those of male shrubs, when many may have belonged to females; 3) size of female was estimated from debris shadows thus potentially introducing significant error. (If, as a result of fire, debris shadows were reduced, then the original size of the parent plant would have been overestimated.); and 4) the range of size estimates was narrow (1-4 m) relative to the size range recorded for living female shrubs (0.5-6.6 m).

Dispersal—As a model of the data to be used for simulating population dynamics, this distribution (Fig. 14) has several advantages: 1) it is convex at the source, reflecting increased dispersal or establishment at a minimum distance (~ 2 m) from the parent shrub, and 2) is highly leptokurtic with 90% of recruits establishing within a 10 m distance of the mother plant, consistent with the mapped data in which juveniles are highly clumped around females.

Because recruits were assigned to the nearest mature female, the resulting gamma probability density distribution of dispersal distances probably underestimates the true distribution. A limitation of this method is the width of the tail of the probability distribution in that realistic estimates of the likelihood of long-distance dispersal events are not captured (Clark et al. 1999). However, this model is adequate for estimating dispersal within a discrete island of sandhill habitat.

Growth—Findings from the growth model reinforce those of survivorship and fecundity: growth rates are already declining by age 25 when fecundity and survivorship begin to decline. Interestingly, growth rates decrease after age 10 (point of inflection of growth curve) by which time most plants become reproductive. This may reflect a tradeoff (Silvertown et al. 1993) between growth and reproduction.

Because the factors determining age-size patterns are unclear, a Bayesian approach is well-suited to an individual-based model of plant population dynamics where individual shrubs can be randomly assigned growth parameters based on a data-derived distribution of values. In this case, drawing values of a, the upper asymptote of the Gomperz growth curve, from a normal distribution while fixing other parameters at mean values yields a range of growth curves based on the distribution of age-size relationships in the data.

Rainfall and annual variation in survivorship and fecundity—A significant effect of rainfall on yearly survivorship or recruitment was not apparent in this short-term data set. Although the highest mortality, aside from the burn year (2003) at Fort Gordon, was a year (2002) of relatively low rainfall at Cobbtown, similarly low rainfall amounts did not appear to result in higher mortality at either of the other sites. However, the effect on seedling survivorship was not detectable under the current sampling schedule. Seeds germinate February-March and many may die by mid-summer in dry years. Annual rainfall is an important determiner of temporal patterns of recruitment in many arid and semi-arid plant communities (Watson et al. 1997, Wiegand et al. 1995, Burgman and Lamont 1992)—a class within which longleaf pine-turkey oak sandhills arguably belongs. Clearly, a longer term data set is required to understand possible patterns and effects of rainfall and climate, and the likely interactive effects of fire and rainfall on recruitment in this system.

GIS--Gathering the data necessary to develop population parameters was greatly facilitated by the use of GIS-based data-gathering methods. By using GPS to map plants, spatial relationships of individuals were easily measured, analysed and used to develop estimates of realized fecundity and dispersal. Field mapping without the aid of GPS would have, by necessity, limited the area sampled and the size of the data set. The initial mapped data set was further enhanced by overlaying it on recent high-resolution air photos facilitating the incorporation of data on the relationship of *C. ericoides* occurrence to sandhill community patterns. In this study, GIS-based data-gathering methods were an essential complement to field-based methods.

Bayesian statistics—Bayesian statistics provide a useful framework for handling the issue of repeated measures and the resulting non-independence of data points inherent in analysing demographic data (Natarajan and Kass 2000). Of particular utility for demographic studies, are hierarchical Bayesian models which allow data across sites and years to be used to inform parameters for individual sites and years. Perhaps most important for the purposes of this project, Bayesian modelling approaches lend themselves to implementing stochastic simulations by estimating a distribution for a given parameter from which values can be randomly drawn (Buckley et al. 2003, Chapter 3). For example, in a demographic model of *C. ericoides* based on data so far collected, annual variation cannot be readily correlated to climatic variables. Yet, annual variation can be simulated by using prior distributions estimated from the data to draw a random annual variation effect. In this way, more realistic stochastic models can be constructed from relatively limited data sets.

Conclusions

Ceratiola ericoides demography—While survivorship is nearly uniform across age and size classes at unburned sites (Type II curve), at the regularly burned site survivorship is lowest in the juvenile and establishment phase (Type III curve) but increases sharply once shrubs reach 3 m because 1) young plants face high mortality if they germinate within fire-prone zones, 2) the longer plants live, the cumulative risk of fire to survival increases (in order to reach the oldest age classes, plants must survive multiple fire threats), and 3) older, larger shrubs become bigger targets for ignition. Estimated rates of survivorship, growth and fecundity decline from maximum at ~3 m (~20 years) suggesting adaptation to a disturbance frequency of 15-30 years.

As a wind-pollinated, dioecious species which exhibits significant pollen limitation, demographic stochasticity in the form of sex ratio and spatial proximity of male and female shrubs offers an additional constraint to colonization of new sites by *C. ericoides* over those experienced by other fleshy-fruited woody plants with more plastic mating systems. The presence of a persistent seed bank of up to 10 years in a shrub of fire-prone habitats agrees with theoretical studies (Cohen 1966, 1967) which predict that persistent seed banks will be most important to the survival and viability of plant populations in highly variable environments. In the case of *C. ericoides*, seed bank emergence appears to be strongly linked to fire events thus cueing seed germination to mineralization of nutrients and the opening of canopy, and dampening the effect of fire on mortality. In the absence of fire, a persistent seed bank appears to confer little advantage to populations of this fire-adapted shrub.

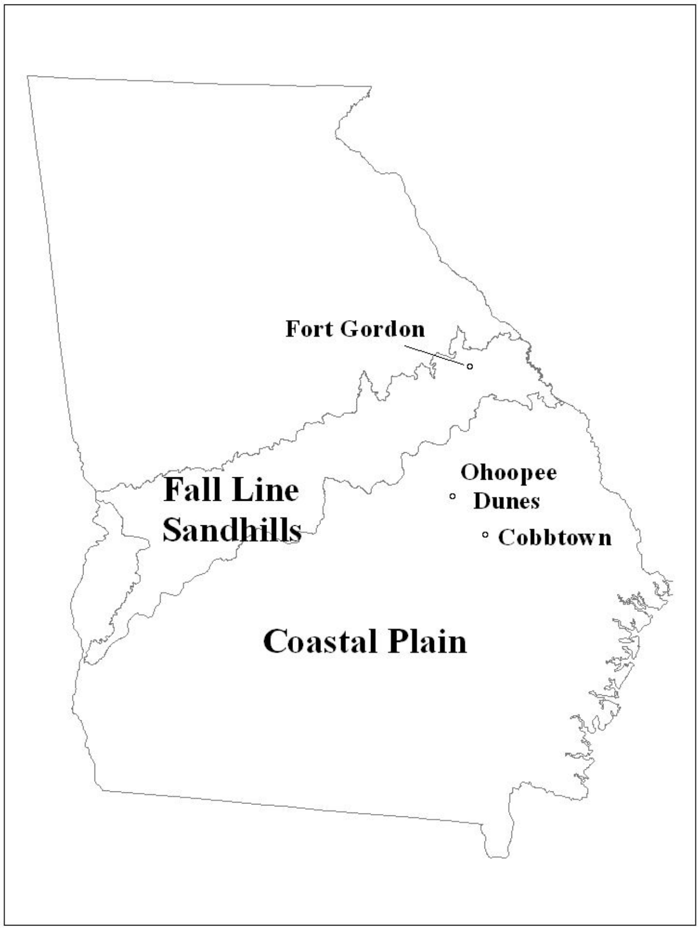


Figure 2.1: Locations of study populations.

Table 2.1: Sites.

	# plants mapped	**fire history**	**location**
Fort Gordon	490	burned every 3 years since 1970	Fall Line
Cobbtown	334	burned within last 10 years	Coastal Plain
Ohoopee Dunes NA	512	last burned 1985-1989	Coastal Plain

Table 2.2. Mapping and recensus schedule.

	2002	**2003**	**2004**	**2005**
Summer	Ohoopee Dunes	Ohoopee Dunes	Ohoopee Dunes	
Summer	Cobbtown	Cobbtown	Cobbtown	
Winter		Fort Gordon	Fort Gordon	Fort Gordon

Table 2.3. Mean and standard deviation in parentheses of parameter values for a logistic regression model of *C. ericoides* survivorship site.

parameter		**mean (95% c.i.)**
$\beta_0$site/year effect	**Fort Gordon 2003**	-0.296 (-0.80, 0.20)
	Fort Gordon 2004	1.01 (0.50, 1.55)
	Cobbtown 2002	1.77 (1.14, 2.43)
	Cobbtown 2003	1.56 (0.98, 2.19)
	Ohoopee Dunes 2002	2.62 (1.77, 3.55)
	Ohoopee Dunes 2003	2.47 (1.65, 3.36)
$\beta_1$diameter		0.88 (0.40,1.38)
$\beta_2$diameter^2		-0.14 (-0.25, -0.02)
$\beta_3$fire*longleaf distance	**fire**	0.018 (0.001, 0.034)
	no fire	-0.004 (-0.019, 0.031)
$betamu_0$*rainfall		0.0017 (-0.010, 0.014)

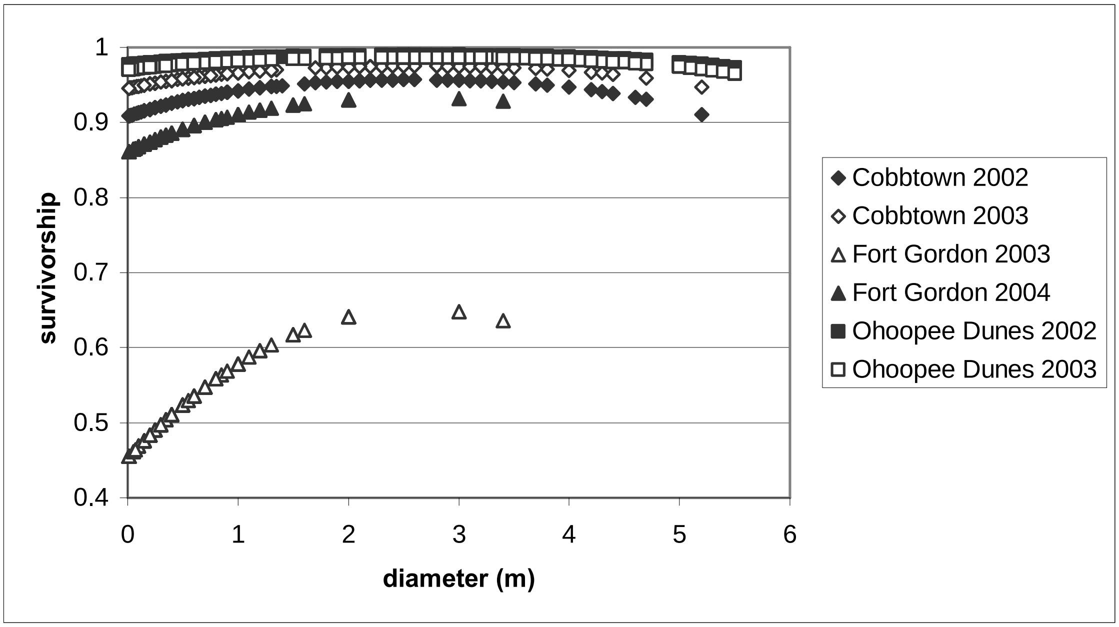


Figure 2.2: Predicted values for a multiple logistic regression model of survivorship by year and site. Only the Cobbtown and Ohoopee Dunes populations were surveyed during 2002, and only the Fort Gordon population has been recensused during 2005.

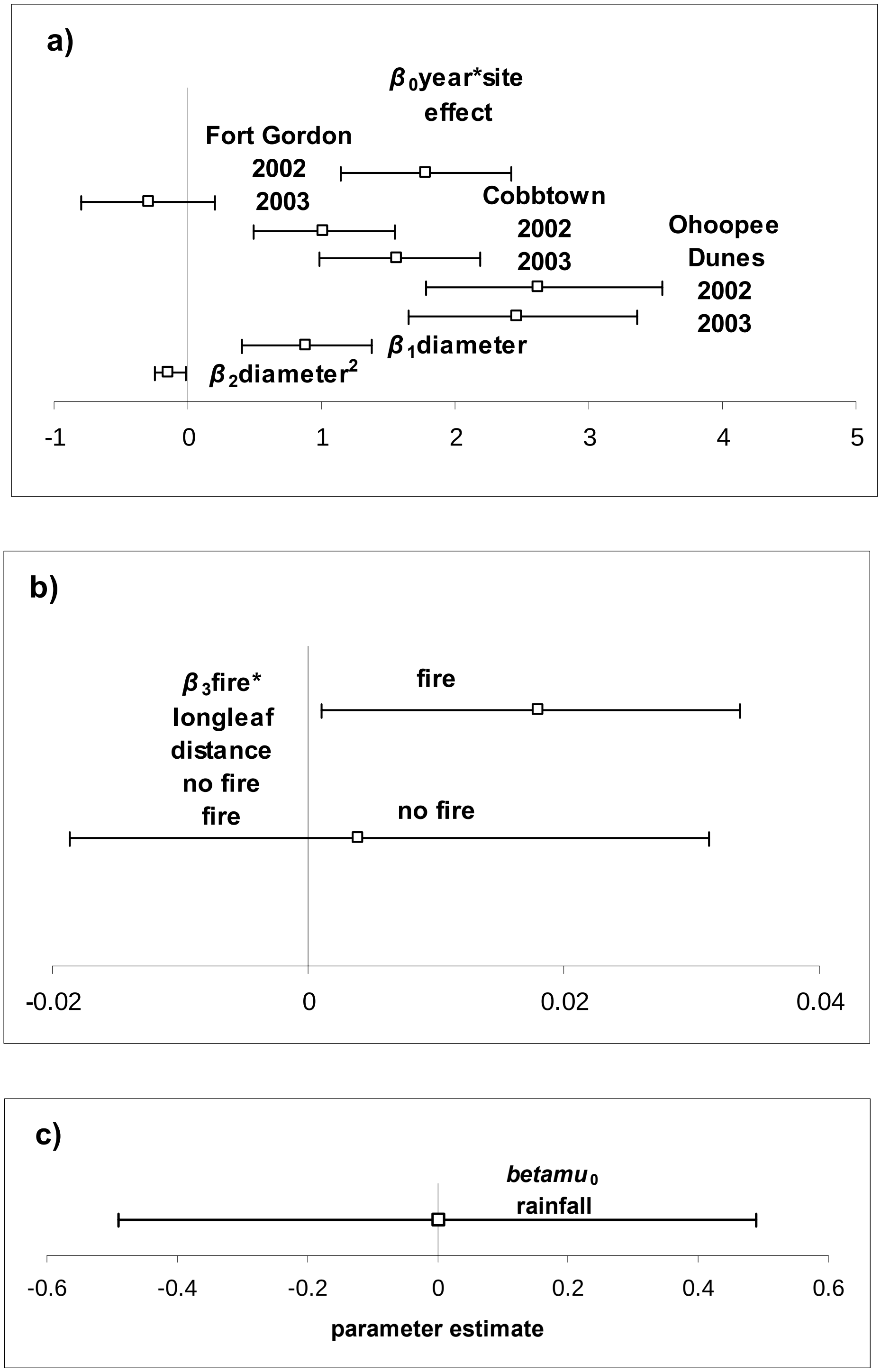


Figure 2.3. Graph of point estimates for mean (□) and 95% confidence intervals for a) site/year parameters; b) size and location parameters; and c) rainfall effect parameters for Bayesian logistic regression of yearly survival likelihood.

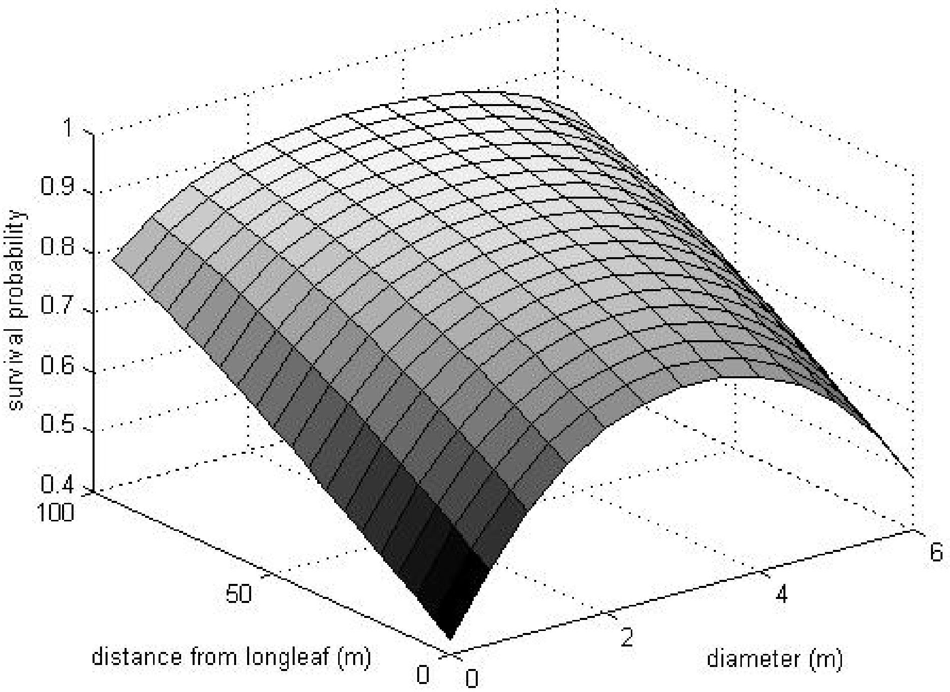


Figure 2.4. Predicted values for survivorship over the sampling interval 2003-2004 at Fort Gordon during which controlled fire reached the survey population.

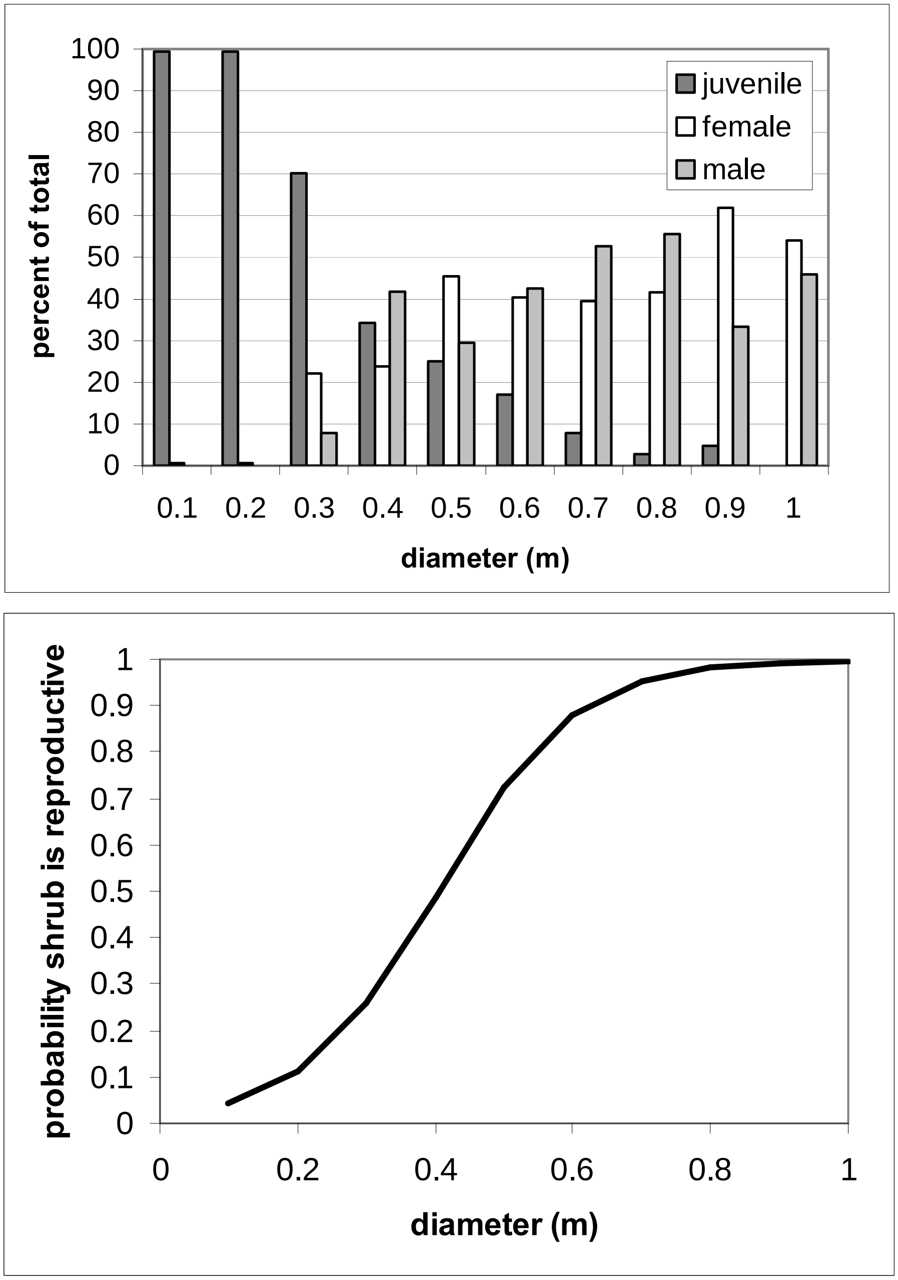


Figure 2.5. Size and reproductive status for shrubs at all sites.

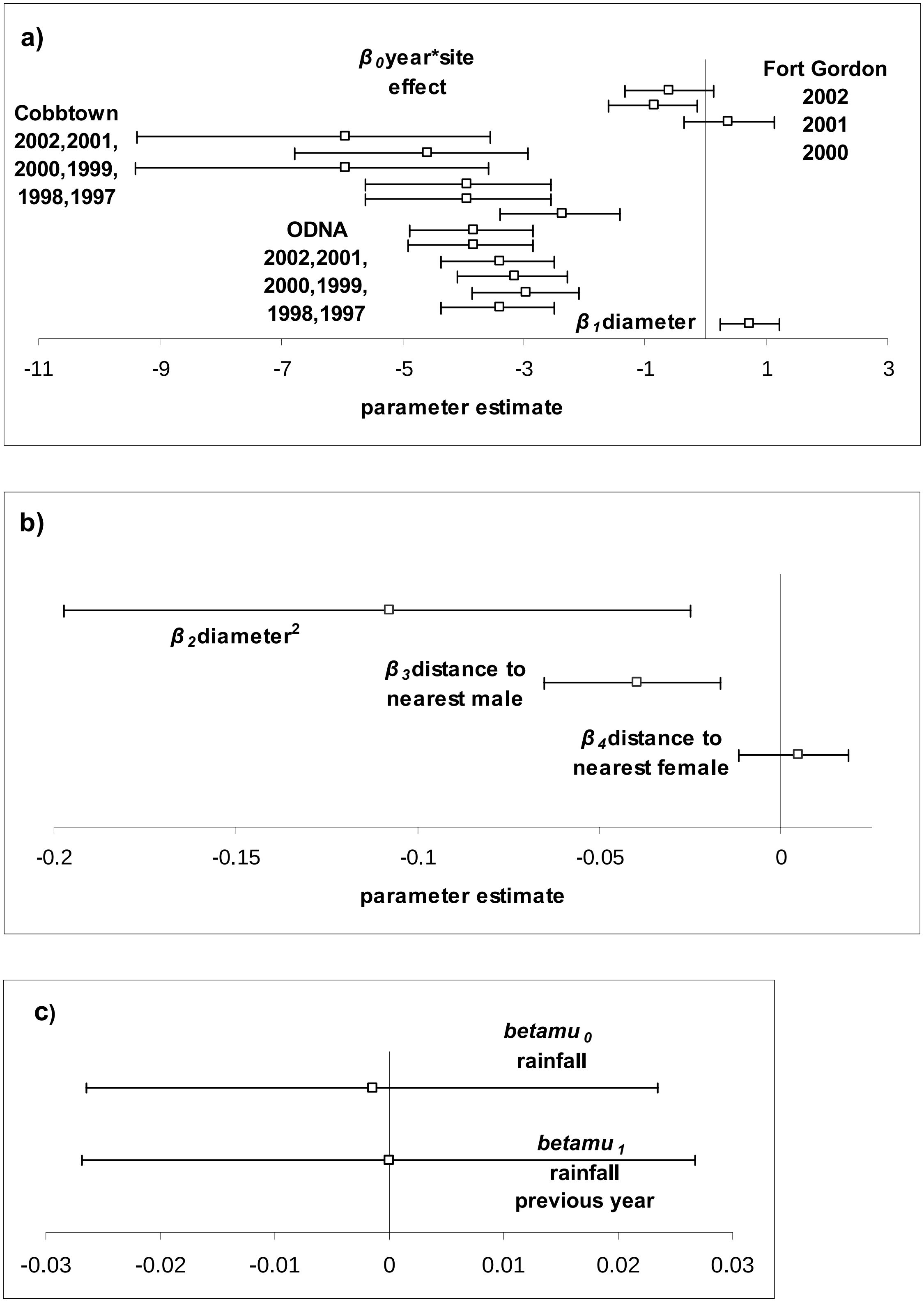
Table 2.4. Point estimates and 95 % Monte Carlo confidence interval estimates (in parentheses) for individual-level parameters of a) Bayesian logistic regression model of probability of female fecundity > 0; and b) Bayesian Poisson regression model of mean number of recruits per reproductive female.

a)	**parameter**		**mean (95% c.i.)**
Logistic regression			
	$\beta_0$site/year effect	**Fort Gordon 2003**	-0.60 (-1.34, 0.12)
		Fort Gordon 2002	-0.86 (-1.60, -0.13)
		Fort Gordon 2001	0.38 (-0.37, 1.14)
		Cobbtown 2002	-5.92 (-9.38, -3.57)
		Cobbtown 2001	-4.58 (-6.77, -2.93)
		Cobbtown 2000	-5.93 (-9.39, -3.60)
		Cobbtown 1999	-3.93 (-5.60, -2.55)
		Cobbtown 1998	-3.93 (-5.60, -2.55)
		Cobbtown 1997	-2.37 (-3.39, -1.41)
		Ohoopee Dunes 2002	-3.83 (-4.89, -2.85)
		Ohoopee Dunes 2001	-3.83 (-4.89, -2.85)
		Ohoopee Dunes 2000	-3.40 (-4.37, -2.49)
		Ohoopee Dunes 1999	-3.16 (-4.82, -2.77)
		Ohoopee Dunes 1998	-2.95 (-4.09, -2.28)
		Ohoopee Dunes 1997	-3.40 (-4.37, -2.49)
	$\beta_1$diameter effect		0.72 (0.24, 1.22)
	$\beta_2$diameter^2		-0.11 (-0.20, -0.02)
	$\beta_3$distance to male (m)		-0.04 (-0.07, -0.02)
	$\beta_4$distance to female (m)		0.005 (-0.01,0.02)
b)			
Poisson regression			
	$\beta_0$site/year	**Fort Gordon 2003**	1.44 (1.11, 1.77)
		Fort Gordon 2002	1.08 (0.71, 1.43)
		Fort Gordon 2001	1.31 (1.00, 3.56)
		Cobbtown-OD 2002	0.25 (-0.53, 0.97)
		Cobbtown-OD 2001	0.85 (0.30, 1.39)
		Cobbtown-OD 2000	0.65 (0.12, 1.16)
		Cobbtown-OD 1999	0.85 (0.34, 1.35)
		Cobbtown-OD 1998	0.60 (0.10, 1.09)
		Cobbtown-OD 1997	0.58 (0.11, 1.04)
	$\beta_1$diameter effect		0.09 (-0.18, 0.37)
	$\beta_2$diameter^2		-0.01 (-0.07, 0.04)
	$\beta_3$distance to male (m)		-0.04 (-0.05, -0.02)
	$\beta_4$distance to female		0.01 (0.003,0.019)

Table 2.5. Point estimates and 95 % Monte Carlo confidence interval estimates (in parentheses) for year-site level rainfall parameters of a) Bayesian logistic regression model of probability of female fecundity > 0; and b) Bayesian Poisson regression model of mean number of recruits per reproductive female.

a)	**parameter**	**mean (95% c.i.)**
Logistic regression		
	***betamu*$_0$*rainfall**	-0.0015 (-0.026,0.023)
	***betamu*$_1$*rainfall previous year**	-0.00004 (-0.027, 0.027)
b)		
Poisson regression		
	***betamu*$_0$*rainfall**	0.0002 (-0.009,0.0095)
	***betamu*$_1$*rainfall previous year**	0.0008 (-0.0094,0.01)

Figure 2.6. Graph of point estimates for mean (□) and 95% confidence intervals for a) site/year parameters; b) size and location parameters; and c) rainfall effect parameters for Bayesian logistic regression of annual female recruitment likelihood.


a)
$\beta_0$year*site effect
Fort Gordon
2002
2001
2000
Cobbtown
2002,2001,
2000,1999,
1998,1997
ODNA
2002,2001,
2000,1999,
1998,1997
$\beta_1$diameter
-11
-9
-7
-5
-3
-1
1
3
parameter estimate
b)
$\beta_2$diameter^2
$\beta_3$distance to nearest male
$\beta_4$distance to nearest female
-0.2
-0.15
-0.1
-0.05
0
parameter estimate
c)
betamu$_0$ rainfall
betamu$_1$ rainfall previous year
-0.03
-0.02
-0.01
0
0.01
0.02
0.03

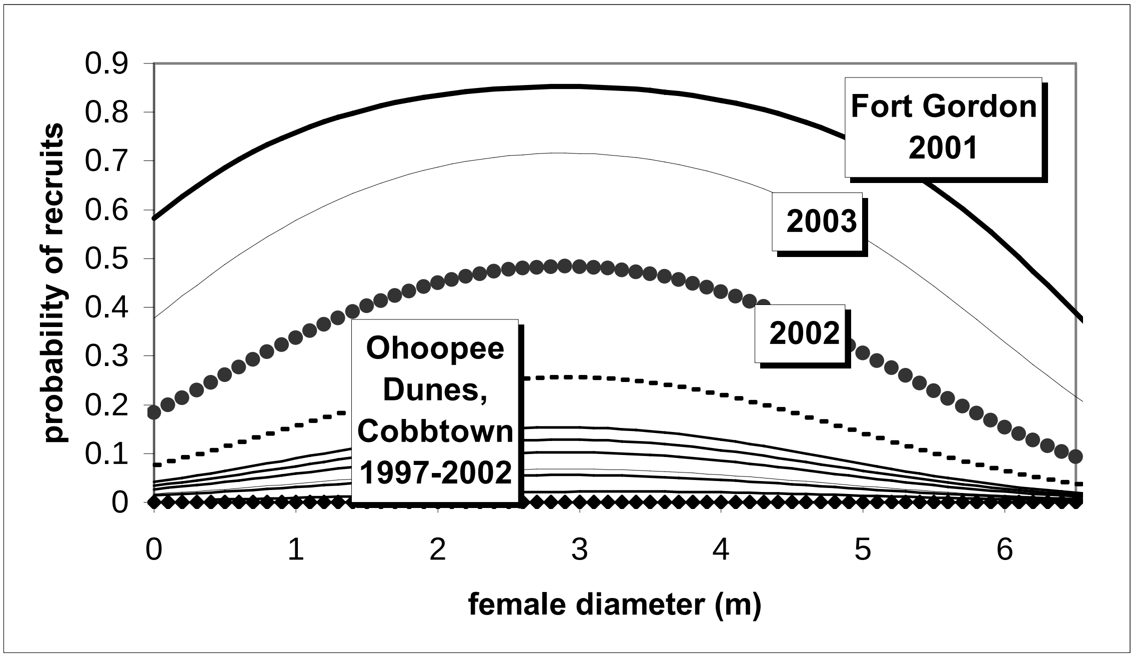
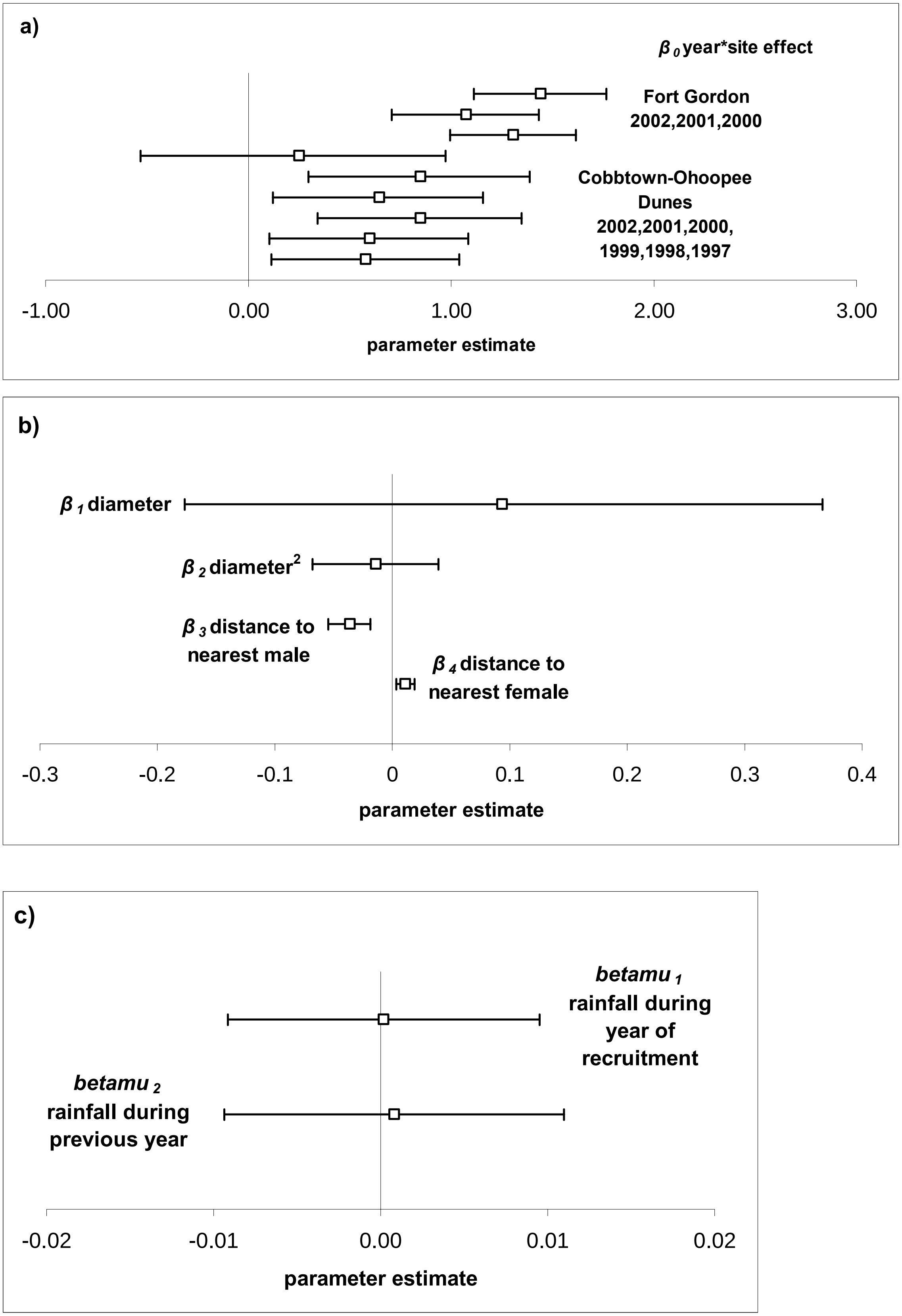


Figure 2.7. Predicted values for likelihood of any recruits/year, given pollen saturation, as a function of female diameter for all sites by year.

Figure 2.8. Graph of point estimates for mean (□) and 95% confidence intervals for a) site/year parameters; b) size and location parameters; and c) rainfall effect parameters for Bayesian Poisson regression of mean number of recruits per females with recruits.


a)
β0 year*site effect
Fort Gordon
2002,2001,2000
Cobbtown-Ohoopee
Dunes
2002,2001,2000,
1999,1998,1997
-1.00
0.00
1.00
2.00
3.00
parameter estimate
b)
β1 diameter
β2 diameter²
β3 distance to
nearest male
β4 distance to
nearest female
-0.3
-0.2
-0.1
0
0.1
0.2
0.3
0.4
parameter estimate
c)
betamu1
rainfall during
year of
recruitment
betamu2
rainfall during
previous year
-0.02
-0.01
0.00
0.01
0.02
parameter estimate

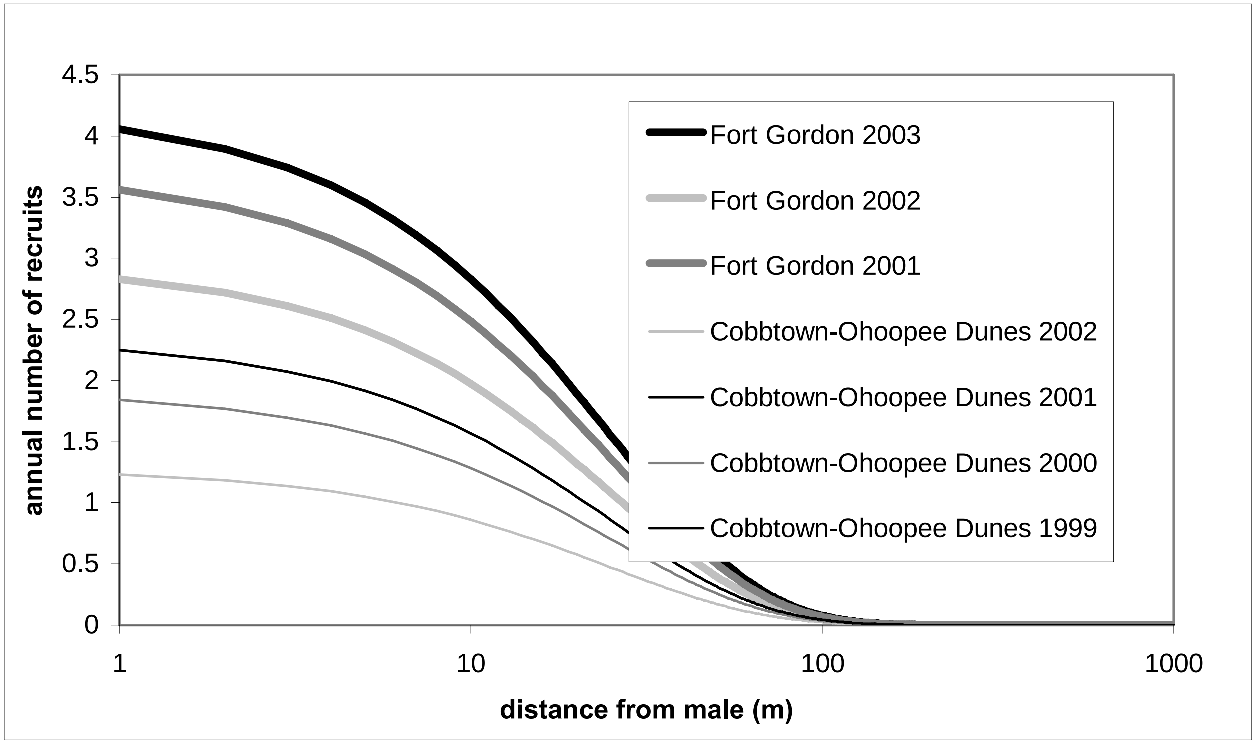


Figure 2.9. Predicted values for a Bayesian Poisson GLM of recruits/female for all females with recruits > 0 as a function of distance from male.

Table 2.6. Point estimates and 95 % confidence interval estimates (in parentheses) for a) Bayesian logistic regression of likelihood of recruitment from seedbank; and b) Bayesian Poisson regression of mean number of recruits per females (dead) with recruits. Parameters are years since death of female and estimated diameter of female.

	parameter	**mean (95% c.i.)**
a)		
	$\beta_1$years	-0.273 (-0.455, -0.101)
	$\beta_2$diameter	0.523 (0.10, 0.965)
b)		0.585 (0.37, 0.796)
	$\beta_1$years	-0.084 (-0.2, -0.015)
	$\beta_2$diameter	0.585 (0.37, 0.796)

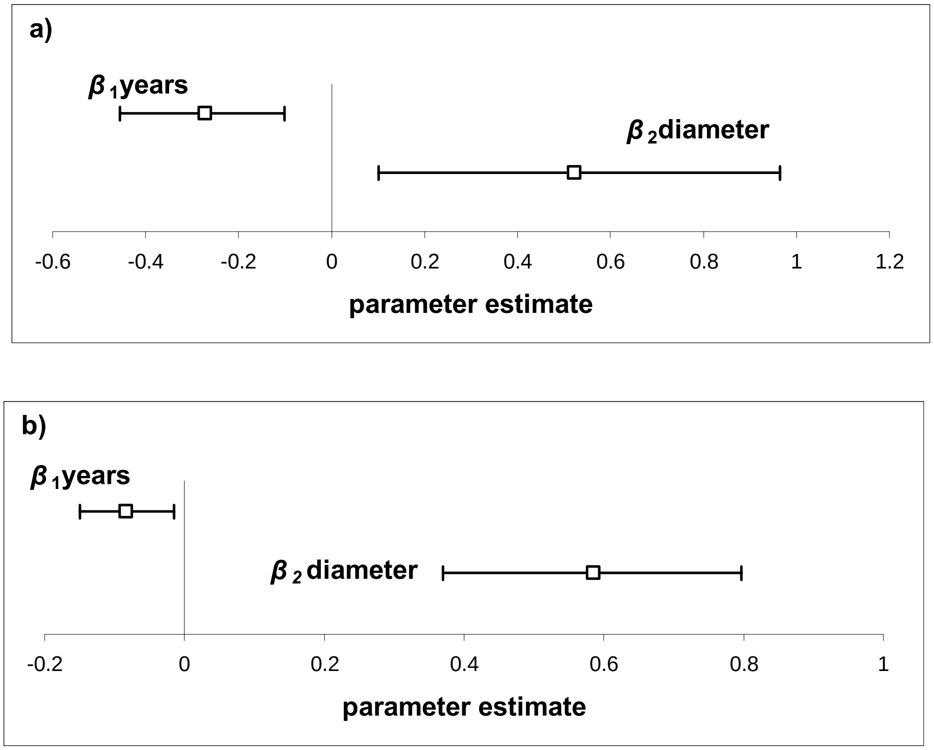


Figure 2.10. Graph of point estimates for mean (□) and 95% confidence intervals for a) Bayesian logistic regression of likelihood of recruitment from seedbank; and b) for Bayesian Poisson regression of mean number of recruits per females (dead) with recruits. Parameters are years since death of female and estimated diameter of female.

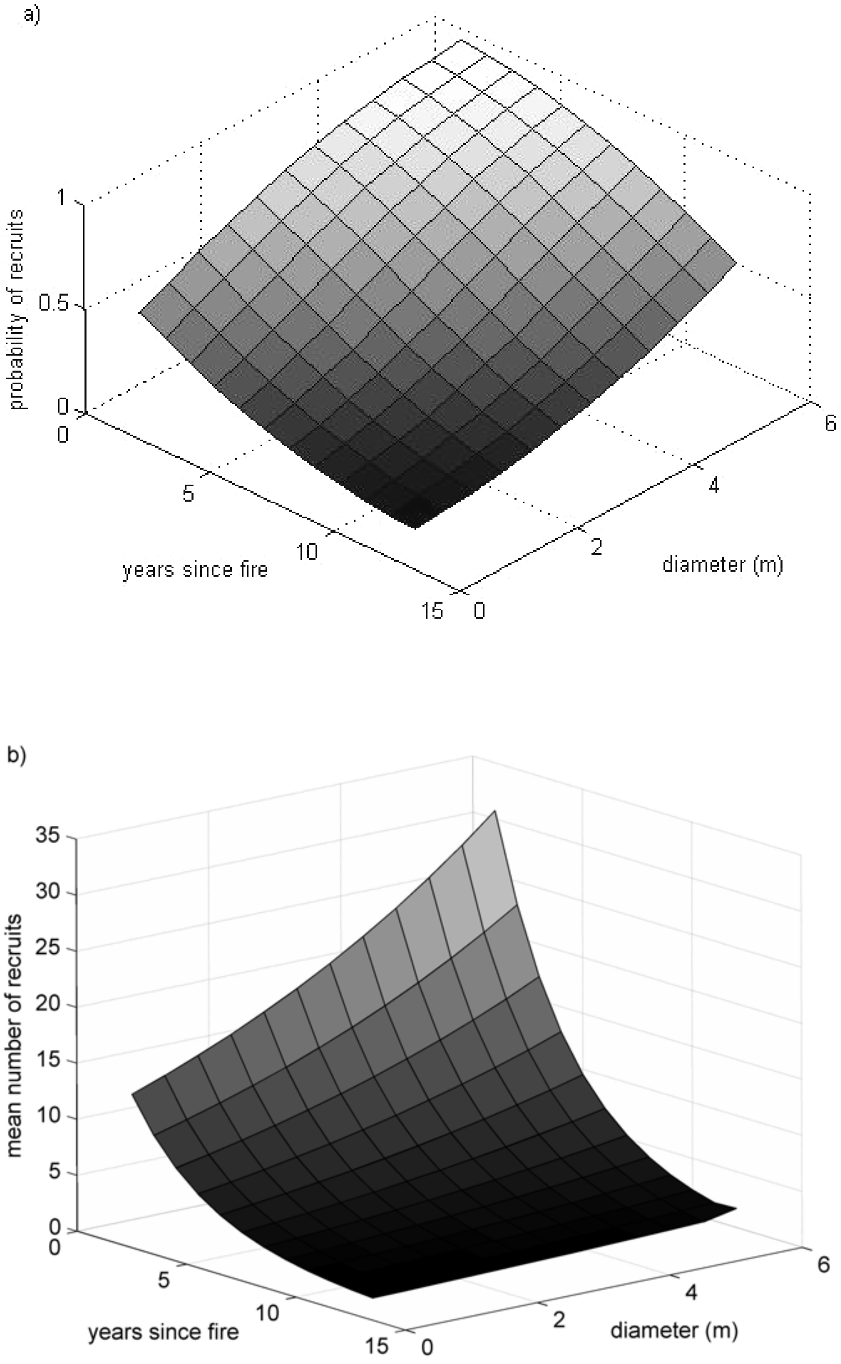


Figure 2.11. Predicted values for recruitment from seedbank as a function of years since death of female shrub and female diameter: a) logistic model of recruitment likelihood; and b) Poisson regression of mean number of recruits.

Table 2.7. Point estimates and 95 % confidence interval estimates (in parentheses) for Bayesian estimation of Gompertz growth parameters from node-diameter data.

growth parameter	**mean (95% c.i.)**
a (upper asymptote)	4.41 (4.17, 4.67)
b (slope)	0.16 (0.14, 0.17)
m (point of inflection)	11.37 (10.86, 11.93)

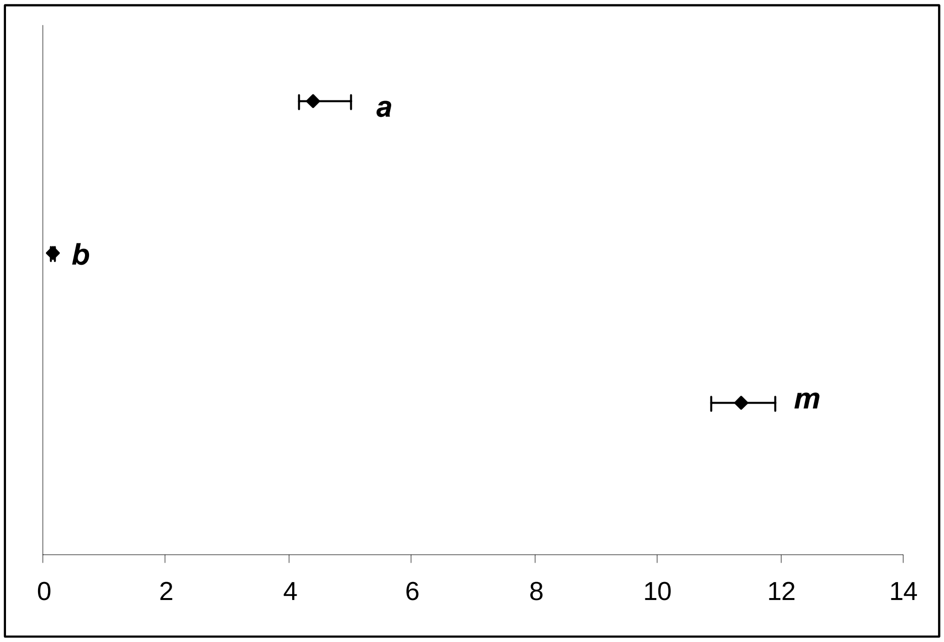


Figure 2.12. Graph of point estimates and 95 % confidence interval estimates (in parentheses) for Bayesian estimation of Gompertz growth parameters from node-diameter data.

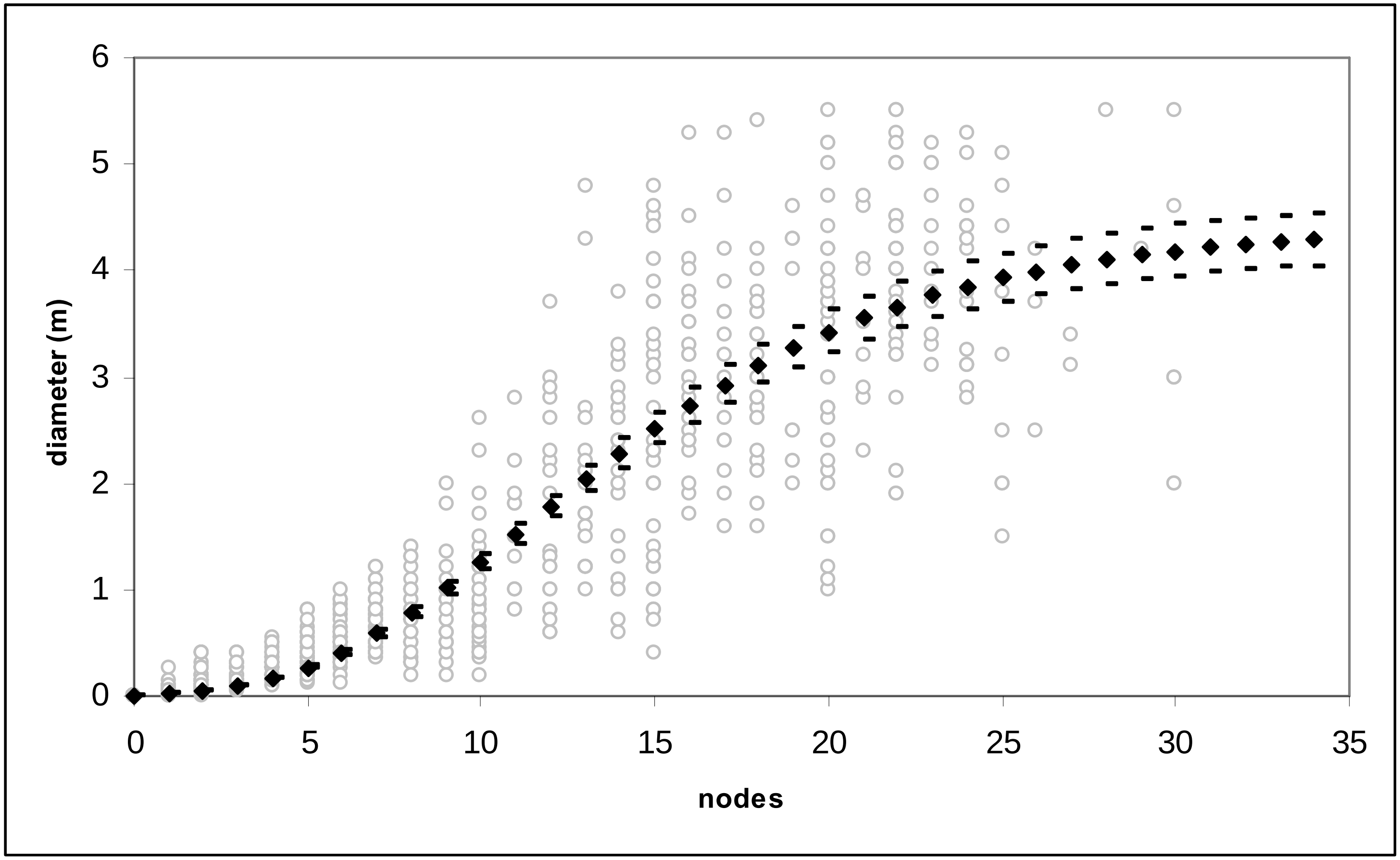


Figure 2.13. Gompertz curve relating nodes to diameter for growth data across sites. Dashed lines represent mean + or – 2 standard deviations of *a*, the upper assymptote.

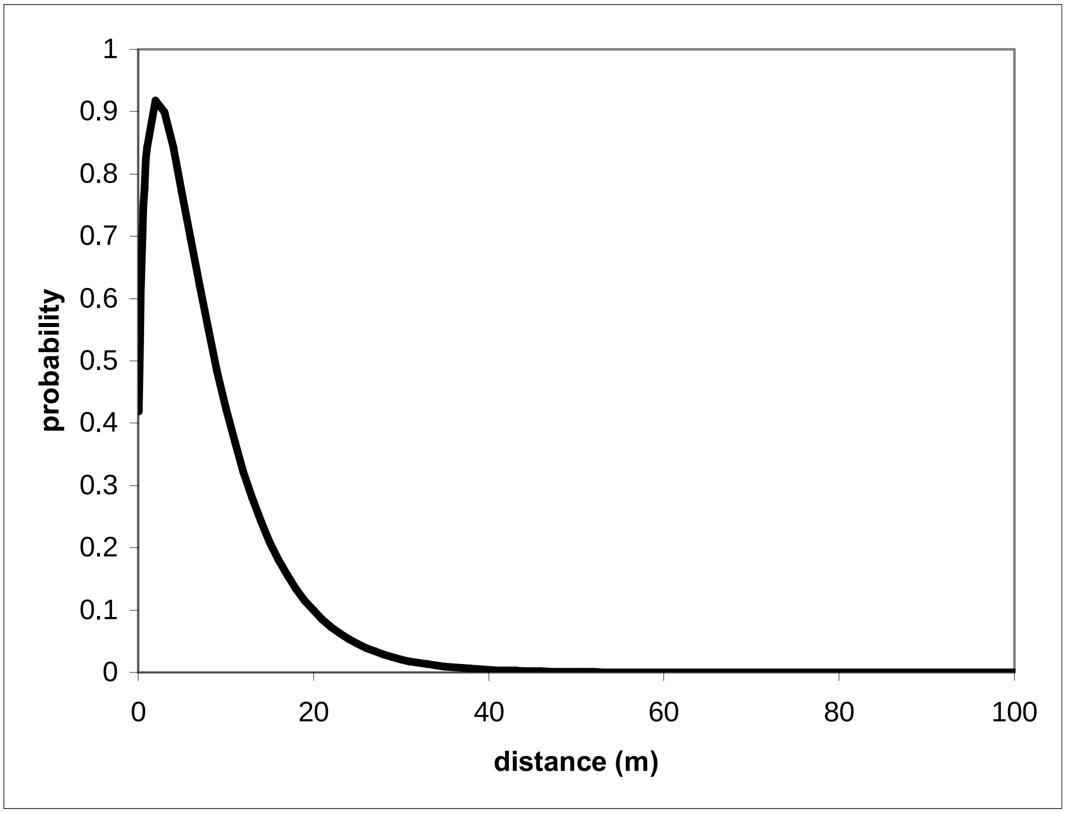


Figure 2.14. Gamma probability density distribution of dispersal distance (from female shrub canopy edge) derived from juvenile to female nearest neighbor distances.

Table 2.8. Annual rainfall by site and year from nearest National Weather Service stations.

site	year	rainfall (mm)	weather station	distance
Fort Gordon	2004	1219.2	August, Georgia	34.0
Fort Gordon	2003	1524	August, Georgia	34.0
Fort Gordon	2002	1031.7	August, Georgia	34.0
Fort Gordon	2001	852.2	August, Georgia	34.0
Fort Gordon	2000	961.4	August, Georgia	34.0
Fort Gordon	1999	933.2	August, Georgia	34.0
Fort Gordon	1998	1215.1	August, Georgia	34.0
Fort Gordon	1997	1278.9	August, Georgia	34.0
Cobbtown	2003	1524	Stillmore, Georgia	5.7
Cobbtown	2002	1219.2	Stillmore, Georgia	5.7
Cobbtown	2000	1080	Stillmore, Georgia	5.7
Cobbtown	2001	922.5	Stillmore, Georgia	5.7
Cobbtown	1999	980.9	Stillmore, Georgia	5.7
Cobbtown	1998	1228.9	Stillmore, Georgia	5.7
Cobbtown	1997	1469.6	Stillmore, Georgia	5.7
Ohoopee	2003	1625.6	Swainsboro, Georgia	12.6
Ohoopee	2002	1320.8	Swainsboro, Georgia	12.6
Ohoopee	2001	1117.6	Swainsboro, Georgia	12.6
Ohoopee	2000	1117.6	Swainsboro, Georgia	12.6
Ohoopee	1999	1062.7	Swainsboro, Georgia	12.6
Ohoopee	1998	994.4	Swainsboro, Georgia	12.6
Ohoopee	1997	1102.9	Swainsboro, Georgia	12.6

CHAPTER 4

OPTIMAL FIRE MANAGEMENT FOR A SANDHILL ENDEMIC SHRUB, *CERATIOLA ERICOIDES*: AN INDIVIDUAL-BASED MODELING APPROACH

Introduction

Appropriate fire and controlled burning regimes are a major topic of management concern on conservation reserves in many plant community types within the Coastal Plain region of the southeastern United States. Although fire is understood as central to the dynamics of communities within the region, developing and implementing a fire management program on many sites is hampered by several concerns: 1) an incomplete understanding of historic fire regimes and the respective roles of natural versus anthropogenic fire, 2) a history fire of suppression which has dramatically altered the density and composition of vegetation at many sites, 3) fear of disturbing remnant populations of locally or regionally rare species, and 4) liabilities associated with controlled burning that limit opportunities for prescribed burns to winter and early spring (Reinhart and Menges 2004, Heuberger and Putz 2003, Glitzenstein et al. 1995, Rebertus et al. 1989a, Myers and White 1987).

Developing models to predict an optimal fire regime with respect to 1) population growth rates of individual species of concern or 2) a patchwork of community types promoting species diversity has been a particular focus of conservation scientists working in Mediterranean environments in Australia and South Africa. Two factors--the role of stochastic episodic events, whether in the form of rainfall, fire or their interaction, and the effects of space or neighborhood interactions--present inherent challenges to population modeling within arid and/or fire-maintained vegetation types. As a result, a variety of modeling approaches have been employed. Among these are spatially explicit, individual-based simulations (IBMs), discrete space cellular automata (Bradstock et al. 1998, Wiegand et al. 1995), other individual-based models (McCarthy et al. 2001), as well as matrix model approaches (Wiegand et al. 2004, Gross et al. 1998, Watson et al. 1997, Burgman and Lamont 1992). Because of the strong spatial dependencies usually present in fire-prone environments, spatially explicit IBMs are increasingly favored since their implementation has been facilitated by the computational power now available to many researchers.

In this paper I present the results of a spatially explicit, continuous space IBM used to predict an optimal fire regime for a dioecious shrub, *Ceratiola ericoides*, endemic to xeric sand environments within the Southeast characterized by sterile soils, drought, and, historically, by periodic fire. *C. ericoides*, a long-lived shrub which commonly occurs on sandhill sites, is not resistant to fire (only very rarely resprouting) and, following fire, reestablishes only by seed (Johnson 1982). However, fire also stimulates germination in *C. ericoides* (Chapter 4, Gibson and Menges 1994). Because *C. ericoides* demography is sensitive to fire frequency, my goal is to develop a model of population dynamics at varying fire-frequencies in order to guide a management regime of controlled burning. A fire regime that promotes long-term persistence of *C. ericoides* is assumed to be beneficial to many other sandhill endemics.

Methods

CONSTRUCTION OF THE IBM

The statistical analyses described in Chapter 3 provided the functions and parameter estimates for each of the plant demographic processes modeled: growth, survival, probability of recruits from living females and from the seedbank, and number of recruits from living females and from the seedbank. Results from Bayesian statistical analyses of field data also provide parameters for the effects of distance from longleaf pine on survivorship and distance from male on female fecundity. Sub-models for each of these individual plant processes were used in an IBM to create virtual plant populations where each plant was configured separately and followed through growth, reproduction and survival trajectories according to a flow diagram (Figure 1). The model has an annual time-step. The code for the IBM was written in Matlab.

The model is stochastic in that probabilities of survivorship, of juveniles achieving reproductive status, and of females and seedbanks producing recruits are generated by a logistic function (binomial distribution). The resulting probability is compared to a random number, and if the random number < P, the plant survives, is reproductive, or the plant produces recruits. The number of recruits given that a living or dead female (seedbank) produces recruits is generated as a Poisson random variable with mean determined by the sub-model function. Growth was modeled stochastically by including a normally distributed random variable that describes the upper growth asymptote of the Gompertz model which determines the growth trajectory of individual shrubs. Stochastic spatial variation is implemented by the dispersal sub-model. Dispersal distance was generated as a gamma random variable with parameters derived from a gamma probability distribution function derived from empirical data (Chapter 3).

Stochastic temporal variation in survivorship was modeled as a random year-site intercept drawn from the distributions of annual variation generated from results of Bayesian logistic regression of survivorship in Chapter 3. Specifically, for either fire or non-fire years, a mean for the year-specific intercept was randomly generated from a normally distributed parent distribution derived from the data. A final value for year-site intercept was then randomly generated using the above mean and a variance derived from the distribution of individual year-site parameters produced from the hierarchical Bayesian model employed in Chapter 3. Parent distributions from which random year-site intercepts were drawn for survivorship in fire and non-fire years are given in Figure 2 as is an example of an individual year-site distribution.

Year-specific intercepts for logistic and Poisson fecundity models were generated in the same way. However, since the data used to parameterize the model were derived from a brief (3-6 year) record for populations in which fire was either very frequent or absent, the shift from relatively high levels of recruitment measured following fire to low levels of recruitment measured in the absence of fire was modeled as a logarithmic decay function occurring over a 10 year period as suggested by Gibson and Menges (1994) who estimated recruitment episodes for *C. ericoides* following fires to span 10 years. Logarithmic decay was modeled with fecundity at Fort Gordon 2003 representing highest (post-fire) levels and levels of fecundity at Ohoopee Dunes where major fire has been absent for at least 15 years representing levels of recruitment 10 years post-fire. In this way, the distributions from which values for year-specific intercepts are randomly generated for the logistic (Figure 3a) and Poisson (Figure 3b) recruitment models are a function of time since fire.

Rather than drawing randomly from the parameter distributions, coefficients of diameter, diameter^2, and distance terms in the survivorship and fecundity models were fixed as the means of the posterior distributions from the Bayesian regression models (Chapter 2). Because the model was parameterized from data gathered over a relatively short time period, correlations between survivorship and fecundity parameters are not known and, therefore, were not incorporated into the model. However, field data demonstrated generally very low levels of recruitment and mortality in the absence of fire, and high levels of recruitment and mortality associated with burning.

Component sub-models

For all of the following models, subscript *i* refers to year-specific effects. Models of survivorship and recruitment have distinct estimates of year-specific effects or intercepts depending on whether or not fire is an effect in a given year. Similarly, parameters estimating the effect of longleaf pine on survivorship also vary by fire or non-fire year.

Probability of survival

$$PS_y = \frac{\exp(\beta_{0(Y_i)} + \beta_1 D + \beta_2 D^2 + \beta_3 DLP)}{1 + \exp(\beta_{0(Y_i)} + \beta_1 D + \beta_2 D^2 + \beta_3 DLP)}$$

PS_y is the probability of surviving in year *y* and is predicted by a logistic function of year-specific intercept $\beta_{0(Y_k)}$, shrub diameter $\beta_1 D$, square of shrub diameter $\beta_2 D^2$, and distance from nearest longleaf pine (positive coefficient in burn years, term drops out in non-fire years) $\beta_{3S_j}DLP$. Distances from longleaf pine are captured from Ohoopee Dunes data which includes coordinates for all longleaf pines and mapped *C. ericoides* shrub. A plant survives if a uniformly distributed random variable between 0 and 1 < PS_y .

Shrub diameter growth

$$S_{y+1} = a_j(\exp(-\exp(-0.16(x - 11.37)))$$

Growth of shrub in year y or size of shrub in year $y + 1$, S_{y+1} is generated by a Gompertz growth model where x = age in years, and a is a normally distributed random variable representing the upper asymptote of shrub growth (Chapter 3). Values of a are randomly assigned to each shrub when they are recruited.

Reproductive status

In each yearly iteration of the IBM,

$$PRP = \frac{\exp(-4.1 + 10.13D)}{(1 + (\exp(-4.1 + 10.13D)}$$

is the probability that a juvenile shrub will become reproductive. A plant is reproductively mature if a uniformly distributed random variable between 0 and 1 < PRP.

Probability of producing recruits

$$PR_y = \frac{\exp(\beta_{0(Y_i)} + \beta_1 D + \beta_2 D^2 + \beta_3 DM)}{1 + \exp(\beta_{0(Y_i)} + \beta_1 D + \beta_2 D^2 + \beta_3 DM)}$$

PR_y is the probability of producing any recruits in year y and is predicted by a logistic function of year-specific intercept $\beta_{0(Y_i)}$, shrub diameter $\beta_1 D$, square of shrub diameter $\beta_2 D^2$, and distance from nearest longleaf pine (positive coefficient in burn years, negative coefficient in non-fire years) $\beta_3 DM$. A plant produces at least one recruit if a uniformly distributed random variable between 0 and 1 < PR_y .

Number of recruits

$$NR_y = \exp(\beta_{0(Y_i)} + \beta_1 DM)$$

NR_y is the mean number of recruits produced in year *y* given that likelihood of producing any recruits is positive, and is predicted by a Poisson function with mean NR_y . Number of recruits is generated in the model by generating a Poisson random variable with mean NR_y .

Probability of seedbank recruitment

$$PSR_y = \frac{\exp(\beta_{0(Y_i)} + \beta_1 D + \beta_2 Y)}{1 + \exp(\beta_{0(Y_i)} + \beta_1 D + \beta_2 Y)}$$

PSR_y is the probability of producing any recruits in year *y* and is predicted by a logistic function of year-specific intercept $\beta_{0(Y_k)}$, shrub diameter $\beta_1 D$, and years since female shrub death $\beta_2 Y$ which is tracked by the model. A plant produces at least one recruit if a uniformly distributed random variable between 0 and 1 < PS_y .

Number of recruits from seedbank

$$NSR_y = \exp(\beta_{0(Y_i)} + \beta_1 D + \beta_2 Y)$$

NSR_y is a the mean number of recruits produced in year *y* and is predicted by a Poisson function of year-specific intercept $\beta_{0(Y_k)}$, diameter of female shrub at death $\beta_1 D$, and years since death of female shrub $\beta_2 Y$. Number of recruits is generated in the model by generating a Poisson random variable (random variance) with mean NSR_y and adding it to NSR_y.

Dispersal distance

For recruitment from living shrubs and from seedbanks, dispersal direction is randomly generated from a uniform circular probability distribution. Dispersal distance is generated from a gamma probability density distribution estimated from the frequency of distance values derived from mapped data. Juvenile shrubs are assigned as offspring to the nearest neighboring mature female and dispersal distances calculated accordingly (Chapter 3). Dispersal distances are calculated as distances from the edge of female shrub canopy. Since seedbanks represent recruitment under what was formerly the canopy of a female shrub, seedbank dispersal distances are generated as normally distributed random number with mean $r/2$, where r = radius of dead female shrub.

MODEL RUNS

The IBM was run with initial values derived from mapped data from two populations, long-unburned Ohoopee Dunes Natural Area, and annually burned Fort Gordon. Coordinates and attributes of these populations were used as starting data arrays. Longleaf pine coordinates recorded from these locations are fixed. The Ohoopee Dunes data were used to investigate four deterministic model scenarios: no fire, fire every 3 years, 10 years and 20 years. The effect of stochastic fire frequency in which fire frequencies were randomly varied between 3 and 20 years was explored as a fifth model scenario. In addition, in order to explore the effect of initial size distributions, versions of the no fire and 3 year fire-frequency scenarios were run using the Fort Gordon data. For each scenario, 500 simulations were run. For 20 year fire and stochastic scenarios, simulations were run for a 50 year time period. For all other scenarios, each simulation was run for a 30 year time period (30 iterations) representing a realistic management time-frame. For each iteration of each simulation, the IBM calculates λ as N_{t+1} / N_t. The effects of fire frequency on λ were analyzed by taking the geometric mean of λ for all simulations within a given treatment.

Sensitivity testing

The sensitivity of λ to seed bank recruitment, and to spatial factors (distance to nearest male for females and distance to nearest longleaf pine) was investigated by comparing mean values of λ for the full model to versions of the model in which single components were dropped. As sensitivity contrasts, model variants were run for all scenarios in which 1) the effect of distance to nearest longleaf pine on survivorship was set to 0, 2) the effect of distance to nearest male on female fecundity was set to 0, and 3) a seed bank module was not included.

Validation

Output from snapshot sample simulations was compared with the data used to parameterize the model. Size-class frequencies from simulations of the 3 year fire frequency scenario using both the Fort Gordon and Ohoopee Dunes data were compared to the size-class distribution of the data from frequently burned Fort Gordon. Similarly, size-class distributions were compared between model output and the Ohoopee Dunes data for the no burn scenario.

Results

Population dynamics

For all three deterministic fire scenarios based on Ohoopee Dunes data, population size fluctuated periodically following an initial increase in response to fire. Initial populations tripled, or in the case of the 3 year fire scenario, quadrupled, as a result of a recruitment surge. This initial response was absent from simulations of the Fort Gordon data where the population is dominated by juvenile rather than large old shrubs. Burning at 20-year intervals resulted in the highest population size increases over a 30-year period (Figure 4b). Population size remained relatively steady over time when fire occurred at ten-year intervals (Figure 4c). Following a large initial surge, 3-year fire intervals resulted in a steady population reduction over time (Figure 4d). While individual simulations were characterized by irregular periodic fluctuations in response to fires, mean values across all simulations of the stochastic fire scenario produced a large initial increase in population size followed by steady rather than periodic growth cycles. Mean population sizes of the stochastic scenario were comparable to that of the 20-year scenario (Figure 4a). In the absence of fire, simulations of the Ohoopee Dunes population exhibited a steady decline (Figure 4e). Simulations of the no-fire scenario using the Fort Gordon data exhibited a much slower decline.

The finite rate of increase, λ, was highest following the initial burn when simulations were based on data from the long-unburned Ohoopee Dunes population. By the fifth year following a fire in the 10-year and 20-year fire scenarios, values of λ fall below 1 indicating negative mean population growth rates (Figure 5). High mean growth rates ($\lambda > 1.3$) in the first years after a burn balance relatively low mean rates of decline ($\lambda \sim 0.95$) thereafter.

Longer fire return times, at least up to 20 years, result in higher mean rates of population growth when fire returns. Although lacking a between-fire period of population decline, 3-year fire intervals result in low mean population growth rates because mean growth rates in non-fire years are low ($\lambda<1.2$) relative to mean population declines ($\lambda>0.8$) during fire years.

Sensitivity

In all of the fire scenarios, λ showed the highest sensitivity to presence/absence of a seed bank. Variants of the models run without the seed bank component predicted population declines in all years of every scenario (Figure 6). Congruently, no-fire scenarios, which lack a seed bank component, predict population declines over time. Differences in growth rates of model populations run with and without the inclusion of a distance-from-male pollen limitation parameter in the fecundity models were relatively slight. However, removing the effect of distance from longleaf pine—a negative effect on survivorship in non-fire years and a positive effect on survivorship in burn years--resulted in a much larger change in mean values of λ. Higher mean values of λ occurred in the first years after a burn when the longleaf effect was dropped, but excluding the longleaf effect from the model lowered mortality in fire years only slightly. The relative magnitude of the sensitivity of λ to the two longleaf effects corresponds to the magnitude of the effects, -0.5 versus 0.015.

Validation

As a cross-validation of the model, output from sample simulations was compared to data from regularly-burned Fort Gordon and long-unburned Ohoopee Dunes. Simulations of 30 year length of the 3-year-fire-interval scenario using Ohoopee Dunes data yielded size-distributions similar to the Fort Gordon data (Figure 7a). Likewise, 30-year no-burn scenarios using Fort Gordon data yield size distributions which agree with the Ohoopee Dunes data (Figure 7b). Although this is not a rigorous validation of the IBM, it suggests that the model captures the generalities of shrub growth and survivorship.

Discussion

These results indicate that mean population growth rates are highest at fire return intervals of greater than 10 years. Intervals between 10 and 20 years were not examined separately, but stochastic and 20-year fire return intervals yielded, on average, an increasing population over a 30-50 year time period. At 20 years, populations size frequencies are skewed toward large (>1 m) shrubs which have high fecundity established seed banks. At the other extreme, fire frequencies of 3 years or less result in population declines over time as high mortality in fire years prevents adequate replacement of mature reproductive shrubs. Shrubs may live to 40+ years, but begin to reproduce, on average, at age 10. No-fire scenarios result in slow population declines due to very low levels of recruitment. Silvertown et al. (1993) compared stage projections for 21 species of woody plants and 45 herbaceous perennials and found that woody shrubs had the highest elasticities of population growth to survivorship rather than growth or fecundity. Shrubs of open, fire-prone habitats, which showed population growth rates more dependent on growth and fecundity, formed an exception to this pattern. Evidence from this modeling exercise suggests that *C. ericoides* probably fits this second pattern: population growth appears to depend on older (10-25 year-old) shrubs which exhibit the highest fecundities of any age-size class.

These findings agree well with data on *C. ericoides* demography: growth rates are slow and female fecundity levels off as shrubs reach age 20. *C. ericoides* demography, therefore, suggests that the species has evolved in response to a risk of mortality that increases steadily from ~10 years of age, when most shrubs are sexually mature, onward. Although historic fire frequencies may have been much higher in most communities of the southeastern Coastal Plain, xeric sand environments are characterized by discontinuous fuels and vegetation causing fires to spread into them less often than through surrounding savannas (Glitzenstein et al. 1995). Moreover, population persistence over time in this species is strongly dependent on the presence of a persistent seedbank. All model variants from which a seedbank component was dropped exhibited negative population growth rates over time. Although low levels of recruitment occur continuously, smoke and ash stimulate germination (Chapter 3) and regeneration is dependent on germination pulses following fires when mature females are killed and their seed banks released. There is also the possibility that higher levels of recruitment are stimulated by exogenous smoke entering sites fires burning nearby in the absence of direct fire effects on shrubs.

Since the parameters for this IBM were developed from a brief data set and depend on a number of assumptions, these results offer a guide to management in the broadest sense only. Perhaps most importantly, data on recruitment from seed bank, a key component of the demography of this species, was based on a very small sample (n=25) especially relative to the sample size of adult shrubs (n=1330). Temporally, although a fairly broad range of yearly variation was captured in both survivorship and fecundity data, annual variation is based on data over a short period and may not reflect adequately the extremes of climatic variation and its effects on demography. Wetter years would be expected to promote seedling survivorship in arid or xeric communities and fires may be more likely in dry years resulting in higher mortality of shrubs generally and of seedlings in particular. However, a clear relationship between rainfall and survivorship or realized fecundity was lacking from the data. Therefore, rainfall was not used as a model parameter.

The model is built on survivorship data gathered after a winter burn. Warm season burns are likely to be hotter and, therefore, to result in higher kill rates. Also, the effects of fire frequency over time on the dynamics of dominant sandhill tree species, longleaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*) which may strongly interact with the demography of *C. ericoides*, are not included in these models. Fire suppression results in reduced habitat on many sandhill sites as turkey oak densities increase in the absence of fire. Conversely, frequent fires may boost recruitment of *C. ericoides* by opening up more habitat. Density-dependent mortality was not measurable in the data used to parameterize these models. However, intraspecific competition may be a factor--particularly in scenarios where fire occurs at intermediate frequencies and high levels of recruitment are combined with relatively low levels of mortality.

Sensitivity of λ to pollen limitation was, on balance, minor. This may be attributable to the clumped spatial distribution of shrub populations. Pollen limitation is likely to be a strong effect only in small, isolated, or spatially dispersed populations—where populations are most subject to demographic stochasticity. Sensitivity of the model to either growth rate or dispersal—though potentially high--was not examined. While validation based on size-class distributions suggest that model growth and mortality rates are congruent with empirical data they were developed from, the effect of small changes in growth rate on λ have not been measured. A dispersal kernel which increased mean dispersal distance could have the effect of either depressing λ if the result was for a larger fraction of recruits to be located in isolation, or increasing λ if greater mean dispersal distances lead to more rapid invasion of available habitat.

Beyond general management recommendations, perhaps the most useful outcome of a modeling exercise such as this study is to focus attention on parameters for which robust data are lacking that are most critical in determining demographic processes. Because seed bank persistence and recruitment appear central to *C. ericoides* demography, a larger seed bank recruitment data set would improve the accuracy of model predictions.

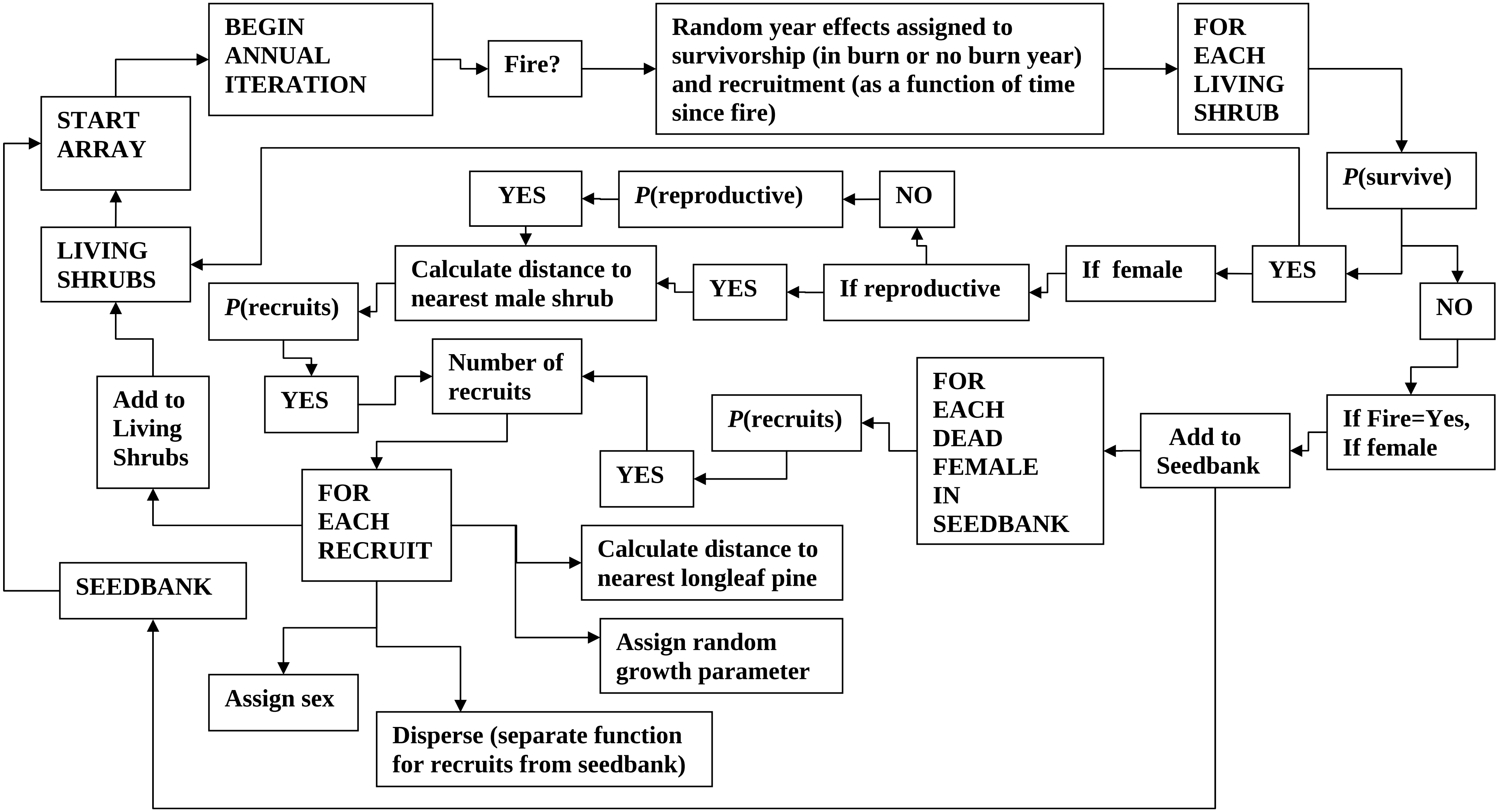


Figure 3.1. Structure of the individual-based model. This diagram represents one replicate population followed for one yearly iteration.

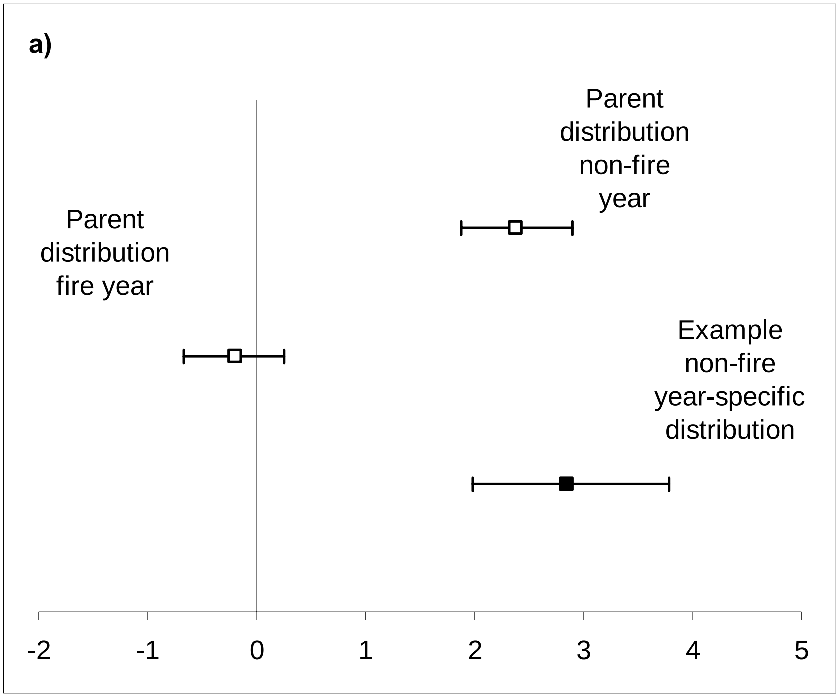


Figure 3.2. Mean and 95% confidence intervals for distributions of year-site intercepts for survivorship in fire and non-fire years.

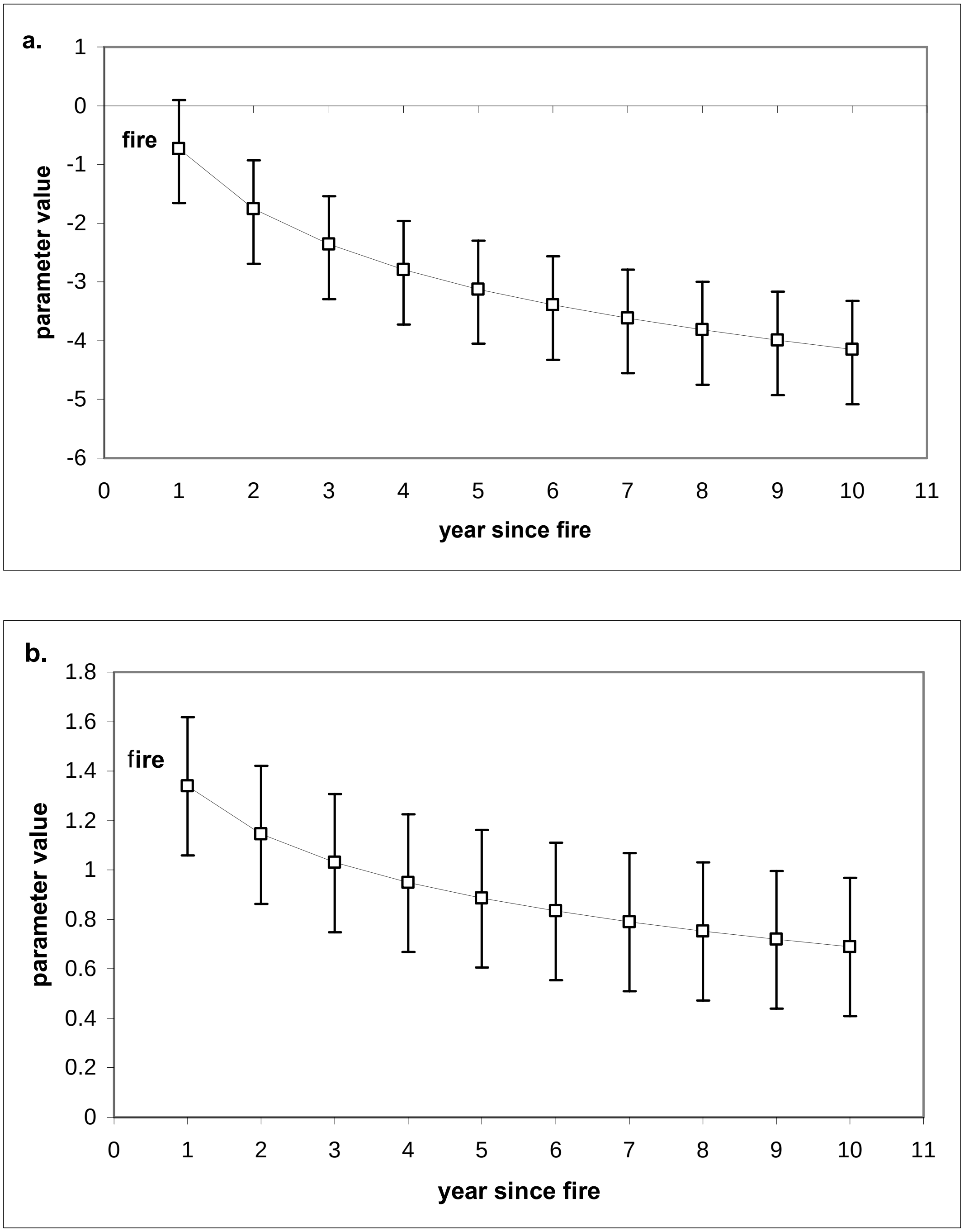
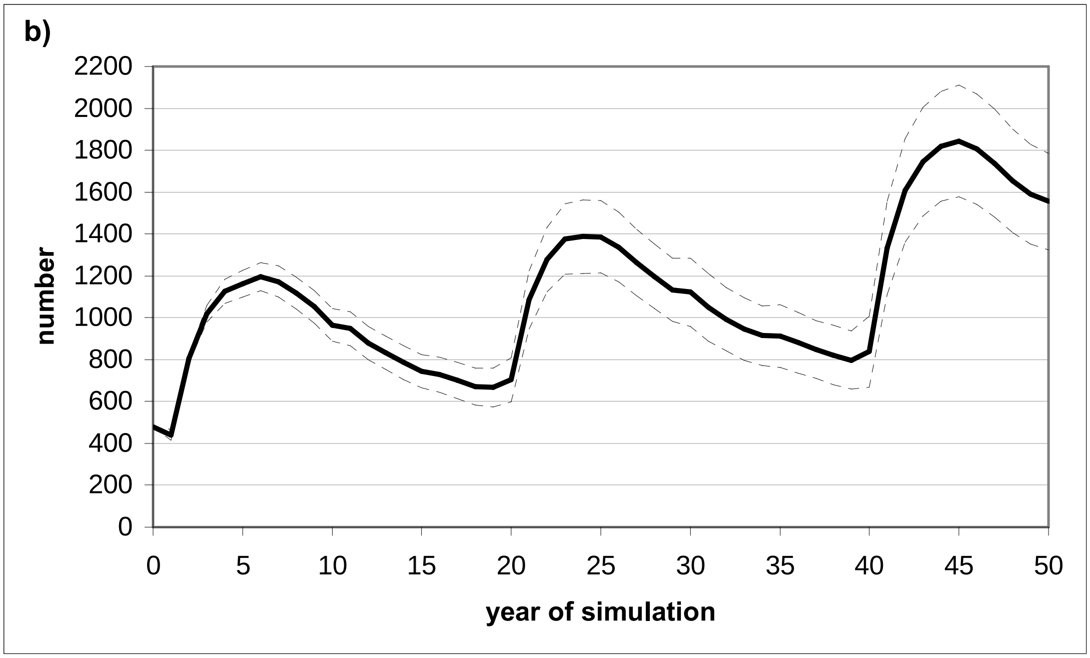


Figure 3.3. Logrithmic decay models of year-site intercepts for a) a logistic model of female shrub recruitment likelihood, and b) a Poisson model of the number of recruits produced by female shrubs with recruits. Points and error bars represent means 95% confidence intervals

of distributions used to generate values of the year-site intercept for each year of each model simulation.

Figure 3.4. Mean and 95% confidence intervals of population size over 30 or 50 year model projections for a) stochastic fire interval, b) 20-year fire interval, c) 10-year fire interval, d) 3-year fire interval, and e) no-fire scenarios. Means are averaged from 500 simulations.


a)
number
year of simulation
0
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
0
5
10
15
20
25
30
35
40
45
50


b)
number
year of simulation
0
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
0
5
10
15
20
25
30
35
40
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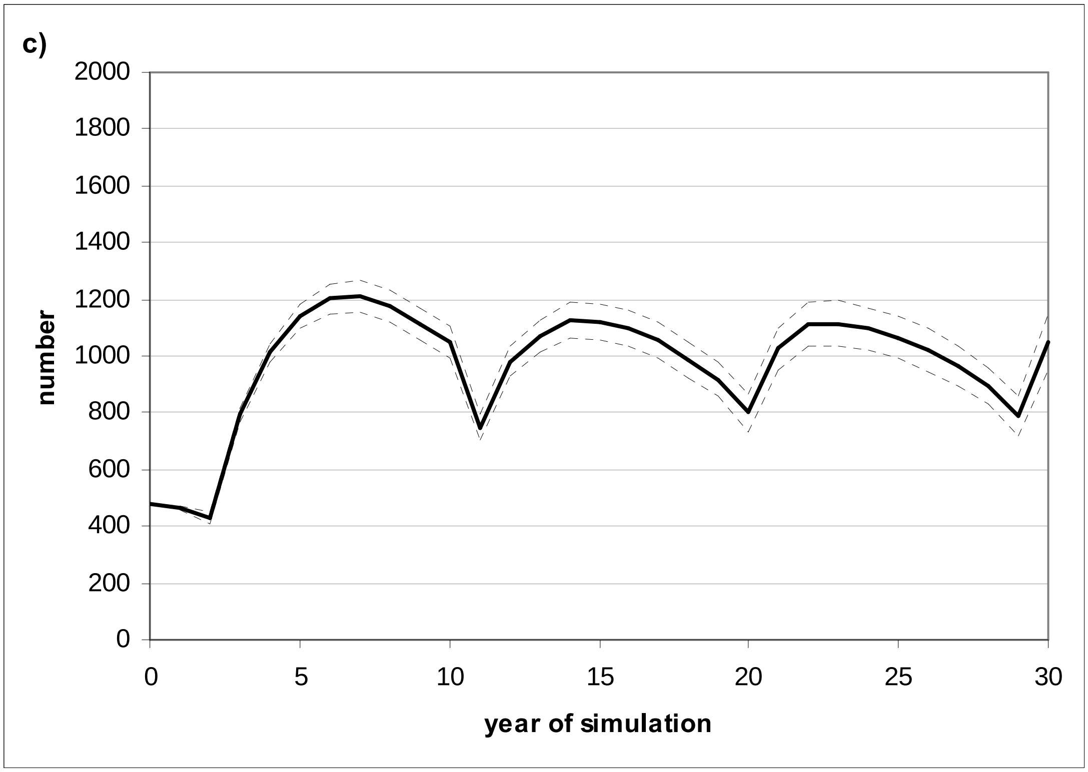
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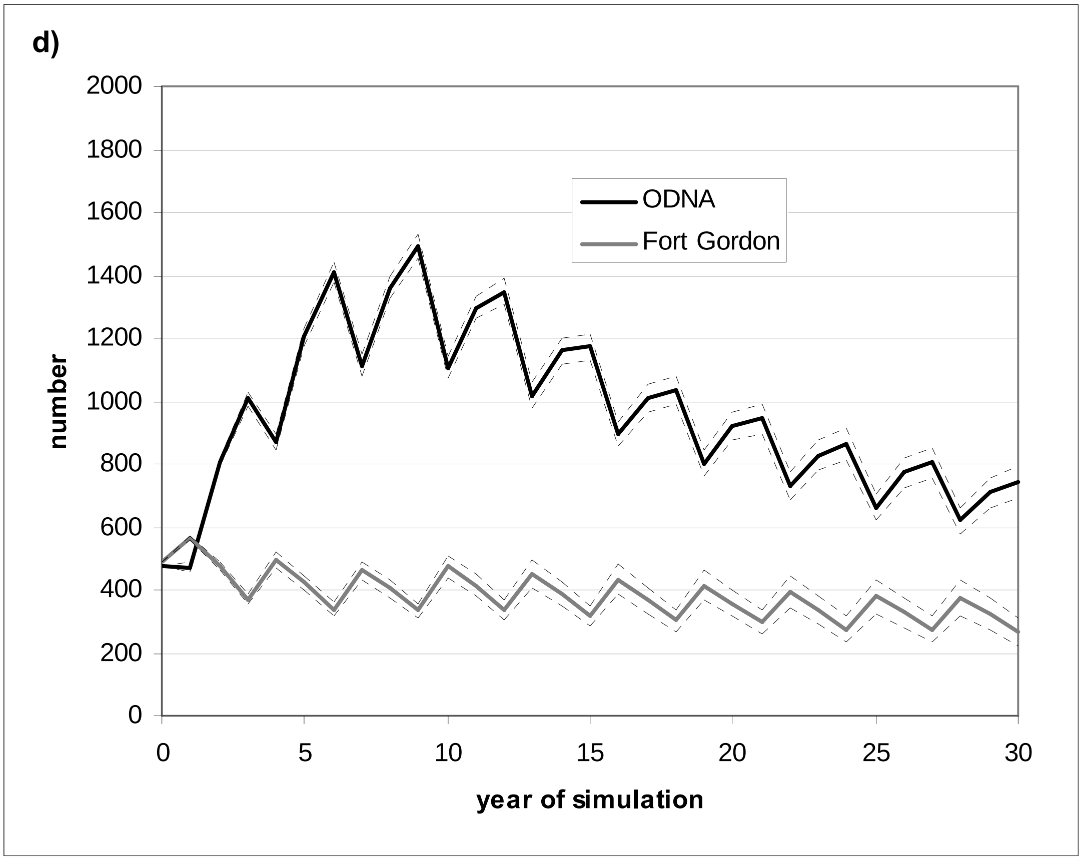
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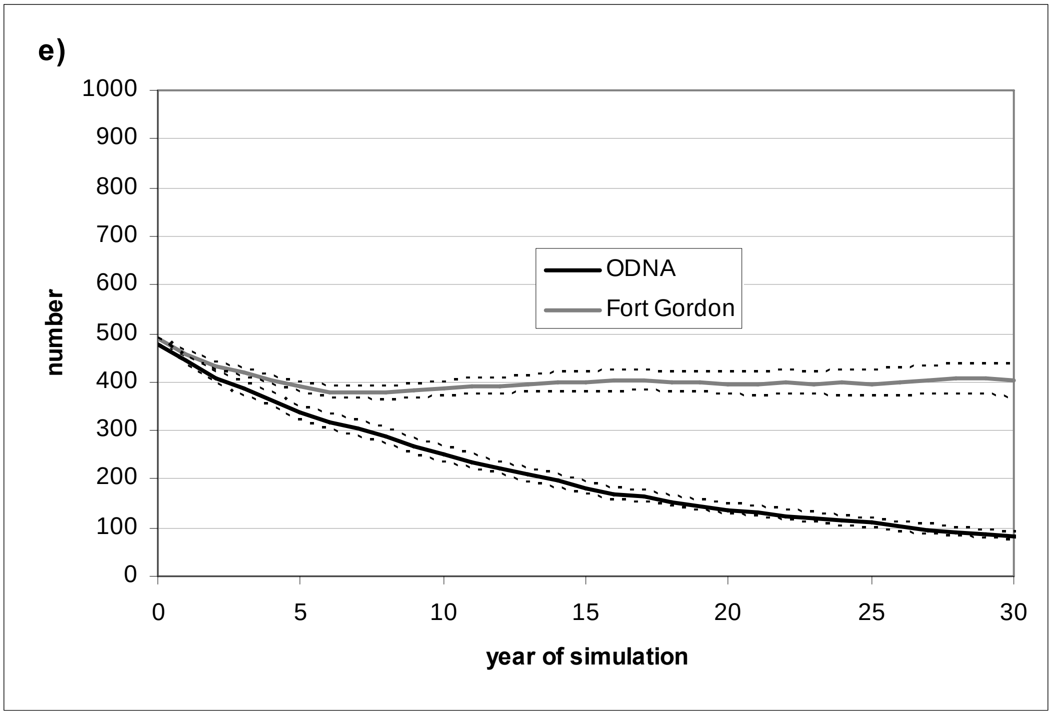
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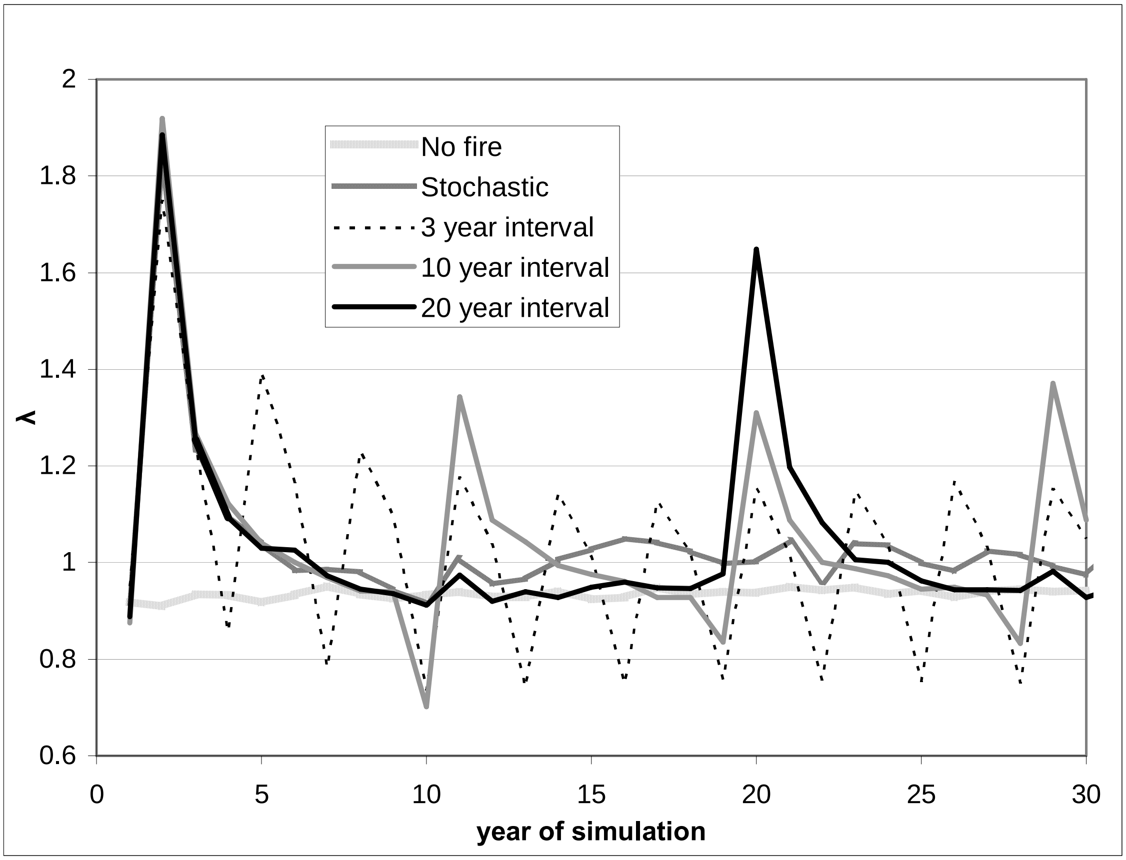
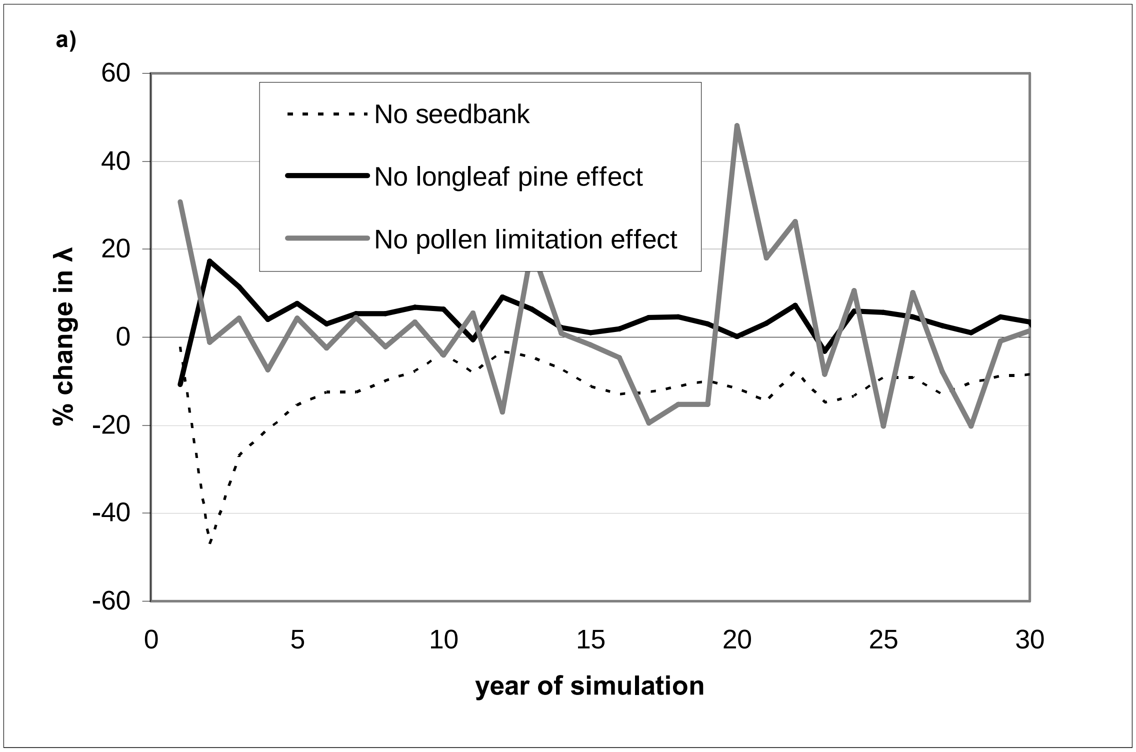


Figure 3.5. Geometric mean of λ over a 30 year model trajectory for all five model scenarios.

Figure 3.6. Model sensitivity as represented by percent change in λ for a) stochastic fire, b) 20-year fire, c) 10 year fire, d) 3-year fire, and e) no-fire scenarios.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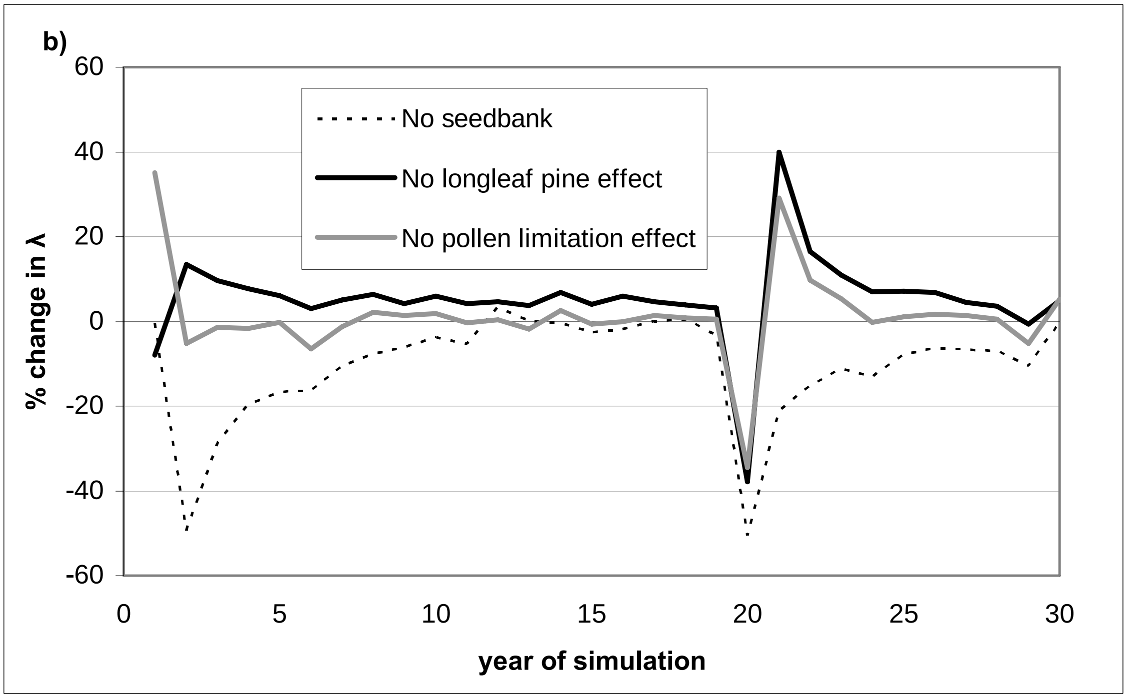
No longleaf pine effect
No pollen limitation effect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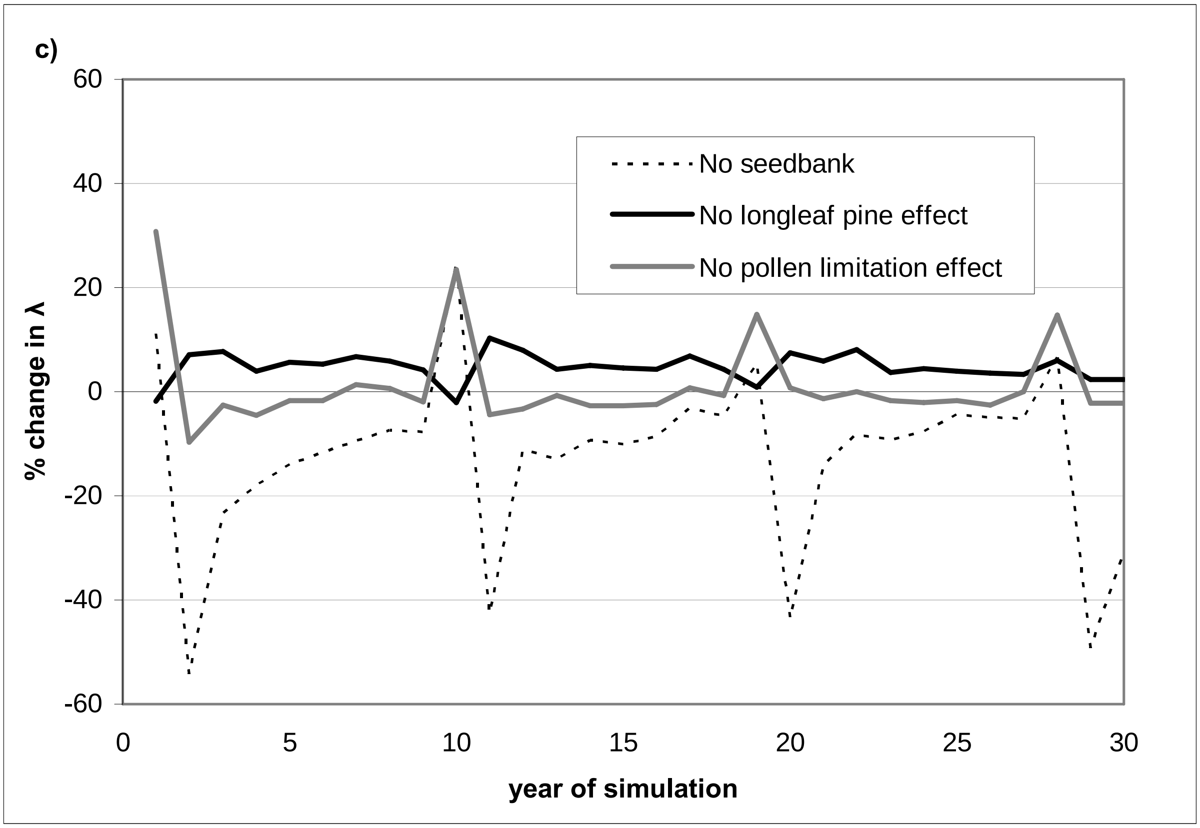
No longleaf pine effect
No pollen limitation effect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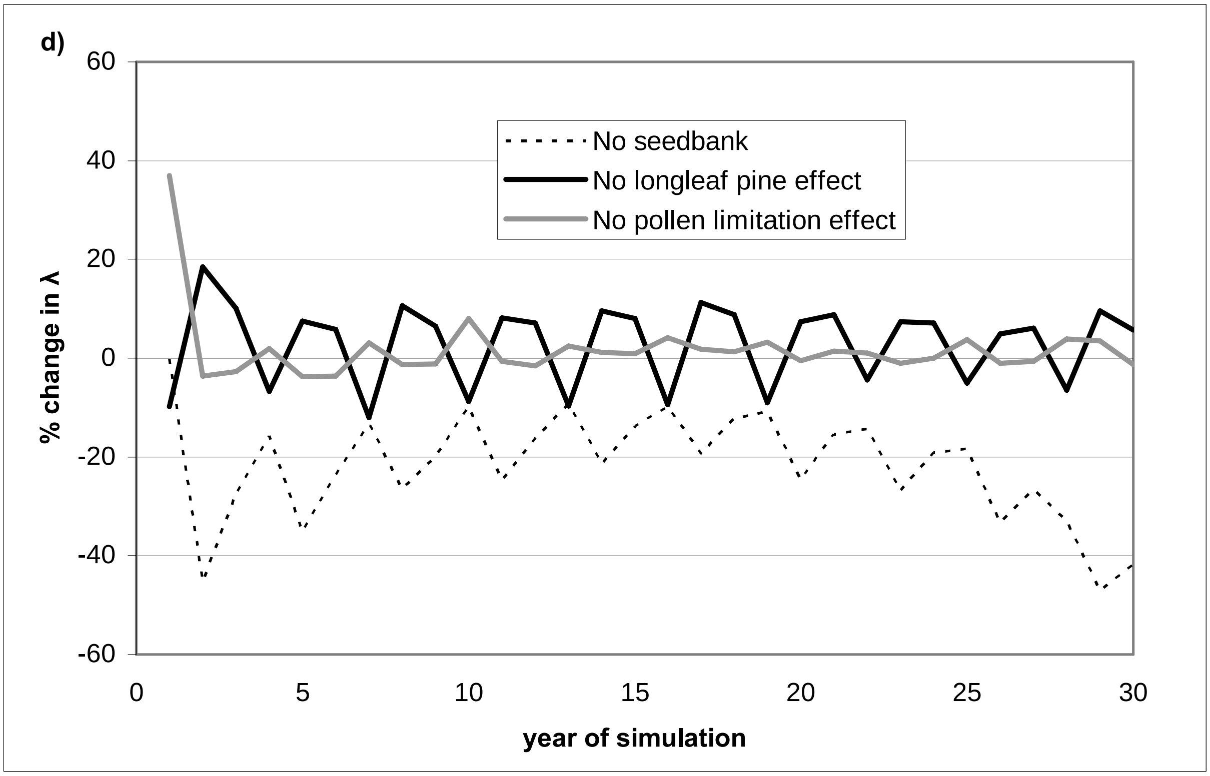
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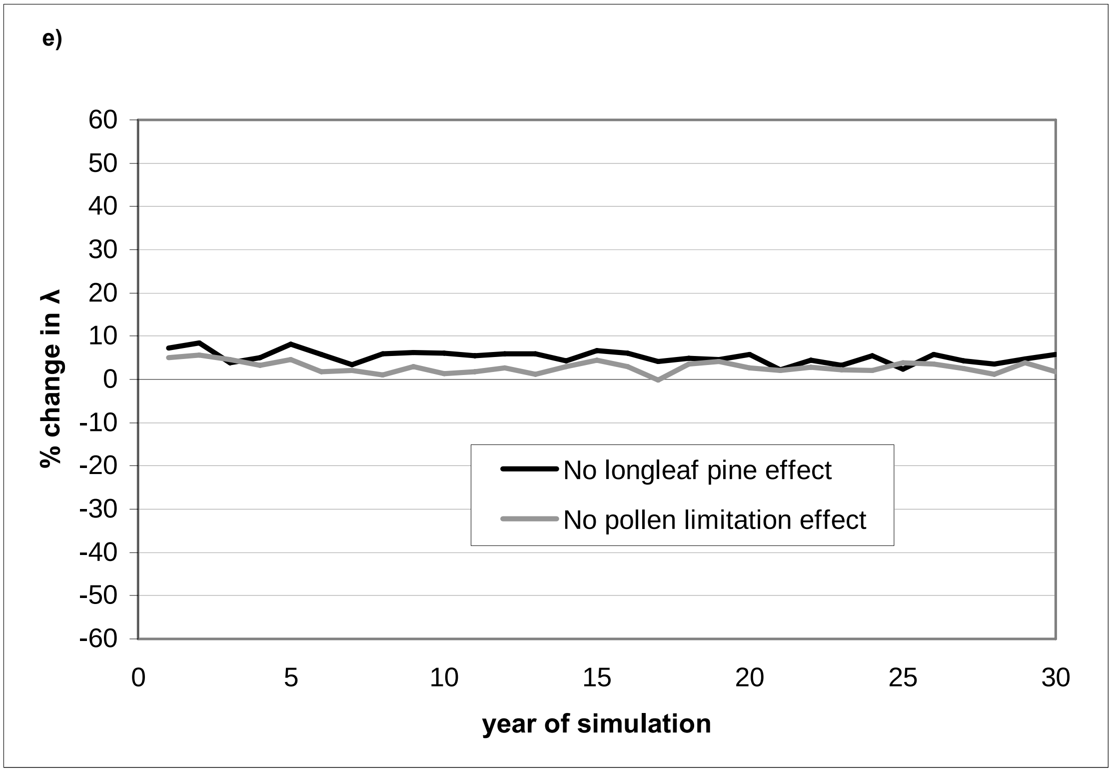
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year of simulation
No longleaf pine effect
No pollen limitation effect

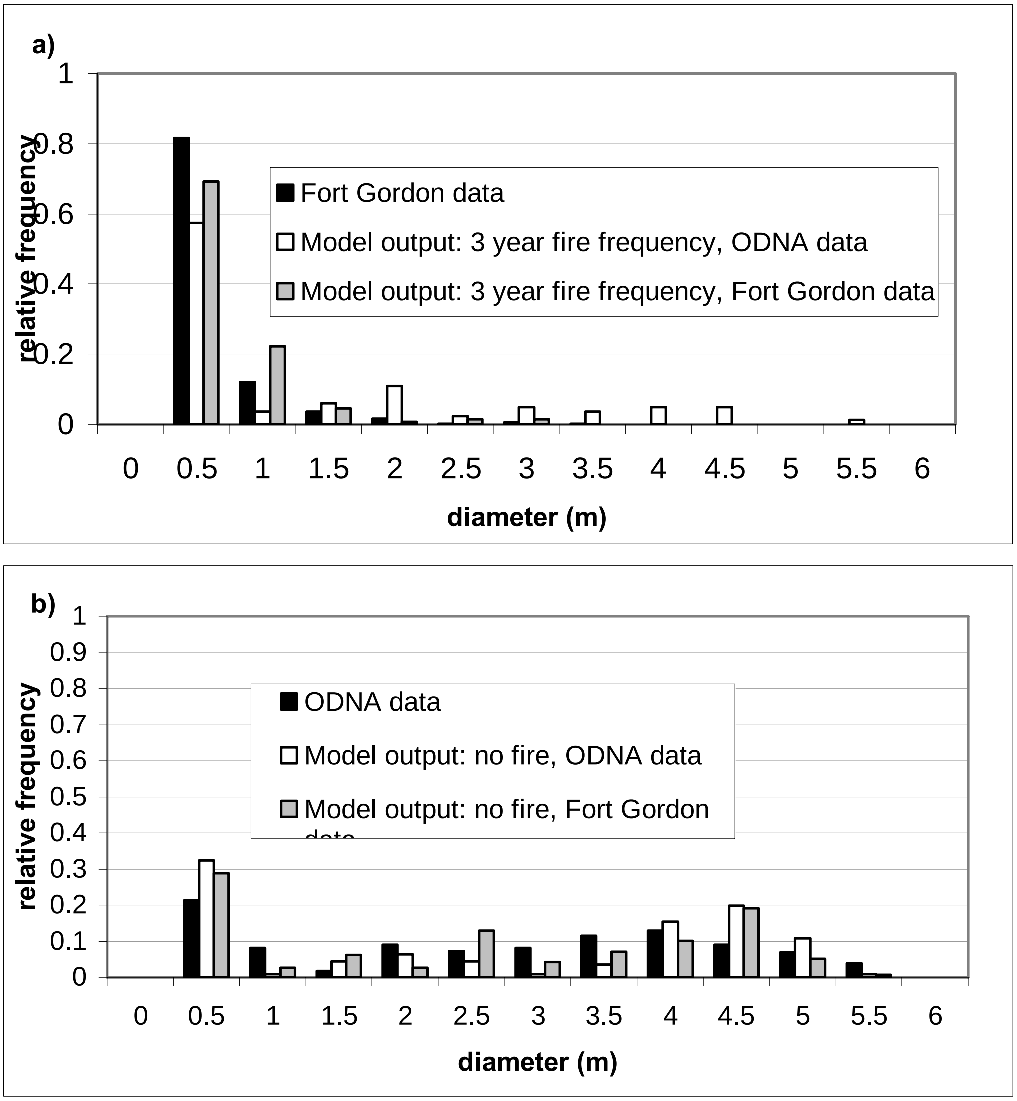

Figure 3.7. Size distributions for a) Fort Gordon data and output from 3-year fire model scenarios, and b) ODNA data and output from no-fire model scenarios.

CHAPTER 5

CONCLUSIONS

1. *Ceratiola ericoides* exhibits evidence of spatial segretation of sexes (SSS) only only at one of the seven sites examined. The site where SSS was pronounced was also the most xeric site sampled based on soil maps—suggesting that SSS occurs in this species only where sites are most stressful. There is no evidence of density-dependent limitation on growth at any of the sample sites. Age/size relationships and size at reproductive maturity do not appear to differ by sex

2. Fire increases seed germination probably because smoke is a trigger to germination. Fire can also cause a more than tenfold increase in mortality. Mortality is highest in the establishment phase, 0-10 years, and the senescent phase, > 25 years. Mortality as a result of fire is highest among shrubs growing in close proximity to longleaf pines. In the absence of fire, rates of both seedling recruitment and of shrub mortality are extremely low. Large (>6 m diameter), old individuals appear to have relatively little reproductive value.

3. The results of individual-based population models parameterized with from field data suggest that an optimal fire return frequency is approximately 20 years. Stochastic fire return intervals of 3-20 years result in positive population growth rates on average. In the absence of fire, mean population growth rates are negative.

4. *C. ericoides* appears to require fire at regular intervals of less than 20 years to persist on sandhill sites. While seasonality of burns and the effects of burns on long fire-suppressed sites may differ from the data gathered at Fort Gordon (where annual burns have been conducted for over 30 years) in this study, the existence of *C. ericoides* populations on any sandhill site suggests that those sites experienced a fire frequency 20 years or less. Given the patchy nature of fire on longleaf pine-turkey oak sandhills, more frequent application of fire to these sites may be more effective in promoting species such as *C. ericoides*.

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