LEGUMES IN LOAMY SOIL COMMUNITIES OF THE CAROLINA SANDHILLS: THEIR NATURAL DISTRIBUTIONS AND PERFORMANCE OF SEEDS AND SEEDLINGS ALONG COMPLEX ECOLOGICAL GRADIENTS

by

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ABSTRACT

MARY MCRAE JAMES: Legumes in Loamy Soil Communities of the Carolina Sandhills: Their Natural Distributions and Performance of Seeds and Seedlings along Complex Ecological Gradients.
(Under the direction of Dr. Peter S. White)

Legumes (Leguminosae) are an important group of plants in the frequently-burned, longleaf pine-wiregrass ecosystem. 58 native taxa occur in the Carolina Sandhills. Within this xeric landscape, legume density and species richness are maximized in small, topographic depressions known as bean dips and pea swales. Major indices of fertility are enhanced in these depressions, and productivity decreases with increasing elevation. Legumes show patterns of sorting along these complex topographic gradients. In the Carolina Sandhills, twenty transects were established along slopes of depressions. Legume stem density, soil texture and chemistry, and relative elevation were measured at regular intervals. Although some legumes occurred most frequently on the upper slopes of depressions, most were confined to mesic bottoms. To clarify these findings, seeds and seedlings of select legume species were introduced to the gradient, and their performance was evaluated over one growing season. The number of germinated seeds surviving one growing season did not differ across the gradient for any single species, but differences between species were observed. Biomass also differed significantly between species, and was nearly twice as great in bottom plots for all but one species. These results provide a valuable supplement to the understanding of a unique community that deserves conservation priority. Restoration of degraded loamy soil communities could be guided by these findings.

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CHAPTER I.

LEGUME RICH COMMUNITIES IN THE CAROLINA SANDHILLS

Introduction

Legumes are frequently encountered in the fire-maintained longleaf pine forest of the southeastern United States, but vary considerably in patterns of occurrence and abundance. Commonly invoked explanations include variation in soil moisture and texture (Peet & Allard, 1990; Taggart, 1990; Hainds, 1999; Walker & Peet, 1993). In this thesis, I set out to describe soil and topographic gradients that control legume distribution through their indirect effects on moisture and nutrient availability in the Carolina Sandhills, a distinct physiographic sub-province of the Atlantic Coastal Plain considered to contain the xeric extreme of longleaf pine vegetation. I had two general objectives: (1) to describe soil and site gradients associated with variation in legume presence and abundance (Chapter 3), and (2) to test whether these gradients controlled seedling establishment and early seedling growth of legumes. I viewed these two objectives necessary steps in determining how to restore these communities (Chapter 4).

In this chapter, I present a summary of the major factors that influence legume distributions with particular emphasis on fire-maintained ecosystems. I then describe the Loamy Soil Variant of the Pine/Scrub Oak Sandhills Community (Schafale & Weakley 1990), the legume-rich community that I studied in the Carolina Sandhills.

Chapter 2 reviews the stratigraphy and geologic history of the Carolina Sandhills. Following this review, I propose a mode of origin for the closed depressions in which moist and fertile soils occur, and consider the relatedness of the legume-rich Sandhill depressions to Carolina Bays, closed depressions which appear on flatter coastal plain terraces east of the Sandhills region.

Chapter 3 describes a survey of legume distributions that I conducted in loamy soil communities within two portions of the Carolina Sandhills: the Sandhills Gameland in North Carolina and the Carolina Sandhills National Wildlife Refuge in South Carolina. At each location, ten transects were anchored near the bottoms of topographic depressions where loamy soil communities occurred, and extended upward in the direction of maximum slope. Legume density, soil texture, soil chemistry, and relative elevation were measured along these transects. These data was used to search for trends in legume species richness and distribution, and assess the correlation of legume distribution with edaphic variation along the sampled gradient. This chapter also compares landscape, legume, and soil characteristics between the two study areas.

In the fourth chapter, I describe a reciprocal-transplant experiment that I conducted along five of the South Carolina transects sampled for legumes and soil. In this study, seeds and seedlings of legume species representing different portions of the gradient were introduced to plots established across a range of soil texture and site slope classes. Performance, measured as germination, survivorship, and biomass, was assessed over one growing season. In the final part of this chapter, I discuss the implications these results have for the restoration of loamy soil communities.

Chapter 5 is a summary and synthesis of the preceding chapters. It also contains suggestions for future studies in these communities.

Legumes in Fire-maintained Systems

Despite their world-wide distribution, legumes are not evenly distributed across landscapes. Perhaps the most universal characteristic of legume-rich plant communities is their tendency to occur in high-light environments, a prerequisite for the energy-demanding, nitrogen-fixation process (Davidson & Davidson, 1993). Fire, grazing, mowing, and other forms of disturbance create this condition and thereby often promote legume occurrence.

Fire also favors many legumes by altering soil chemistry. Depending upon fuel characteristics, 30-70% of total N can be volatilized by fire (Debell & Ralston, 1970). This periodic loss provides a temporary competitive advantage for N-fixing species, such as legumes, when other resources are not limiting (Norman & Wetselaar, 1960). Additional chemical benefit from fire to legumes and soil bacteria is afforded by ash deposition. These pulses enhance the availability of nutrients, such as calcium, potassium, and phosphorus, needed for nitrogen-fixation (Davidson & Davidson, 1993). The effects of these nutrient pulses are especially important in oligotrophic ecosystems where fires are generally more frequent (Christensen, 1987).

Legume seeds are also well-adapted for fire-maintained systems. Most legume seeds are surrounded by a thin, waxy cuticle that serves two important functions. First, this cuticle prevents rapid desiccation of the seed (Grace, 1986). As a result, legume seeds can remain viable in the seed bank for extended periods until conditions are favorable for germination. The second advantage afforded by the waxy cuticle is its tendency to be weakened by heat.

Auld & O'Connell (1991) examined 35 legume species from southeastern Australia, and found that while only 50% germinated in soil that was heated to 60°C, 100% germination was achieved at exposure to 80°C. In a laboratory setting, Martin & Cushwa (1966) demonstrated that legume germination was dramatically enhanced when seeds were exposed to moist heat, the type more frequently associated with growing-season burns in the southeastern longleaf pine forest. They also determined that individual heat and moisture treatments had no significant effect on germination, except that at very high temperatures seeds were destroyed.

Although legumes are associated with both extremely xeric and hydric moisture regimes, evidence suggests that most legumes occur at intermediate moisture levels. In longleaf pine savannas, legumes are uncommon in wetter sites. Instead, legume cover is maximized in the comparatively dry ultisol savannas, where soil pH is slightly higher and the water table is lower (Taggart, 1990; Walker & Peet, 1983). In longleaf pine forests of southwest Georgia, Hainds (1999) investigated legume patterns, and found soil moisture to be the best predictor of their distribution. However, only three of 43 species were associated with the wet or dry extremes; all others occurred at intermediate moisture levels. In the Florida panhandle, Clewell (1971) observed a conspicuous absence of legumes in wet longleaf savannas, and suggested a correlation with the long hydroperiod characteristic of these soils. Soil moisture has also been correlated with inoculation activity of nitrogen-fixing bacteria. In the Australian sclerophyll forest, studies have shown that nodule activity is reduced during dry summer months, and that infection of legume roots is enhanced during cool, moist seasons (Davidson & Davidson, 1993). This trend may help explain the aboveground patterns in legume distribution that have been recognized in other ecosystems.

Legume-rich ecosystems can be found wherever the right combinations of light, nutrients, moisture, and microbial populations permit. As these resources vary, individual legume distributions vary according to their individual tolerances. Several studies have focussed on these patterns in legume distributions. In the Nebraska Sandhills, Barnes et al (1984) addressed distributions of common legumes, grasses, and forbs according to ridge, slope, and valley landforms. Strong sequential replacement of species occurred across these landforms. Species rooting morphology and rooting depth, and the implications they have for water use, were cited as the primary mechanisms controlling these distributions. In the loamy soils of the tallgrass prairie, Towne and Knapp (1996) compared legume distributions between uplands and lowlands. In this ecosystem, total legume density increased significantly in the lowlands, although individual species were distributed differently along the coarse elevation gradient. Similar studies have been conducted in other legume-rich habitats (Vasquez de Aldana et al, 1996; Arianoutsou & Thanos, 1996).

Legumes-rich Communities in the Carolina Sandhills

The Carolina Sandhills region of the Upper Coastal Plain is widely regarded as the extreme xeric expression of the longleaf pine—wiregrass forest (Peet & Allard, 1993). The prevalence of deep, coarse, well-drained sands in the area presents significant challenges to plant growth. As a result, plant density and diversity are generally lower here than in subxeric, mesic, and seasonally wet longleaf forests. A number of deep-rooting legumes, however, appear to cope successfully with these perennially dry and infertile conditions. *Baptisia cinerea, Galactia regularis, Lupinus diffusus,* and *Tephrosia virginiana* are perhaps the most commonly encountered legumes in the Carolina Sandhills. Apparently, they are able to persist in the most commonly encountered soil type—deep sand.

Nested within this severe landscape, however, are small, isolated pockets of loamy soils where the effects of drought and infertility are ameliorated. These areas have been formally identified as the Loamy Soil Variant of the Pine/Scrub Oak Sandhill Community (Schafale & Weakley, 1990), and they may represent the most species-rich community in the Sandhills (Sorrie, 1998). Compared to other Sandhill communities, the Loamy Soil Variant usually supports a diverse subcanopy, including blackjack oak (*Quercus marilandica*), bluejack oak (*Quercus incana*), sand post oak (*Quercus margaretta*), and occasionally southern red oak (*Quercus falcata*). Equally distinctive is the dense and diverse understory (Table 1.1). Grasses, composites, and especially legumes achieve levels of diversity here that are unmatched in other Sandhill communities. Relative to their area, a disproportionate number of rare taxa are also associated with this habitat (Sorrie, 1998). At least eighteen rare species, including six legumes, are either restricted or most frequently encountered in the Loamy Soil Variant (Table 1.2). In addition to supporting a wealth of plant diversity, these communities also provide critical habitat for Sandhills fauna. Throughout the course of this study, bob-white quail (*Colinus virginianus*), turkeys (*Meleagris gallopavo*), white-tail deer (*Odocoileus virginianus*), and many insects were observed utilizing these habitats.

Loamy soil communities include a variety of landforms that promote the accumulation of moisture and nutrients. Sorrie (1998) names three examples: bean dips, dry troughs above streamheads, and loamy flats, all of which occur on upland divides above saturated soils. The three are similar in their ability to promote both nutrient and moisture retention, but they differ in degree of containment. In this paper I have elected to distinguish

Table 1.1. List of potential Loamy Soil Variant Indicator Species.

FAMILY	Species	Common Name
ACANTHACEAE	*Ruellia caroliniensis* ssp. *ciliosa*	Sandhills wild petunia
AGAVACEAE	*Yucca filamentosa*	bear-grass
ANACARDIACEAE	*Rhus copallinum*	winged sumac
ANACARDIACEAE	*Rhus michauxii*	Michaux's sumac
ANACARDIACEAE	*Toxicodendron pubescens*	poison-oak
APOCYNACEAE	*Amsonia ciliata*	fringe bluestar
ASCLEPIADACEAE	*Asclepias tuberosa*	butterfly weed
ASTERACEAE	*Ambrosia psilostachya*	lesser ragweed
ASTERACEAE	*Aster concolor*	eastern silvery aster
ASTERACEAE	*Silphium compositum*	rosinweed
BORAGINACEAE	*Onosmodium virginianum*	Virginia marbleseed
CORNACEAE	*Cornus florida*	flowering dogwood
ERICACEAE	*Vaccinium arboreum*	sparkleberry
EUPHORBIACEAE	*Stillingia sylvatica*	queen's delight
FAGACEAE	*Quercus incana*	bluejack oak
FAGACEAE	*Quercus margaretta*	sand post oak
FAGACEAE	*Quercus marilandica*	blackjack oak
JUGLANDACEAE	*Carya tomentosa*	mockernut hickory
LAMIACEAE	*Salvia azurea*	blue sage
LAURACEAE	*Sassafras albidum*	sassafras
ONAGRACEAE	*Oenothera fruticosa*	sundrops
POACEAE	*Andropogon gerardii*	big bluestem
POACEAE	*Anthaenantia villosa*	green silkyscale
POACEAE	*Aristida lanosa*	woolysheath 3-awn
POACEAE	*Paspalum bifidum*	pitchfork crowngrass
POACEAE	*Sorghastrum elliottii*	nodding indiangrass
POACEAE	*Sorghastrum nutans*	yellow indiangrass
POACEAE	*Tridens carolinianus*	Carolina tridens
POLYGALACEAE	*Polygala grandiflora*	showy milkwort
POLGONACEAE	*Eriogonum tomentosum*	dog-tongue
RHAMNACEAE	*Ceanothus americanus*	New Jersey tea
RUBIACEAE	*Galium pilosum*	hairy bedstraw
SCROPHULARIACEAE	*Penstemon australis*	hairy beardtongue
SCROPHULARIACEAE	*Schwalbea americana*	American chaffseed
SOLANACEAE	*Physalis lanceolata*	Sandhills groundcherry
VERBENACEAE	*Stylodon carneus*	Carolina false-vervain
VIOLACEAE	*Viola pedata*	bird's-foot violet
VIOLACEAE	*Viola villosa*	southern wooly violet

Table 1.2. Rare Species Associated with the Loamy Soil Variant in the Carolina Sandhills

FAMILY	Species	Common Name	Global	US	NC	NC Rank	SC Rank
ACANTHACEAE	*Ruellia caroliniensis* ssp. *ciliosa*	Sandhills wild petunia	G?		C	S1	S?
ANACARDIACEAE	*Rhus michauxii*	Michaux's sumac	G2	E	E-SC	S2	SX
APOCYNACEAE	*Amsonia ciliata*	fringed bluestar	G5?		W1	S2	
BORAGINACEAE	*Onosmodium virginianum*	Virginia marbleseed	G4		W1	S3	
LAMIACEAE	*Salvia azurea*	azure sage	G4G5		SR	SH	
LEGUMINOSAE	*Astragalus michauxii*	Sandhill's milkvetch	G3	FSC	PT	S3	S?
LEGUMINOSAE	*Dalea pinnata* var. *pinnata*	summer farewell	G5		W1	S2	
LEGUMINOSAE	*Galactia mollis*	soft milkpea	G4G5		C	S2	
LEGUMINOSAE	*Orbexilum lupinellum*	lupine scurfpea	G3G4		W1	S3	S?
LEGUMINOSAE	*Pediomelum canescens*	buckroot	G3G4		W7	S2	
LEGUMINOSAE	*Phaseolus sinuatus*	Sandhill bean	G3		C	S3	
POACEAE	*Paspalum bifidum*	pitchfork crowngrass	G5		W1	S3	S?
POACEAE	*Tridens carolinianus*	Carolina tridens	G3?		C	S3	S?
POLYGALACEAE	*Polygala grandiflora*	showy milkwort		G5?	SR	S2	
POLYGONACEAE	*Eriogonum tomentosum*	southern wild-buckwheat	G4G5		C	SH	
SCROPHULARIACEAE	*Schwalbea americana*	American chaffseed	G2	E	E	S1	S2
SOLANACEAE	*Physalis lanceolata*	Sandhills ground cherry	G3?	PC2	W1	S2?	
VIOLACEAE	*Viola villosa*	Carolina violet	G5		W7	S1?	

among the three groups according to their geomorphology. The term "bean dip," coined by Sorrie, is reserved for the small, shallow depressions of probable deflationary origin exhibiting centripetal drainage. Pea swale is an alternative term for the dry troughs above streamheads described by Sorrie (1998); they are bounded on two sides with a distinct inlet and outlet, and exhibit containment that is intermediate between bean dips and loamy flats. Loamy flats represent the least-contained landform of the group. As their name implies, these areas exhibit little topographic relief and sub-surface waterflow is presumably slow and subtle. In spite of the variation among these groups, fertility is generally highest in the topographic lows. Extending upslope from these low spots, a strong and complex gradient of soils texture and moisture can be recognized over relatively short distances.

Ironically, the conditions that promote the existence of the Loamy Soil Variant are the same as those that have propelled its destruction. Recognizing the advantages to plant growth, land managers in the Sandhills have tended to concentrate their agricultural activities in bean dips and related landforms. Of the bean dips that have been converted on public lands, most have been planted as wildlife food plots, although row-cropping is occasionally practiced on a small scale. In either case, the fields generally mimic the shape of the depression and remnants of the original community are relegated to the unplowed margins. However, due to the decreasing popularity of wildlife food plots, many of these fields have been abandoned over the last several decades. Unfortunately, they do not appear to recover toward the original composition of the Loamy Soil Variant within this time frame, though observations are limited. This apparent lack of natural recovery was a major stimulus in the formulation of this research project.

CHAPTER II.

PHYSIOGRAPHY OF THE CAROLINA SANDHILLS AND ORIGIN OF TOPOGRAPHIC DEPRESSIONS

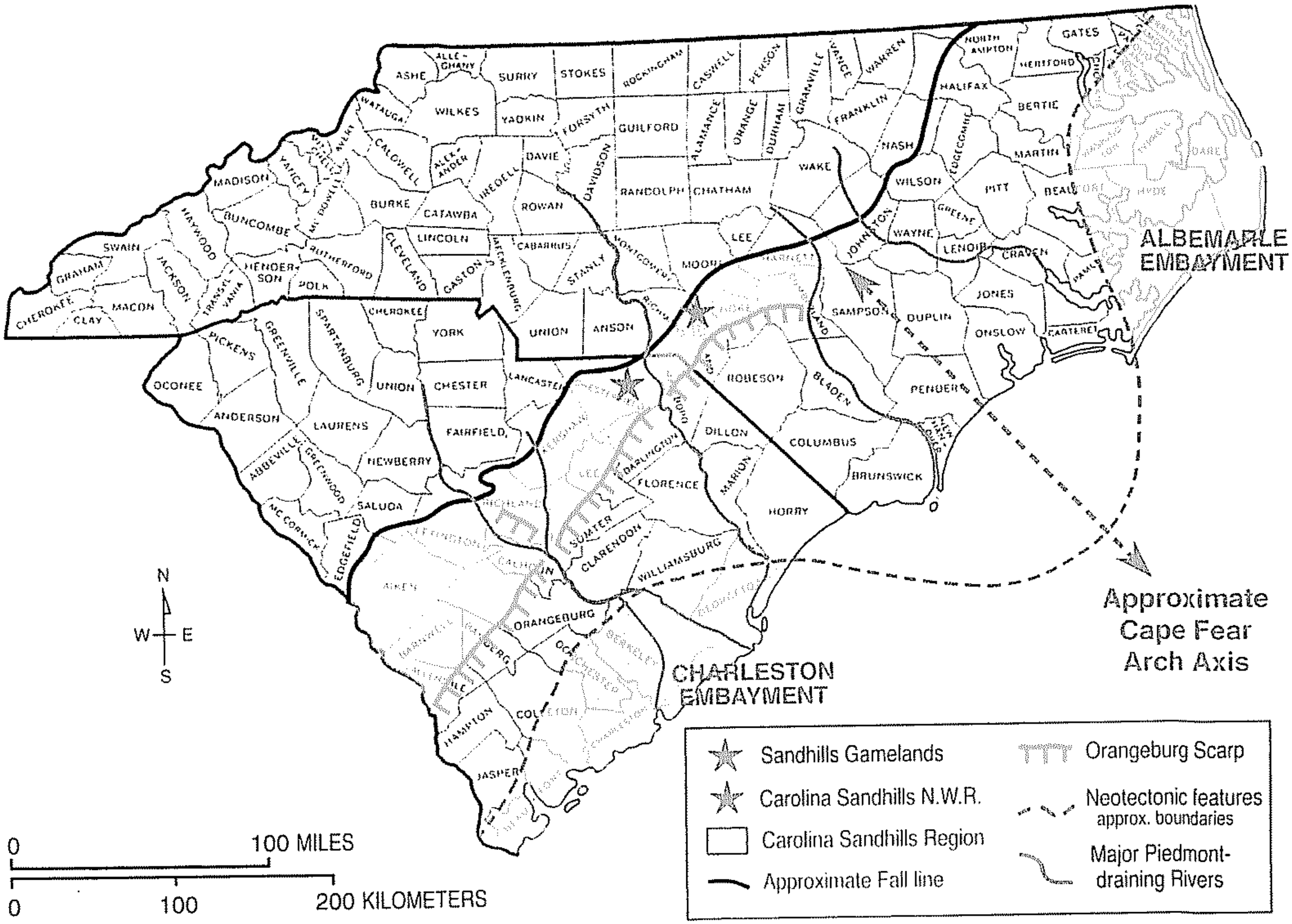
The geologic history of the Carolina Sandhills is regarded as one of the most complex in the United States. Despite the dedication of many geologists, key questions regarding the origins and development of the Upper Coastal Plain remain unanswered. Much of the mystery stems from the great antiquity of this landscape, which is considered to be among the oldest exposed surfaces in the United States. To a large degree, the characteristic sands that mantle the region are responsible for much of the uncertainty that surrounds the origins and development of the Upper Coastal Plain. Due to the extremely porous nature of these sands, the interstream divides in the Sandhills have remained relatively stable and erosion-resistant, despite dramatic climatic fluctuations during the recent geological past. In addition, these sands are not conducive to fossil preservation, forcing geologists to rely, instead, on more imprecise dating methods based on relative stratigraphy.

In this chapter, I synthesize what is known about the origin and development of the Carolina Sandhills in order to clarify the conditions under which the closed topographic basins known as bean dips developed. In doing so, I characterize the general physiography and stratigraphy of the region, and describe how these features structure the dominant gradients that appear to regulate plant distribution. Included in this summary are some original field observations regarding the formation of bean dips, which I propose are eolian deflation features known as pans that formed during the fluctuating climates of the Pleistocene and Holocene. Following a description of the global distribution, nature, and formation of pans, I argue that closed depressions on the Middle and Lower Coastal Plains known as Carolina Bays show a striking similarity to bean dips that may indicate a common origin. I also describe some of the differences between my two study areas, the North and South Carolina Sandhills, as a function of geology and physiography. Additional work will be needed to validate my conclusions, but it is hoped that the following summary will, at least, provide some guidance and motivation for future studies.

Physiography

The Carolina Sandhills are a northeast-southwest-trending sub-province of the Atlantic Coastal Plain that stretches across South Carolina and the southern half of North Carolina as a belt typically less than 50 km wide (Fig. 2.1). The southeastern boundary of the Sandhills, is defined by the Orangeburg Scarp, a subtle wave-cut cliff formed during a highstand of sea level in the early Pliocene (Cabe et al, 1992). The Fall Line, intermittently exposed in major river valleys as the most easterly outcrop of Paleozoic rocks, delimits the northwestern edge of the region (Beyer, 1991). The elevation between these two features generally ranges from 70-180 m above sea level, although relict knobs and exceptionally deep river valleys occasionally occur outside this range. To the north, the Sandhills terminate rather abruptly in southern Harnett County, just north of the Cape Fear River and south of the Albemarle Embayment, for reasons perhaps related to neotectonics (Soller, 1998; Newell et al, 1980). Southward, the Sandhills belt extends through central Florida, albeit with declining elevation, where it is known as the Trail Ridge and the Lake Wales

Figure 2.1. Map of Study Areas in the Carolina Sandhills and Approximate Location of Coastal Plain Tectonic Features.


ALBEMARLE EMBAYMENT
CHARLESTON EMBAYMENT
Approximate Cape Fear Arch Axis
N
W
E
S
0
100 MILES
0
100
200 KILOMETERS
Sandhills Gamelands
Carolina Sandhills N.W.R.
Carolina Sandhills Region
Approximate Fall line
Orangeburg Scarp
Neotectonic features approx. boundaries
Major Piedmont-draining Rivers
ASHE
ALLE-GHANY
SURRY
STOKES
ROCKINGHAM
CASWELL
PERSON
GRANVILLE
VANCE
WARREN
NORTH AMPTON
GATES
HERTFORD
HALIFAX
BERTIE
WATAUGA
WILKES
YADKIN
FORSYTH
GUILFORD
ALAMANCE
ORANGE
DURHAM
FRANKLIN
NASH
EDGECOMBE
MARTIN
AVERY
CALDWELL
ALEX-ANDER
DAVIE
IREDELL
DAVIDSON
RANDOLPH
CHATHAM
WAKE
WILSON
PITT
BEAUFORT
HYDE
DARE
MADISON
YANCEY
MC DOWELL
BURKE
CATAWBA
ROWAN
LEE
JOHNSTON
GREENE
WAYNE
LENOIR
CRAVEN
PAMLICO
SWAIN
HAYWOOD
BUNCOMBE
RUTHERFORD
LINCOLN
CLEVELAND
GASTON
MECKLENBURG
CABARRUS
STANLY
MONTGOMERY
MOORE
HARNETT
SAMPSON
DUPLIN
JONES
ONSLOW
CARTERET
GRAHAM
JACKSON
HENDER-SON
POLK
TRANSYL-VANIA
MACON
CHEROKEE
CLAY
UNION
ANSON
RICHMOND
HOKE
CUMBERLAND
ROBESON
BLADEN
PENDER
NEW HANOVER
COLUMBUS
BRUNSWICK
PICKENS
GREENVILLE
SPARTANBURG
CHEROKEE
YORK
OCONEE
ANDERSON
LAURENS
UNION
CHESTER
LANCASTER
CHESTERFIELD
MARLBORO
DILLON
FAIRFIELD
NEWBERRY
ABBEVILLE
GREENWOOD
SALUDA
MC CORMICK
EDGEFIELD
KERSHAW
LEE
DARLINGTON
FLORENCE
MARION
HORRY
RICHLAND
SUMTER
CLARENDON
WILLIAMSBURG
LEXINGTON
CALHOUN
AIKEN
ORANGEBURG
BERKELEY
GEORGETOWN
BARNWELL
BAMBERG
DORCHESTER
ALLENDALE
HAMPTON
COLLETON
CHARLESTON
JASPER
BEAUFORT

Ridge. The Orangeburg Scarp also marks the eastern boundary of these Sandhills, although the Fall Line is imperceptible at this southern extreme (Doering, 1960; White, 1970).

As the name suggests, the Carolina Sandhills have variable topography and, in most places, are mantled in deep sand. Changes in elevation greater than 60 m may occur within distances less than 0.5 km, although broad plateaus are also common. This topography contrasts strikingly with the flat terrain of the Middle and Lower Coastal Plains east of the Orangeburg Scarp. Interstream divides in the Sandhills represent some of the oldest geomorphic surfaces in the United States (Daniels et al, 1978). They may be relatively flat and plateau-like, or distinctly ridged. They are separated by many small blackwater streams, most of which arise within the Sandhills and receive their color from tannic acids that are readily leached through the porous sands. Only four major Piedmont-draining river systems bisect the Carolina Sandhills region. They are regularly spaced approximately 100-115 km apart, and include, from northeast to southwest: the Cape Fear River, the Pee Dee River, the Santee River (Congaree + Wateree), and the Savannah River.

Stratigraphy

The surficial sands that cap the interfluves in the Sandhills are generally poorly-sorted and variable in origin. Those exhibiting steeply dipping crossbeds are widely regarded as eolian dune deposits, and, in the Carolinas, have been named the Pinehurst Formation (Bartlett, 1967). This unit is discontinuously distributed across the Carolina Sandhills region, but does not overlie Piedmont rocks, nor is it known to occur east of the Orangeburg Scarp (Cooley, 1970; Bell et al, 1974). The position of this unit suggests that the Pinehurst was deposited during the period of sea level rise that carved the Orangeburg Scarp, and, in all likelihood, these sands represent coastal dunes that blew inland from this former shoreline. According to Vail curves, this period of global sea level rise occurred approximately 4 Ma in the Early Pliocene (Haq et al, 1988). The most southerly Pinehurst deposits have been mapped in Aiken County, South Carolina, near Foxtown, (Nystrom et al, 1991), and the most northerly on the Cape Fear-Neuse River divide in North Carolina (Daniels et al, 1978). The Pinehurst Formation is synonymous with the Lafayette of Stephenson (1912) and is part of the Citronelle Formation of Doering (1960), a widely distributed surficial sand unit found at higher elevations along the south Atlantic and Gulf Coastal Plains.

Maximum thickness of Pinehurst deposits is achieved in close proximity to major Piedmont-draining rivers where vigorous incisement of indurated Cretaceous sediments provided a source of loose sand susceptible to entrainment by strong winds (Nystrom et al, 1991; Markewich & Markewich, 1994). A period of vigorous incisement has been associated with broad uplift of the Appalachian Mountains during the Oligocene (White, 1970). The thickest Pinehurst deposits are in the vicinity of the Congaree and Wateree River Valleys near Lugoff, South Carolina. These deposits were nearly 50 m thick prior to extensive sand-mining in the area (Nystrom, pers. comm). In northeastern South Carolina, where the width of the Upper Coastal Plain is comparatively narrow, Pinehurst deposits are scant and occur primarily on isolated knobs at the highest elevations (Nystrom et al, 1991). Northeast of the Pee Dee River valley, in southeastern North Carolina, the width of the Upper Coastal Plain again increases, and eolian Pinehurst sands are widely distributed (Owens, 1989).

Others sand deposits in the Sandhills appear to be of either fluvial or colluvial origin, having accumulated through weathering of the underlying Cretaceous formations, masswasting, and sheet-wash (Newell et al., 1980). Although they differ from eolian sands in their mode of deposition, they are similar in their susceptibility to wind transport in the absence of stabilizing vegetation. They are also similar in their poor fossil preservation and long-term evolution, evidenced by multiple weathering horizons, rendering them extremely difficult to date. Based on stratigraphic position, most geologists believe they were originally deposited in the late-Miocene or early-Pliocene, but have been extensively reworked and modified during the Pleistocene (Newell et al, 1980). It is probably during the Pleistocene that many of the eolian deflation basins of interdune swales--today's bean dips--were formed (Markewich, Dennison, Farrell, Nystrom, pers. comm., Goudie & Wells, 1995).

Sandhill sands typically overlie compact, Late Cretaceous sediments. These deposits belong to either the Middendorf or Tar Heel Formation in the Carolinas, both deltaic deposits of sands, clayey sands, gravelly sands, and lenses of clay representing rapid facies changes in the depositional environment (Sohl & Owens, 1991; Cabe et al, 1992; Owens, 1989; Bartlett, 1967). These Cretaceous sediments outcrop only in the Carolina Sandhills region. To the east they dip steeply and are overlain by nearly 450 m of marine sediment near Wilmington (Soller, 1985). The irregular sub-surface topography of the Cretaceous sediments suggests that they were highly weathered prior to deposition of the overlying sands. The depth of the sand:clay contact is, therefore, highly variable. Nevertheless, the occurrence of clay near the soil surface can exert a strong force on moisture availability, a major determinant of community structure in the Sandhills. The average 1250 mm of rain that falls on the Sandhills each year rapidly percolates through the overlying sandy matrix until reaching an underlying clay horizon where water is forced to flow in a comparatively horizontal direction. The sand:clay contact is sometimes exposed along steep slopes, and these perennially wet zones are known as Sandhill seeps (Wells, 1942). At higher elevations, the amount of sub-surface flow is generally less because of the decreased area of upstream watershed.

The sand:clay contact appears to have played a large role in the formation of bean dips. These depressions are believed to be the result of eolian deflation (Markewich, Dennison, Farrell, Nystrom, pers. comm., Goudie & Wells, 1995). By this mechanism, the downward limit of deflation was determined by the depth at which sediments unsusceptible to entrainment occurred. In other words, the loose sands blanketing the Sandhills region were reasonable candidates for deflation, but the compacted Cretaceous sediments below these sands were not. Hence, many geologists believe that this sand:clay unconformity marks the downward limit of deflation. This hypothesis is supported by unpublished mapping of the Sandhills Gameland done by Farrell of the North Carolina Geological Survey. Together we found elevations of the Pinehurst-Middendorf contact to be coincident with the elevations of nearby bean dips, the bottoms of which occur 2 to 3 m above the elevation of the mapped contact. Presumably, slow infilling of these depressions has ensued since they were formed, and continues presently.

Pans

Eolian deflation basins, such as bean dips, can be found in many arid parts of the world today, or in places that have experienced episodic aridity in the recent geological past. Collectively, these basins are known as pans (Goudie & Wells, 1995). They include both oriented and non-oriented depressions formed in a variety of susceptible sediments. Unlike other closed depressions associated with karstic collapse or meteoritic impact, pans are the product of weathering (by salt, water, termites, wallowing ungulates, etc.) and/or subsequent eolian deflation. On a global scale, the regions with the highest pan densities include southern and central Africa, central North America, the Pampas and Pantanal of South America, southern and western Australia, Manchuria in China, and the western Siberian plain. In the United States, pans occur in four general areas: 1) isolated intermontane basins west of the Rocky Mountains, 2) the High Plains from South Dakota to Texas, 3) the south Texas coastal plain, and 4) the Atlantic coastal plain from New Jersey to Florida (Goudie & Wells, 1995).

Pans may differ in morphology and their mode of formation, but there are several characteristics that these closed depressions hold in common. Perhaps the most universal feature is their tendency to form in sediments that are susceptible to wind transport. In most cases, loose sand has provided this necessary substrate, but pans have also formed in dry, powdered shale and clay. Pans are also restricted to areas where fluvial processes are not integrated due to broad-scale tectonic deformation that may have disrupted previously organized drainage patterns, or, more often, because the region where they form is mantled in highly permeable soils and the amount of run-off is negligible. A final prerequisite for pan formation, and subsequent preservation, is that the rate of eolian deposition must not exceed the rate of eolian deflation, otherwise depressions would be filled by the susceptible material and be, at least surficially, undetectable (Goudie & Wells, 1995).

In addition to these essential pan features, there are several others that are usually associated with pans or the environments in which they are found. In most cases, pan density is maximized in terrain that is characterized by a low angle slope, probably due to the lack of topographic interference with wind velocity in such areas. For example, in South Africa, where pan density may exceed 100/km^2, Hall (1913) noted that "their numbers increase in proportion as the physical features approach more closely to a flat table land." The prevalence of pans on coastal plains around the world provides additional support for this premise.

Many pans have a distinctive morphology and/or consistent orientation, such that long axes are transverse to formative winds. Shapes vary from circular to elliptical (with elongation ratios up to 3.5:1) to pork chop-shaped with crenulate margins on the windward side. Some pans exhibit no distinctive configuration. This variation in morphology is probably due to differences among depressions in water-holding capacity and the consistency of wind velocity and direction (Goudie & Wells, 1995). Lunette dunes are another feature commonly encountered along the leeward side of pans, and provide the most irrefutable evidence that pans are of eolian origin. In many cases, more than one set of dunes is present, indicating multiple formation episodes and dramatic alternations from humid to arid climates during the Holocene and Late Pleistocene (Goudie & Wells, 1995; Markewich & Markewich, 1994; Gamble et al, 1977; Thom, 1968). Furthermore, it should be understood that most pans existing today are relict features, formed by processes that are no longer operative. In a transition to more humid conditions during the mid-Holocene, many dunes became stabilized by vegetation, thereby arresting and, to some extent, reversing deflationary trends.

Carolina Bays

On the Atlantic Coastal Plain, Prouty (1952) reported that approximately 500,000 pans known as Carolina Bays occurred in flat areas with abundant surface sand. However, more recent reviews indicate that this number is exaggerated, and that less than 900 Carolina

Bays with relatively unaltered hydrology remain (Nifong, 1998). Nearly 80% of these are found on the Middle and Lower Coastal Plains of the Carolinas. Within this subset, the region with the highest concentration of large Carolina Bays is within the Cape Fear River basin, in an area known as Bladen Lakes region (Nifong, 1998; Soller, 1988).

Carolina Bays are perhaps most noted for their distinctive morphology and orientation. In shape, they are moderately elliptical to ovoid, with a mean elongation ratio of 1.5:1; in alignment, bays trend northwest-southeast with little deviation. This peculiar disposition has sparked much debate regarding the origins of Carolina Bays, and numerous theories have been proposed to explain them (Price, 1968). Recent studies have attributed bay formation to the combined action of wind and water, relating them to other oriented basins on the coastal plains of Texas, Chile, Alaska, and Australia (Thom, 1968, 1970; Kaczorowski, 1977; Goudie & Wells, 1995). This theory proposes that southwesterly winds blowing across the surface of ponded water resulted in currents that carved the distinctive shape and orientation of the bays.

Most Carolina Bays have a characteristic sandy lunette dune along their eastern rims. In some cases, multiple, overlapping, and juxtaposed lunettes are present, representing shifts in the timing and direction of wind flow. Presumably, these lunettes were formed during episodes that were drier than those that allowed for initial and periodic ponding of water in the bays. Goudie and Wells (1995) suggest that while carving of bay shape by wave current action provided the source of these loose sands, only during drier times would they be susceptible to entrainment and deposition on the bay margins. At least two stages of dune development along Carolina Bays have been identified based on mineralogic differences and radiocarbon dating of peat beneath dune deposits. The youngest of these dunes, by conservative estimates, are between 15,000 and 3,000 years old (Markewich & Markewich, 1994), although Soller (1985) ascribed a narrower range of 7,700 to 5,720 yBP. The older dunes, which are probably associated with the primary deflationary period of the Carolina Bays, exceed the limits of radiocarbon dating, but were most likely formed between 100 to 60 ka (Soller, 1985). This evidence suggests that not all Carolina Bays were formed during one cataclysmic event. On the contrary, their presence on multiple coastal plain terraces of varying age, and their association with at least two dune-forming episodes, suggests that conditions favorable for pan development on the Atlantic Coastal Plain have occurred more than once during the recent geologic past.

A Comparison of Carolina Bays and Bean Dips

Given the fact that both Carolina Bays and bean dips occur within the same geological province, it is natural to assume that these pans are related in origin. Since geological provinces are delineated based on the similarity of their history and modifying influences, we can also assume that the landscapes where bean dips and bays occur have witnessed comparable changes in climate and broad-scale tectonic activity. The numerous publications addressing Carolina Bay distribution, with few exceptions, set their western limit at the toe of the Orangeburg Scarp, where the Middle Coastal Plain meets the Upper Coastal Plain. This same feature marks the eastern limit of bean dips, although no description of these Sandhills depressions are known to exist prior to this thesis. In an exhaustive review of the geological literature, only one source was found that mentioned their existence. As partial evidence to support the stability and antiquity of the interstream divides in the Sandhills, Daniels et al (1978) cite the "presence of numerous depressional areas."

In a global review of the nature, distribution, and formation of pans, Goudie & Wells (1995) specifically cite the Carolina Bays as examples. Although bean dips in the Sandhills were not mentioned, similar, irregularly-shaped depressions were described from South America, Africa, and Australia, where the authors conducted most of their study. Given the large scale of the study, the remote location of the authors, the abundant literature on Carolina Bays, and the dearth of bean dip documentation, it is not surprising that the Sandhill depressions of this thesis were not mentioned. Nevertheless, based on my own experience, and discussions with local geologists, I propose that Carolina Bays and bean dips are related in the following ways:

1) Both bays and bean dips are widely distributed closed depressions that occur on the North and South Carolina Coastal Plain.

2) Both bays and bean dips were formed, in part, by eolian deflation, and, therefore, belong to the same geomorphological group known as pans.

3) Both bays and bean dips were formed in sandy substrates that are weathering products associated with transgressions and regressions of the Atlantic Ocean.

4) Both bays and bean dips currently support unique ecological communities and an abundance of "special status" plants (See Nifong, 1998; Chapter 1, this thesis).

5) The Atlantic Coastal Plain has witnessed dramatic alternations from humid to arid climates associated with glacial-interglacial cycles during the past 200,000 years. Strong winds during this period were necessary for deflation of bean dips and Carolina Bays.

6) The largest and best-developed Carolina Bays are in North Carolina, in the Cape Fear River basin. Based on a comparison of bean dips in North and South Carolina study sites (see Chapter 3), the largest and best-developed bean dips also occur in North Carolina, in the vicinity of the Cape Fear River basin. The proliferation of pans in this area may be due to a temporally persistent tectonic feature known as the Cape Fear Arch whose main axis is approximately parallel to the Cape Fear River. The lack of well-developed bays in the northern half of the South Carolina coastal plain has been correlated with the location of this area along the southern flank of the Arch, where the effects of uplift are not as pronounced. Lower sinuosity values and the presence of paired, symmetrical terraces within the upper Pee Dee River basin are cited as primary evidence of this north to south gradient in erosion and sedimentation patters (See Soller, 1985).

The most obvious dissimilarity between Carolina Bays and bean dips is the lack of regular shape and orientation exhibited by bean dips. I propose that these differences are attributable to differences in substrate characteristics and topographic setting. Since bay shape and alignment are considered the products of wind blowing across ponded water (Kaczorowski, 1977; Goudie & Wells, 1995), the lack of uniformity in shape and orientation in bean dips is probably due to their inability to hold water. This inability is probably caused by two factors. First, the sands in the Sandhills are relatively coarse and poorly-sorted, whereas sands of the Middle and Lower Coastal Plain, where Carolina Bays are found, are comparatively fine and well-sorted. Second, the depth of the water table in the Sandhills is considerably greater than it is on the Middle and Lower Coastal Plain. Consequently, precipitation in the Sandhills percolates rapidly through the coarse sandy matrix and reaches base level more quickly. Even if water could be ponded in the Sandhills, the more variable topography in this region would probably prevent the occurrence of sustained, unidirectional winds. However, on the flat-lying Middle and Lower Coastal Plain, the highest topographic features are generally less than 5 m above ground surface (i.e. lunettes associated with bays and dunes on northeastern segments of some rivers), and present little disruption to wind velocity.

Conclusions

Both Carolina Bays and bean dips are eolian deflation basins known as pans that developed on the Carolina Coastal Plain as a result of dramatic climate fluctuations in the Holocene and Pleistocene. They share many features in common, but differences in their formative substrate and topographic position, and the effects they have had on wind and water, have produced different basin morphologies and alignment. Variation in the size and distribution of pans between the North and South Carolina Coastal Plain are potentially explained by the presence of the Cape Fear Arch, and the position of these two areas relative to its main axis. This feature may also help to explain some of the broad environmental differences between the North and South Carolina Sandhills that are discussed in Chapter 3.

CHAPTER III.

NATIVE LEGUME DISTRIBUTIONS ALONG EDAPHIC AND TOPOGRAPHIC GRADIENTS OF BEAN DIPS AND PEA SWALES

Introduction

The frequently-burned longleaf pine forest of the Carolina Sandhills supports an abundance and diversity of native legume species (Leguminosae). In North Carolina, floristic surveys of the Sandhills Gameland and Ft. Bragg/Camp Mackall indicate that 56 and 58 native legumes occur within these boundaries, respectively (Sorrie, 1998; Sorrie et al, 1993). 48 native legumes have been identified in preliminary surveys on the Carolina Sandhills National Wildlife Refuge in Chesterfield County, South Carolina (Mejeur et al, 2000).

Despite their abundance, legumes are not evenly distributed in the Sandhills. Within this predominantly xeric landscape, legume species richness and density are maximized in small, isolated depressions. These landforms, also know as bean dips and pea swales, have been formally identified as the Loamy Soil Variant of the Pine/Scrub Oak Sandhill Community (Schafale & Weakley, 1990), and they may represent the most species-rich community in the Sandhills (Sorrie, 1998; See Chapter 1, this thesis). Along the slopes of these depressions, strong patterns in legume species sorting can be viewed over relatively short distances.

The distribution of legumes has been correlated with physical environmental gradients in several studies of southeastern longleaf pine communities. In southwest

Georgia, Hainds (1999) also found an abundance of legumes, and determined that soil moisture, which was inversely correlated with percent sand, was the variable that most strongly influenced legume distributions. Approximately 100 km south of this study location, in the Apalachicola National Forest, Clewell (1971) observed a conspicuous absence of legumes in wet longleaf pine savannas, and suggested a negative correlation with the anoxic conditions characteristic of these soils. In the northeastern part of the longleaf range, Walker & Peet (1983) described 3 classes of savannas—wet, mesic, and dry—from the Green Swamp in North Carolina, and noted that legumes were generally absent from wet and mesic savannas, but a common component of the dry savannas. Taggart (1990) confirmed this observation, and classified these legume-rich communities as dry, ultisol savannas.

Collectively, the above-mentioned studies indicate that legumes in longleaf pine forests are distributed along a complex ecological gradient shaped by soil moisture and texture. These results are supported by the findings of Peet & Allard (1993) who proposed a regional classification system for all longleaf pine-dominated communities. They identified four major series, also defined by a soil moisture gradient: xeric, sub-xeric, mesic, and seasonally wet. It is important to remember, however, that the terms mesic or xeric are situation-dependent, and relative to the dominant moisture conditions in an area. For example, on the longleaf pine savannas of the Lower and Middle Carolina Coastal Plain, where saturated soils dominate, legume abundance is maximized under more xeric conditions found on small, isolated, convex islands. To the contrary, my preliminary observations in the Sandhills, where xeric conditions are overwhelming dominant, indicated that legume density and diversity were enhanced in mesic, concave basins known as bean dips. Clarification of these regional differences in legume response was also a major stimulus to the implementation of this research.

In this chapter, I describe a survey of legume distributions along the slopes of bean dips and pea swales at two study sites in the Carolina Sandhills, one in South Carolina and one in North Carolina. Two study sites were selected because of preliminary observations that species diversity and productivity were generally lower on the Carolina Sandhills National Wildlife Refuge (SC) than on the Sandhills Gameland (NC). At each study site, legume density, soil texture and chemistry, and relative elevation were measured at regular intervals along transects established on the slopes of bean dips and pea swales. This experimental design allowed me to answer the following questions: 1) Does bean dip size, frequency, and elevation differ between study sites? 2) Do soil texture and chemistry vary across the topographic gradient from the lowest point to the adjacent upland? 3) Are legume distributions correlated with the physical factors that change along this gradient? and 4) Are the legume and soil gradients similar in North Carolina and South Carolina study sites?

Methods

Study Area

The two study sites were located in the Carolina Sandhills, a northeast-southwest-trending sub-province also known as the Upper Coastal Plain (Fig. 2.1). Unlike the flat-lying Middle and Lower Coastal Plains east of this region, Sandhills topography is moderately rolling and, in most places mantled in deep, coarse, and highly-weathered sands (See Chapter 2).

The Sandhills Gameland in North Carolina served as the northern study site because of the many well-developed bean dips and other loamy soil communities located there. This 23,000 ha property is managed by the North Carolina Wildlife Resources Commission for recreation and 100-year rotation timber production. It lies in portions of Moore, Scotland, and (mostly) Richmond Counties, approximately 65 km northeast of the Great Pee Dee River where it flows over the Orangeburg Scarp near Cheraw, South Carolina (Doering, 1960). The Pinehurst Formation is generally continuous across the upland surfaces of the Gamelands (Owens, 1989). Soil surveys of the Richmond County portion of the Gamelands show Ailey, Wakulla, and Candor series to be dominant. Respectively, these ultisols are loamy, siliceous, thermic Arenic Kanhapludults, sandy siliceous, thermic Psammentic Hapludults, and sandy siliceous thermic Arenic Paleudults (Evans, 1999). The Moore County Gamelands are also dominated by Candor-Ailey, but include the Vaucluse series instead of Wakulla. Vaucluse is characterized as a fine-loamy siliceous thermic typic Kanhapludult (Wyatt, 1995).

The 20,000 ha Carolina Sandhills National Wildlife Refuge in Chesterfield County, South Carolina, served as the southern study site. This federal property is primarily managed to maximize wildlife habitat and timber production. The Refuge also boasts the southeast's highest red-cockaded woodpecker density. Based on 7.5' USGS topographic maps, the Refuge appears to have fewer plateau-like interfluves, and more narrow ridges with distinct divides. Thus, the Refuge landscape is characterized by more broken topography than the Gamelands. In addition, the distribution of Pinehurst sands in this part of South Carolina is extremely scant and discontinuous. Only the crests of the highest hilltops are thinly mantled with the deposit (Nystrom et al, 1991). Instead, most of the deep sands on the Refuge appear to be colluvium, a weathering product of the Cretaceous sandy-clays that have subsequently crept downslope (Nystrom, pers. comm; Newell et al, 1980). The type locality of the Middendorf Formation lies within the Refuge proper along a railroad cut just east of Black Creek. Approximately 70% of the soils on the Refuge have been mapped as the excessively-drained Alpin-Candor series. Respectively, these are thermic, coated Quartzipsamments and sandy, siliceous thermic Arenic Paleudults.

Field Methods

Site Selection

Between June and August 1998, ten bean dip or pea swale sites were selected from each study area. Criteria for inclusion in the study were 1) the sites had to have been burned at least once since 1995, 2) the sites had to show no evidence of recent human disturbance, and 3) the sites had to occur between the elevations of 90-130 m. This sampling range was selected because it included 97% of all Gameland bean dips and eliminated the numerous bean dips that occurred above 130 m on the Refuge (75%). Due to the decreased area of upstream watershed at these high elevations, patterns in legume response (turnover, density, and richness) to local elevation are not as pronounced. In order to control for differences between sites that might be related to elevation, it was deemed preferable to restrict the sampling range to one that included the maximum number of bean dips at both sites.

With these criteria in mind, potential sites were first identified as topographic depressions on 7.5' USGS quadrangle maps, then verified for fire history using records at Gamelands and Refuge headquarters. A field visit was then conducted to determine the disturbance condition of the potential sites. On the Refuge, this final step in the site selection process eliminated 13 of the 15 bean dips that occurred between 90-130 m, mostly due to conversion of the land for agricultural purposes. Consequently, eight pea swales and two bean dips were selected. On the Gamelands, most bean dips met the criteria for site selection. Nine of these were randomly selected, and one pea swale site was included for comparison to pea swales on the Refuge. Although this imbalance of landforms between study sites was not desirable, it is indicative of some of the important landscape and management differences between study sites.

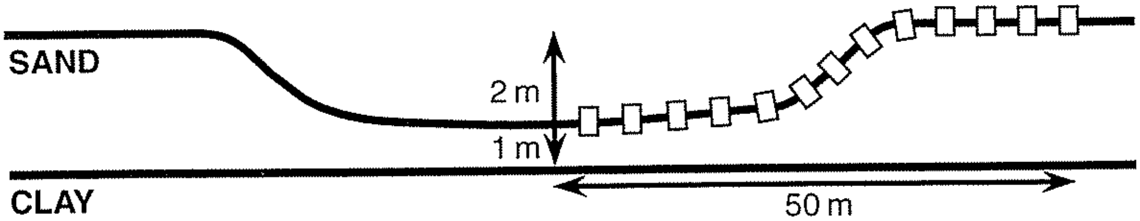
Transect Establishment

At each site, transects of 40 to 60 m were established along a topographic gradient. Most transects were anchored near the lowest point of the site, and extended upwards in the direction of maximum slope (Fig. 3.1). Three of the sites were so small that it was necessary for transects to completely bisect the site to provide adequate sample size; for these, the lowest point occurred near the middle of the transect. Transects ended at the approximate boundary between the Loamy Soil Variant and the Pine/Scrub Oak Sandhill community, or just upslope of this interface, where legume turnover, and plant productivity in general, diminished considerably.

Legume Sampling

At 1 m intervals along each transect, a 0.5 x 1.0 m quadrat was oriented with the long axis perpendicular to the direction of maximum slope. Within these quadrats, all legumes were identified (taxonomy follows Isely, 1990), and the number of stems per species was counted. Some problematic species of *Desmodium* and *Lespedeza* were encountered. These

Figure 3.1. Hypothetical cross-section of bean dip or pea swale with transect.


SAND
2 m
1 m
CLAY
50 m

were identified only to genus. Voucher specimens for all legume taxa encountered during sampling have been deposited in the UNC Herbarium (NCU).

Soil Sampling

Eight or nine soil samples were collected at 10 m intervals along each transect, and from the quadrats containing the highest legume richness and/or density (a total of 161 soil samples). Within these selected quadrats, approximately 500 grams of soil were extracted from 5-15 cm below the soil surface in each half of the quadrat, then combined. These composite samples were sieved using a 2 mm sieve (ASTM #10) to remove coarse fragments, then dried in a 70° C oven for 48 h. 50 g samples were sent to separate soil laboratories for texture and nutrient analysis. Brookside Laboratories, Inc. performed the soil texture analyses for all samples according to the Bouyoucos/Hydrometer Method (ASTM #D422-63). Particle fractionation yielded values for percent sand, silt, and clay for each soil sample. The Agriculture Service Laboratory at Clemson University performed all of the nutrient analyses. Concentrations of P, K, Ca, Mg, Mn, Zn, Cu, and B were determined using a Mehlich I extractant. Cation exchange capacity (CEC) was calculated based on the results of the elemental analyses. Soil pH was determined using a 1:1 dilution of soil and water and a standard pH meter.

Relative Elevation

Relative elevations were measured at 5 m intervals along all transects. At each site, a Lietz-Sokkisha Model 115 transit was mounted and leveled on a tripod at the upper end and in line with the transect. Readings were made to the nearest centimeter, and subsequently standardized to make the elevation of each quadrat equivalent to the height above the lowest point encountered along the transect (HALP).

Slope Classes

Relative elevations and field observations were used to divide each transect into the following slope classes: 1=bottom; 2=lower slope; 3=mid-slope; and 4=upper slope/rim. Consequently, each quadrat was assigned to one of these slope classes. Although extreme variation in slope between transects prevented the establishment of exact elevation parameters, all slope class 1 quadrats were less than 0.3 m above the lowest point.

Analytical Methods

Landform Analysis

7.5' USGS topographic maps were used to compare differences in size and elevation of bean dips between North and South Carolina study sites. For the Gamelands, this information was gleaned from the Marston, Hoffman, Silver Hill, Pinebluff, and Millstone Lake quadrangles. The Refuge lands are mapped on portions of the Middendorf, Ruby, Bethune, Angelus, Jefferson NE, and Lake Robinson quadrangles. All bean dips that could be identified as contained topographic depressions on these maps were estimated for area and elevation. The error of the elevation estimates was +/- 10 feet, based on the contour intervals of these maps. Bean dip area was estimated using a transparent, 1 x 1 inch grid divided into 100 cells, each of which was approximately equal to one acre at the 1:24,000 scale of these maps. This grid was overlain on each bean dip and the number of cells (acres) occupied was counted to the nearest ¼ cell.

Data Analysis

An assortment of statistical methods was used to compare differences in legume distributions and soil texture and nutrient levels between and within study sites. Few of the measured parameters approximated a normal distribution, therefore, mostly non-parametric methods were chosen. Each dataset was originally tabulated in spreadsheet format using Excel 1997. The remainder of the operations were performed using SAS 7.0.

Spearman correlation coefficients, and measures of their significance were determined for each possible pair of soil variables (PROC CORR). Each quadrat with soil data was treated as an independent sample point. A non-parametric version of a one-way ANOVA (PROC NPAR1WAY) was used to analyze differences in nutrients and texture between slope classes within each study area and between study areas by slope class. Wilcoxon scores for each soil parameter were calculated and compared using the Kruskal-Wallis test to determine if differences were significant between slope classes.

For each legume species encountered, percent occurrence per slope class was calculated for each study site separately, then for both study sites combined (PROC FREQ). For each of these permutations, a likelihood ratio chi-square statistic was calculated to determine whether differences were significant among slope classes. Queries regarding total legume species richness were made following the same procedure described above for comparing soil parameters by slope class and between states.

The only manipulation of the slope dataset involved interpolation of unknown relative elevations between quadrats with measured height above lowest point (HALP). This was accomplished using the Econometric and Time Series function available in SAS 7.0. ETS averages values between two known points and estimates values that occur between them.

Results

Landscape Comparisons Between Study Sites

USGS 7.5' topographic map coverage of the study sites reveal that bean dips occur at similar frequencies on the Gamelands (n=66) and the Refuge (n=58). Relative to the size of each property, bean dip frequency in the Gamelands is 1/350 ha, and 1/335 ha on the Refuge. However, the mean size of bean dips is 65% larger on the Gamelands (p<.0057) (Fig. 3.2). On the Refuge, 71% of dips are less than 1 ha, and no dips larger than 8 ha are known to exist. On the Gamelands, dips less than 1 ha are also common (53%), but larger size classes are well-represented, too. The 3 largest dips on the Gamelands are approximately 12, 11, and 7.4 ha. On the Refuge, the three largest are 8.0, 7.9, and 3.8 ha.

Study sites also differ significantly in terms of average bean dip elevation (Fig. 3.3). The mean elevation of bean dips on the Gamelands is 20 m lower than on the Refuge (p<.0001). Across sites, bean dips are located between 85-170 m above sea level, but 47% of the dips on the Refuge occur above the maximum bean dip elevation on the Gamelands. 97% of all Gameland bean dips occur between 90-130 m, whereas, 75% of Refuge bean dips are located at higher elevations.

Legumes

Combined, the twenty transects from each study area contained a total of 1,060 quadrats with legume composition and density data. 540 of these were located on the Refuge

Fig. 3.2. Area of Bean Dips on the Refuge & Gamelands

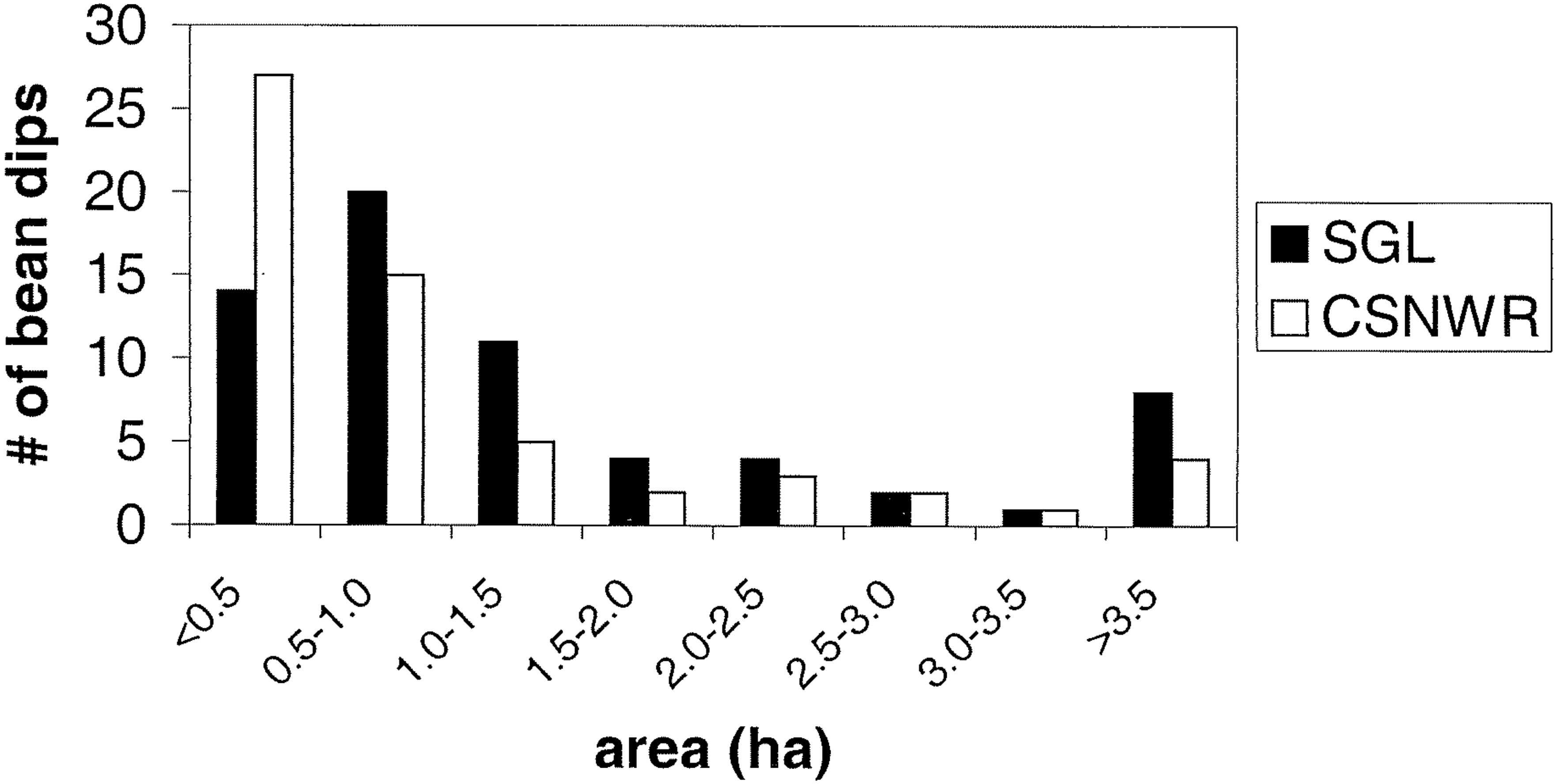
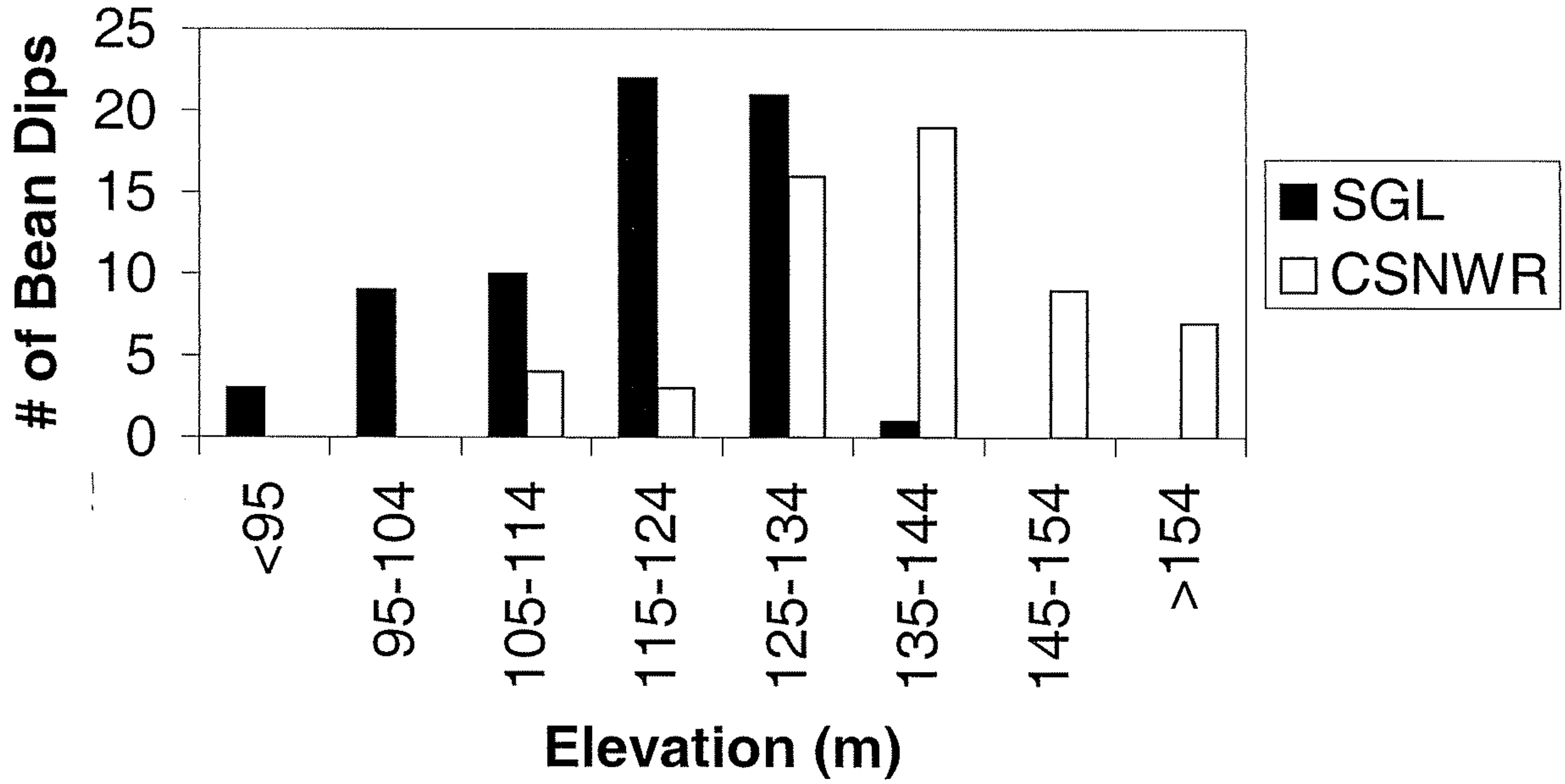


Fig. 3.3. Elevation of Bean Dips on the Refuge & Gamelands



and contained a total of 7,067 legume stems, whereas the Gamelands had 520 quadrats containing 7,441 stems. The number of quadrats per slope class was also evenly distributed among the Gamelands and Refuge study sites (Fig. 3.4).

Across all transects, 37 native legume taxa representing twenty genera were encountered. 27% of all taxa encountered occurred only in Refuge quadrats or only in Gamelands quadrats. Table 3.1 presents these results, also indicating which taxa are only known to occur in either of the study areas, based on the floristic surveys of Sorrie (1998) on the Gamelands and Mejeur et al (2000) on the Refuge. Non-native legumes were rarely present within the sampled quadrats. *Lespedeza cuneata* (Chinese lespedeza), an Asian species, occurred in only three Refuge plots, all slope class 1.

Legume Species Richness

A strong decline in legume species richness with increasing slope position was detected in both study areas (Fig. 3.5). Differences in species richness between slope classes were highly significant in both cases ($p<.0001$). On the Refuge, mean legume richness decreased by 51% from slope class 1 to 2, 44% from slope class 2 to 3, and 47% from slope class 3 to 4. On the Gamelands, the decline in species richness between slope classes 1 to 2 and 2 to 3 was slightly less precipitous (38 and 41%), but the change from class 3 to 4 was more pronounced (70%). The maximum species richness recorded in one quadrat occurred on the Gamelands, which contained *Chamaecrista nictitans* var. *nictitans, Desmodium strictum, Galactia mollis, Galactia regularis, Lespedeza virginica, Phaseolus sinuatus, Stylosanthes biflora,* and *Tephrosia floridana*. 268 quadrats (25%), mostly in slope classes 3 and 4 contained no legume species. Of these, 103 (38%) were Gamelands quadrats, and 165 (62%) were Refuge quadrats (Fig. 3.6).

Fig. 3.4. Number of Quadrats Sampled per Slope Class on the Refuge & Gamelands.

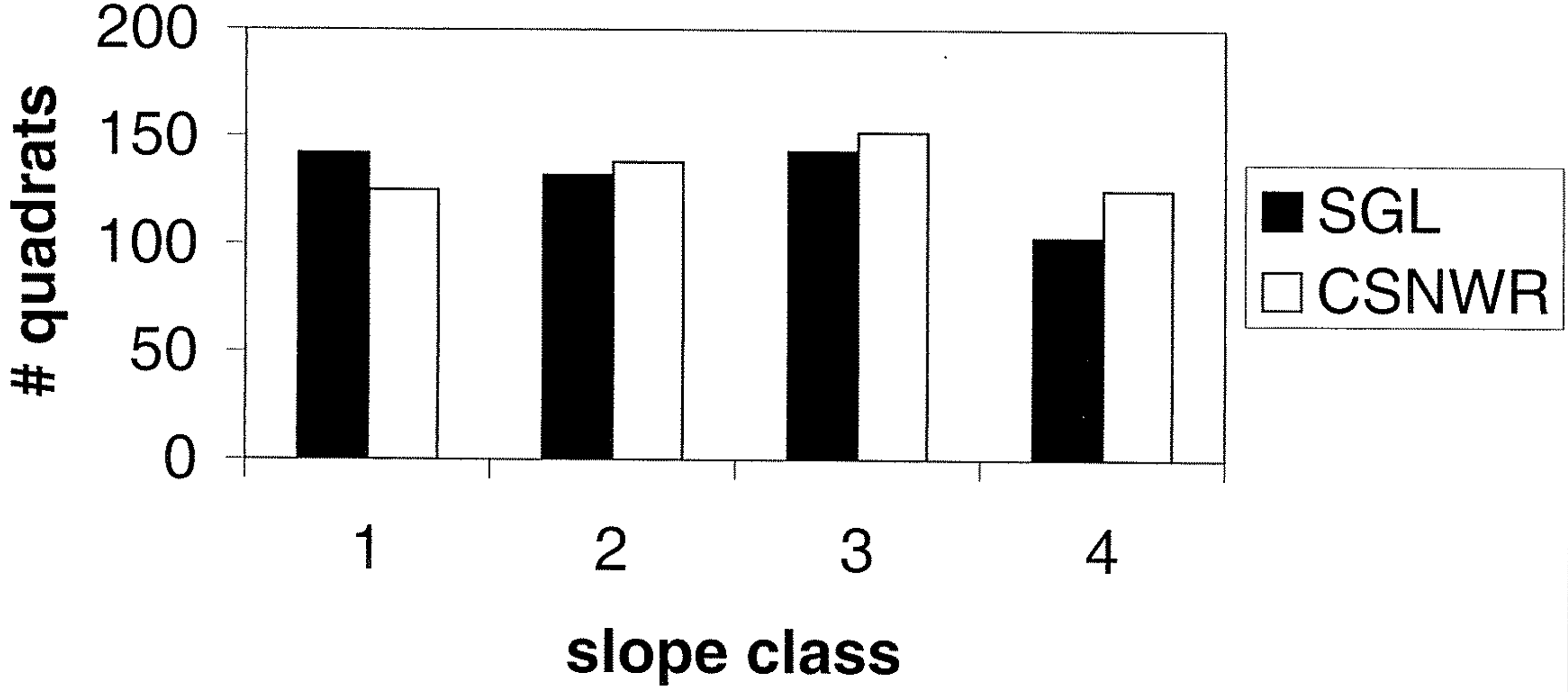


Table 3.1. Legumes Encountered during 1998 Sampling on the Refuge and Gamelands.

Native Legumes Encountered at both Study Sites

- *Amorpha herbacea* var. *herbacea*
- *Astragalus michauxii**
- *Baptisia cinerea*
- *Baptisia tinctoria*
- *Centrosema virginianum*
- *Chamaecrista nictitans*
- *Clitoria mariana*
- *Crotolaria purshii*
- *Crotolaria rotundifolia*
- *Dalea pinnata* var. *pinnata*
- *Desmodium ciliare*
- *Desmodium laevigatum*
- *Desmodium lineatum*
- *Desmodium nuttallii*
- *Desmodium obtusum*
- *Desmodium strictum*
- *Galactia erecta*
- *Galactia mollis**
- *Galactia regularis*
- *Galactia volubilis*
- *Indigofera caroliniana*
- *Lespedeza hirta* var. *hirta*
- *Lespedeza procumbens*
- *Lespedeza repens*
- *Lespedeza stuevii*
- *Lespedeza virginica*
- *Lupinus diffusus*
- *Orbexilum lupinellum**
- *Pediomelum canescens**
- *Phaseolus sinuatus**
- *Rhynchosia reniformis*
- *Rhynchosia tomentosa*
- *Schrankia microphylla*
- *Stylosanthes biflora*
- *Tephrosia florida*
- *Tephrosia spicata*
- *Tephrosia virginiana*

* rare plant (see Table 1.2 for status)

Legumes in Refuge quadrats only

- *Amorpha herbacea* var. *herbacea*
- *Baptisia tinctoria*
- *Indigofera caroliniana*
- *Lespedeza cuneata*
- *Lupinus diffusus*

Legumes in Gameland plots only

- *Astragalus michauxii*
- *Dalea pinnata* var. *pinnata*
- *Galactia mollis*
- *Lespedeza stuevii*
- *Pediomelum canescens*

Species only on Refuge

(Mejeur, 2000)

- *Amorpha herbacea* var. *herbacea*
- *Desmodium floridanum*

Species only on Gamelands

(Sorrie, 1998)

- *Desmodium glabellum*
- *Desmodium marilandicum*
- *Desmodium nudiflorum*
- *Desmodium perplexum*
- *Desmodium rotundifolium*
- *Desmodium tenuifolium*
- *Galactia mollis*
- *Lespedeza angustifolia*
- *Lespedeza intermedia*
- *Lupinus perennis*
- *Pediomelum canescens*
- *Zornia bracteata*

Fig. 3.5. Mean Legume Richness by Slope Class on the Refuge & Gamelands.

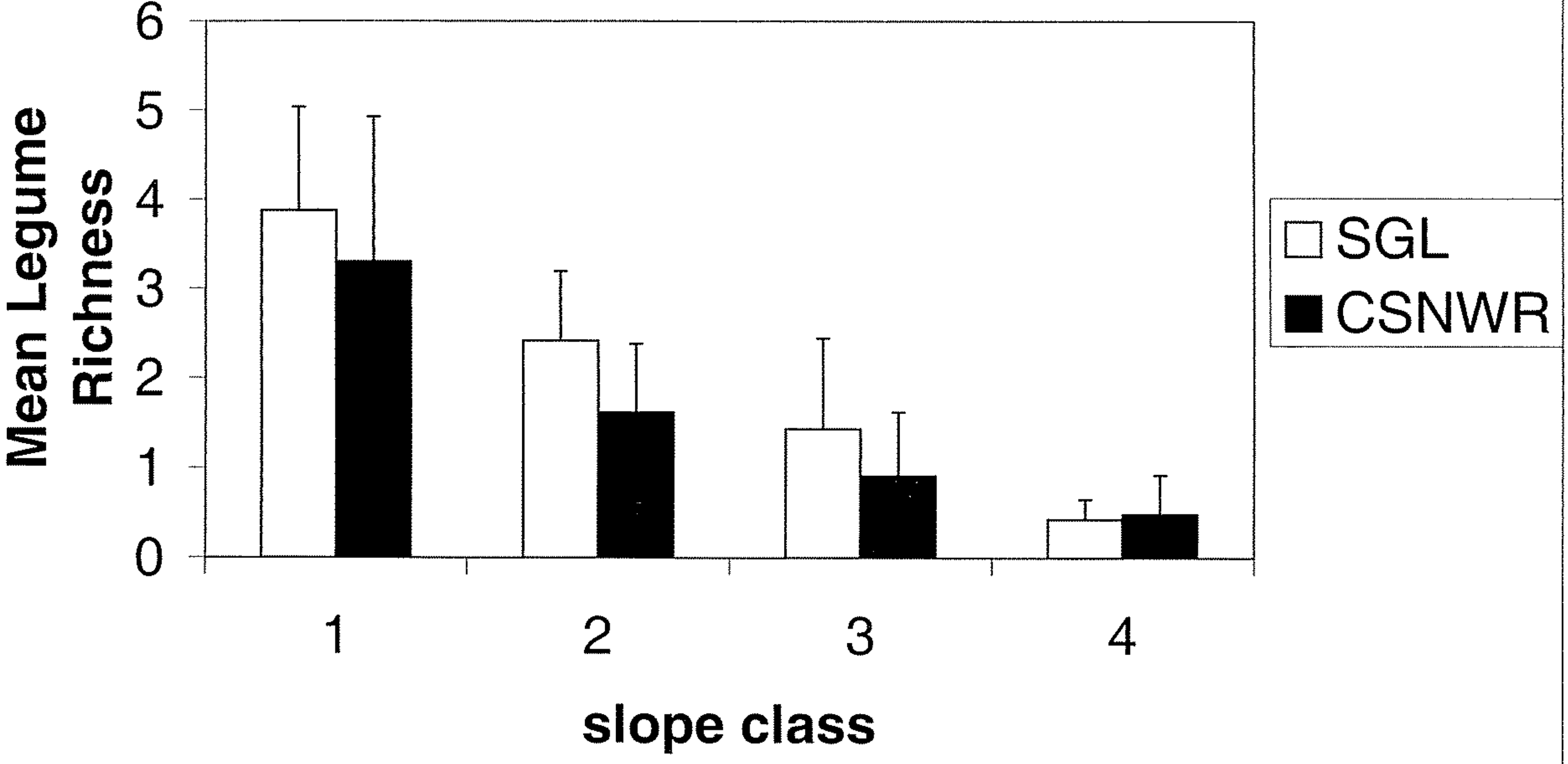
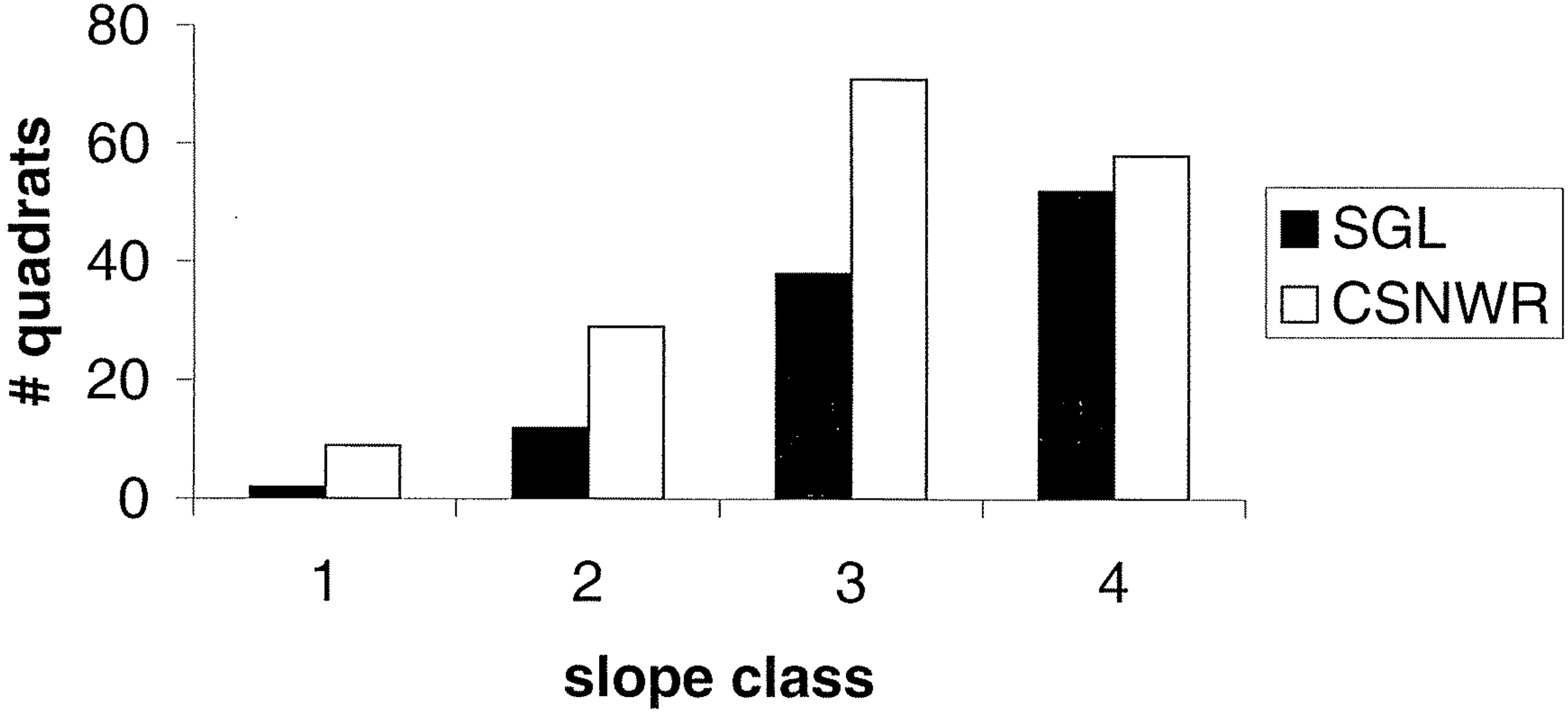


Fig. 3.6. Number of Quadrats without Legumes by Slope Class on the Refuge & Gamelands.



Comparisons between study sites indicate that legume species richness was generally higher in the Gamelands quadrats. This trend was highly significant for slope classes 1, 2, and 3 (p<.0005, p<.0001, p<.0037), but there were no detectable differences between slope class 4 quadrats. When classes 1 and 2 were lumped as "bottoms" and 3 and 4 as "tops," species richness was significantly higher on the Gamelands for both "bottoms" (p<.0001) and "tops" (p<.0237).

Individual Legume Distributions

Of the 37 species encountered during sampling, sixteen on the Gamelands and fourteen on the Refuge occurred frequently enough to warrant further exploration of their distribution trends (Fig. 3.7 & 3.8). The differences in percent occurrence between slope classes were highly significant for these species (Gamelands: .0068<p<.0001; Refuge: .0086<p<.0001). Fig. 3.9-3.20 show percent occurrence by slope class for the species that occurred with sufficient frequency in both study areas. *Amorpha herbacea* var. *herbacea* occurred with sufficient frequency to be studied further on the Refuge, but not on the Gamelands (Fig. 3.21). All *Desmodium* and *Lespedeza* species not included in the preceding group were combined and compared in an identical fashion. The percent occurrence by slope class for these genera is shown in Fig. 3.22-3.23.

On the Gamelands, twelve species occurred less frequently as slope class increased. Those occurring most often in slope class 1 include *Desmodium ciliare, Desmodium obtusum, Galactia erecta, Galactia volubilis, Lespedeza procumbens, Lespedeza repens, Rhynchosia reniformis,* and *Stylosanthes biflora.* Of these, *Desmodium obtusum, Galactia erecta, Galactia volubilis,* and *Lespedeza procumbens* were never recorded in slope class 4. When all other *Desmodium* and *Lespedeza* species were combined, they also occurred most

Fig. 3.7. Legume Species Presence by Slope Class on the Gamelands.

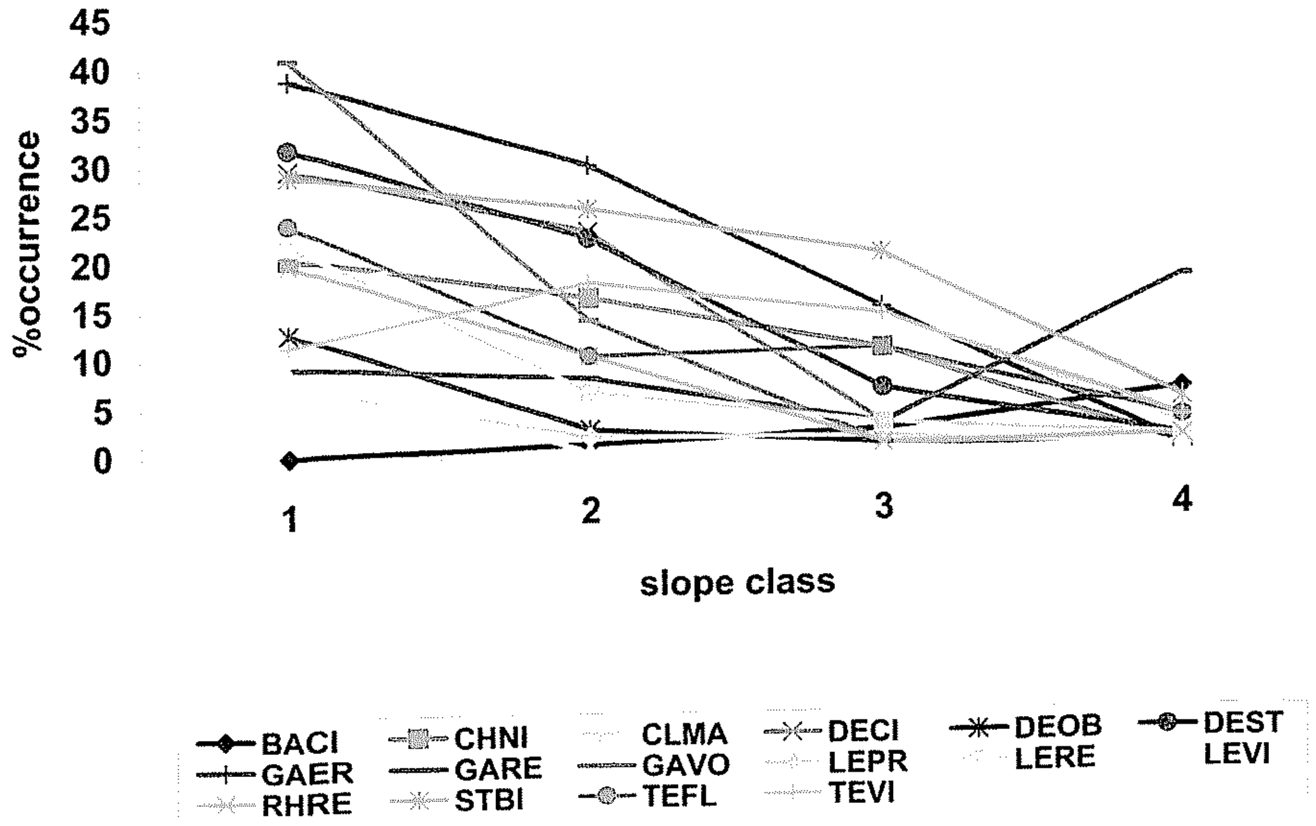


Fig. 3.8. Legume Species Presence by Slope Class on the Refuge.

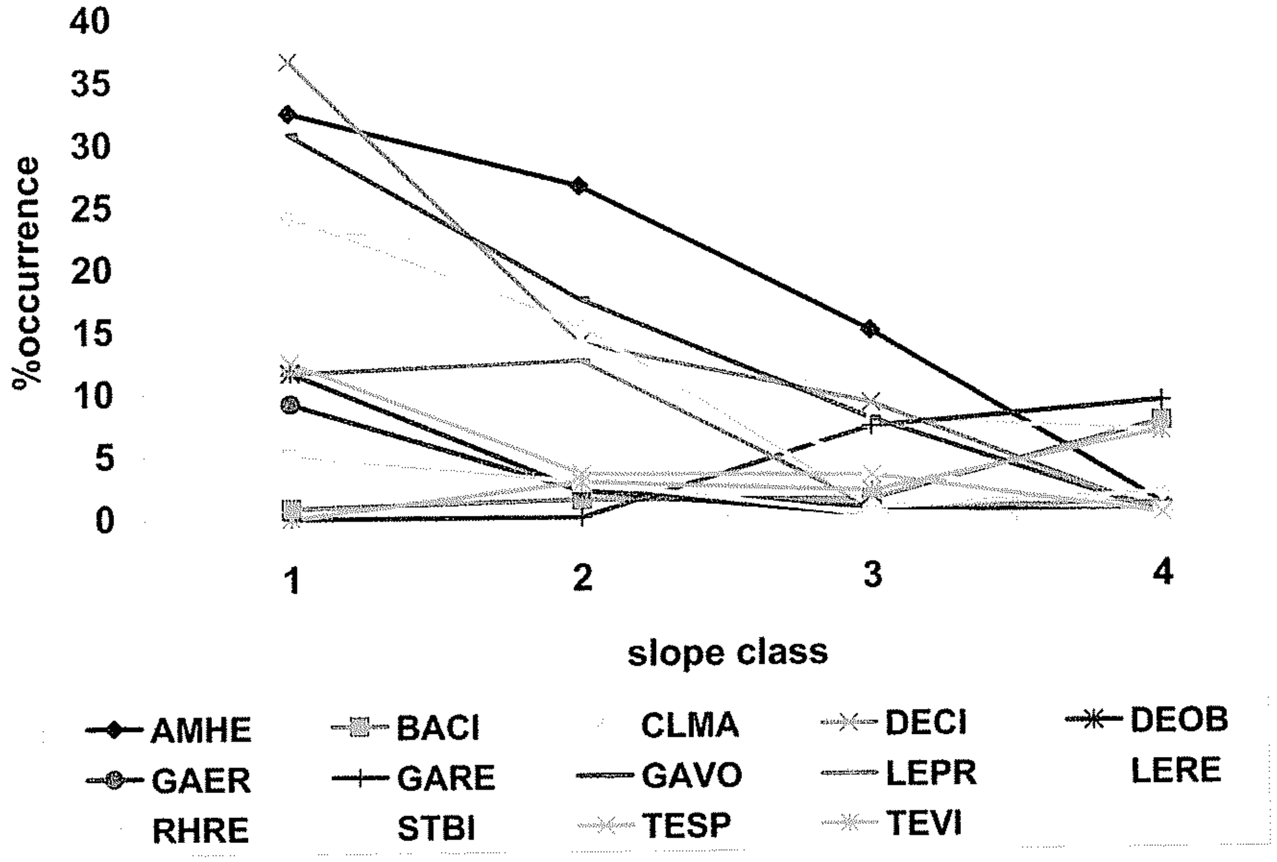


Fig. 3.9. Percent Occurrence of *Baptisia cinerea* by Slope Class on the Refuge and Gamelands.

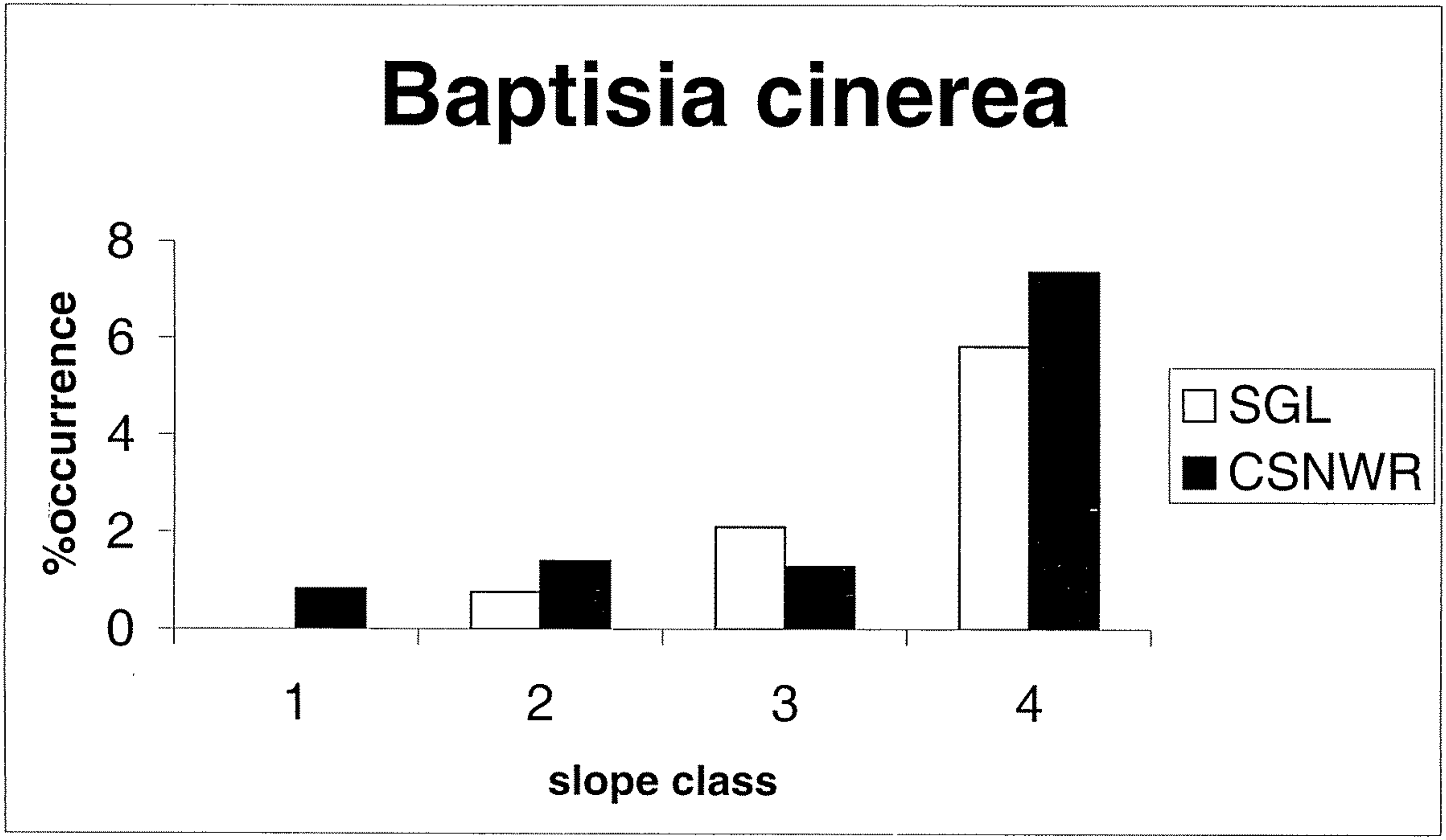


Fig. 3.10. Percent Occurrence of *Clitoria mariana* by Slope Class on the Refuge and Gamelands.

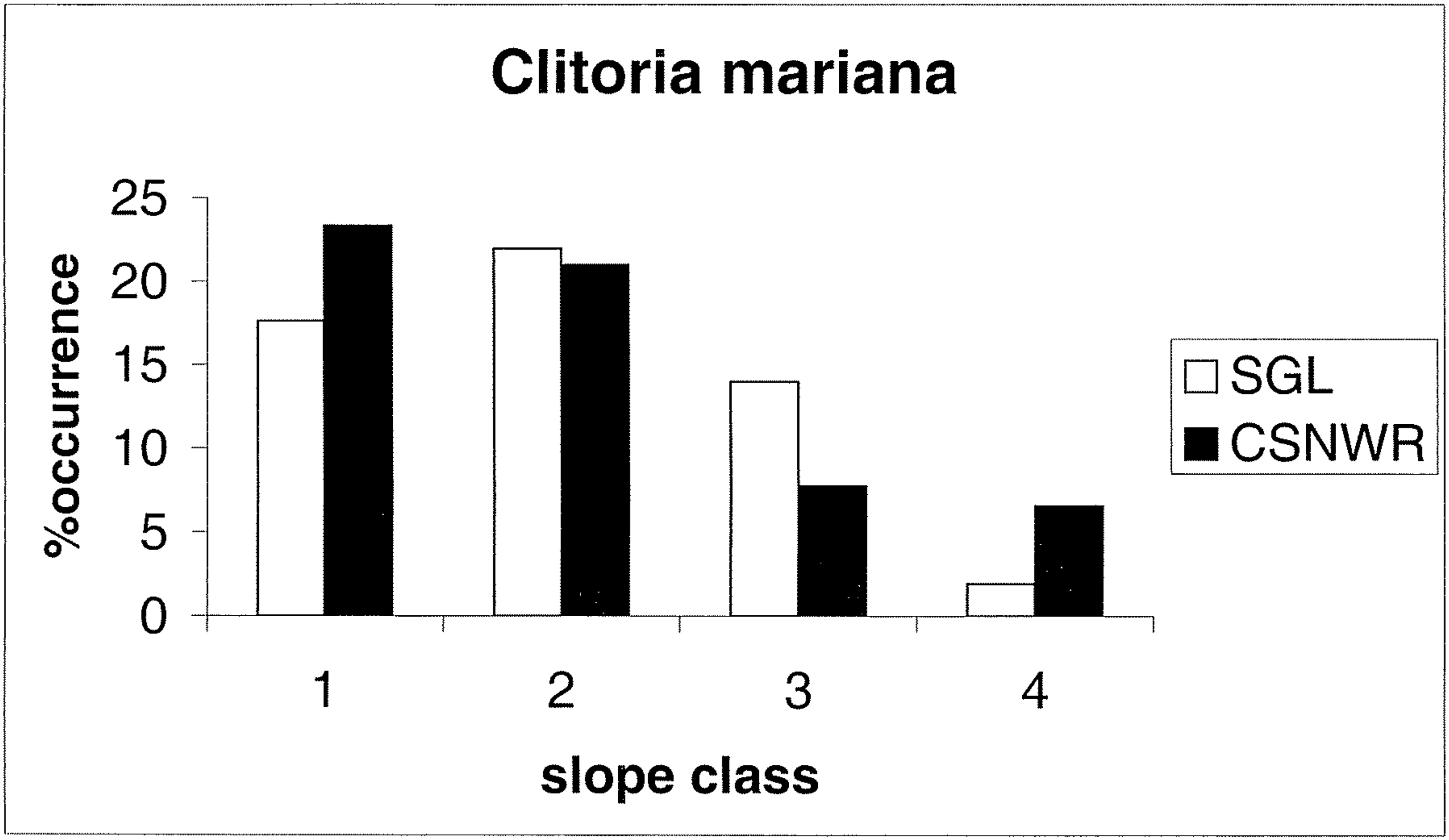


Fig. 3.11. Percent Occurrence of *Desmodium ciliare* by Slope Class on the Refuge and Gamelands.

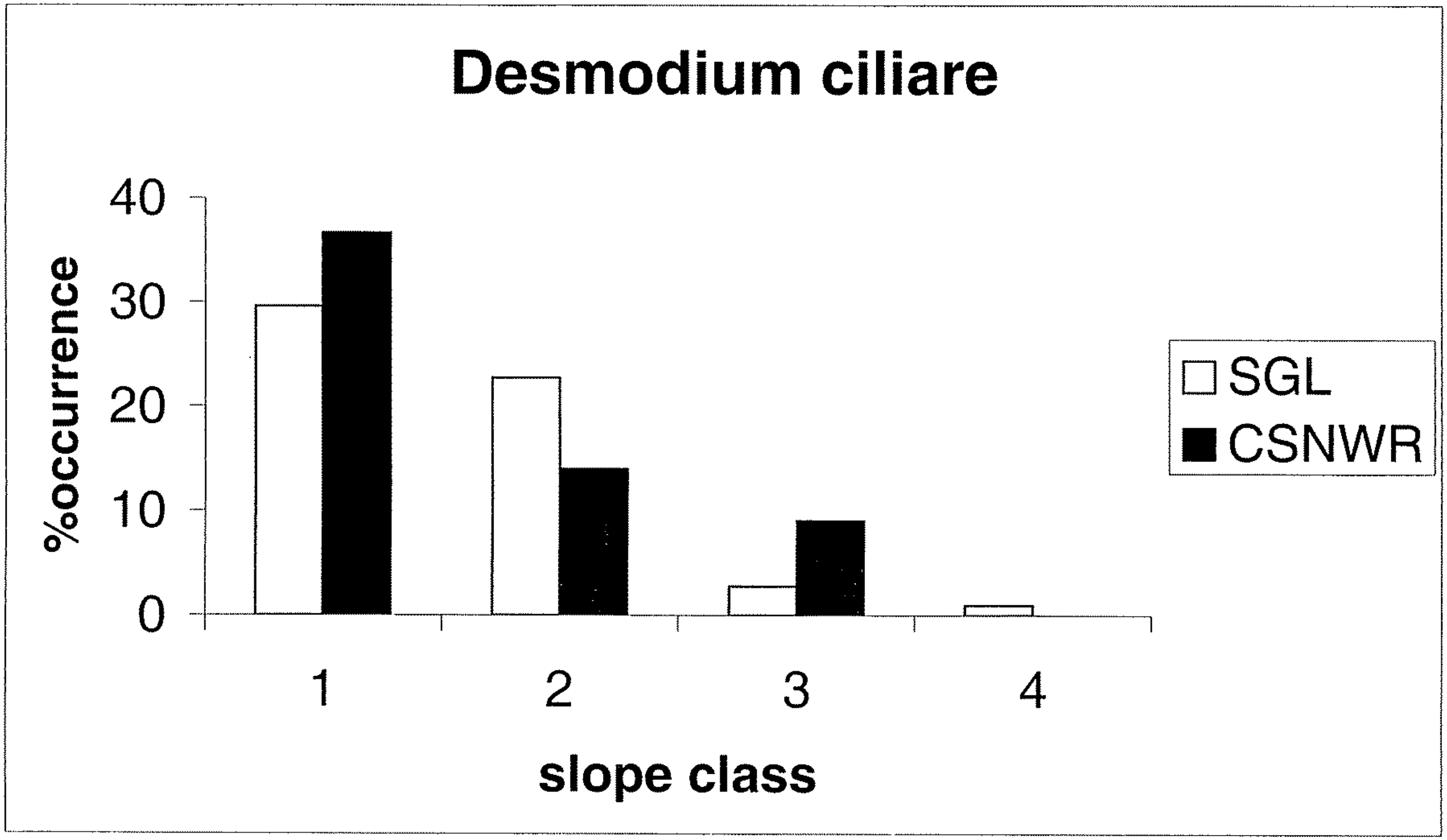


Fig. 3.12. Percent Occurrence of *Desmodium obtusum* by Slope Class on the Refuge and Gamelands.

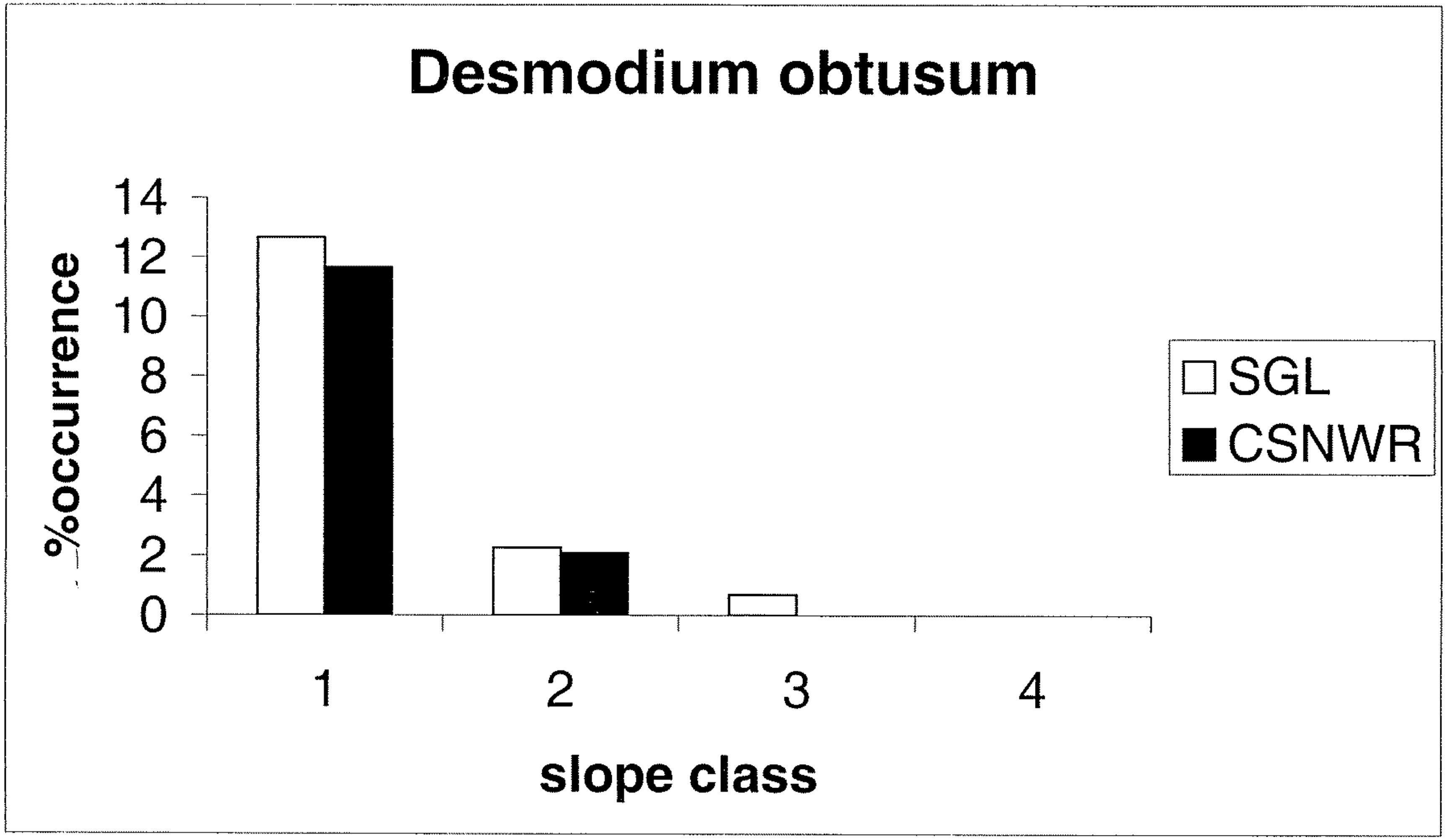


Fig. 3.13. Percent Occurrence of *Galactia erecta* by Slope Class on the Refuge and Gamelands.

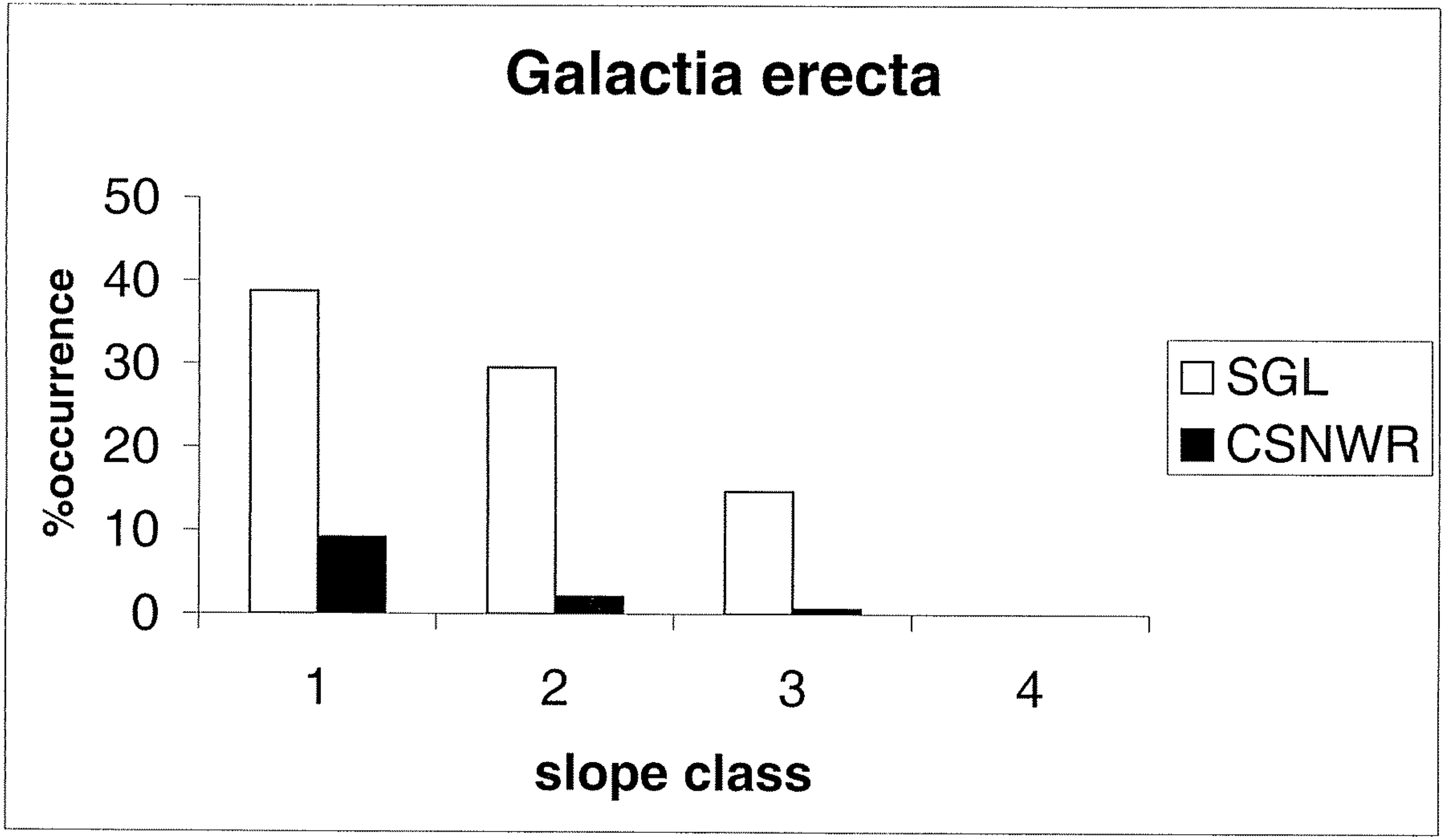


Fig. 3.14. Percent Occurrence of *Galactia regularis* by Slope Class on the Refuge and Gamelands.

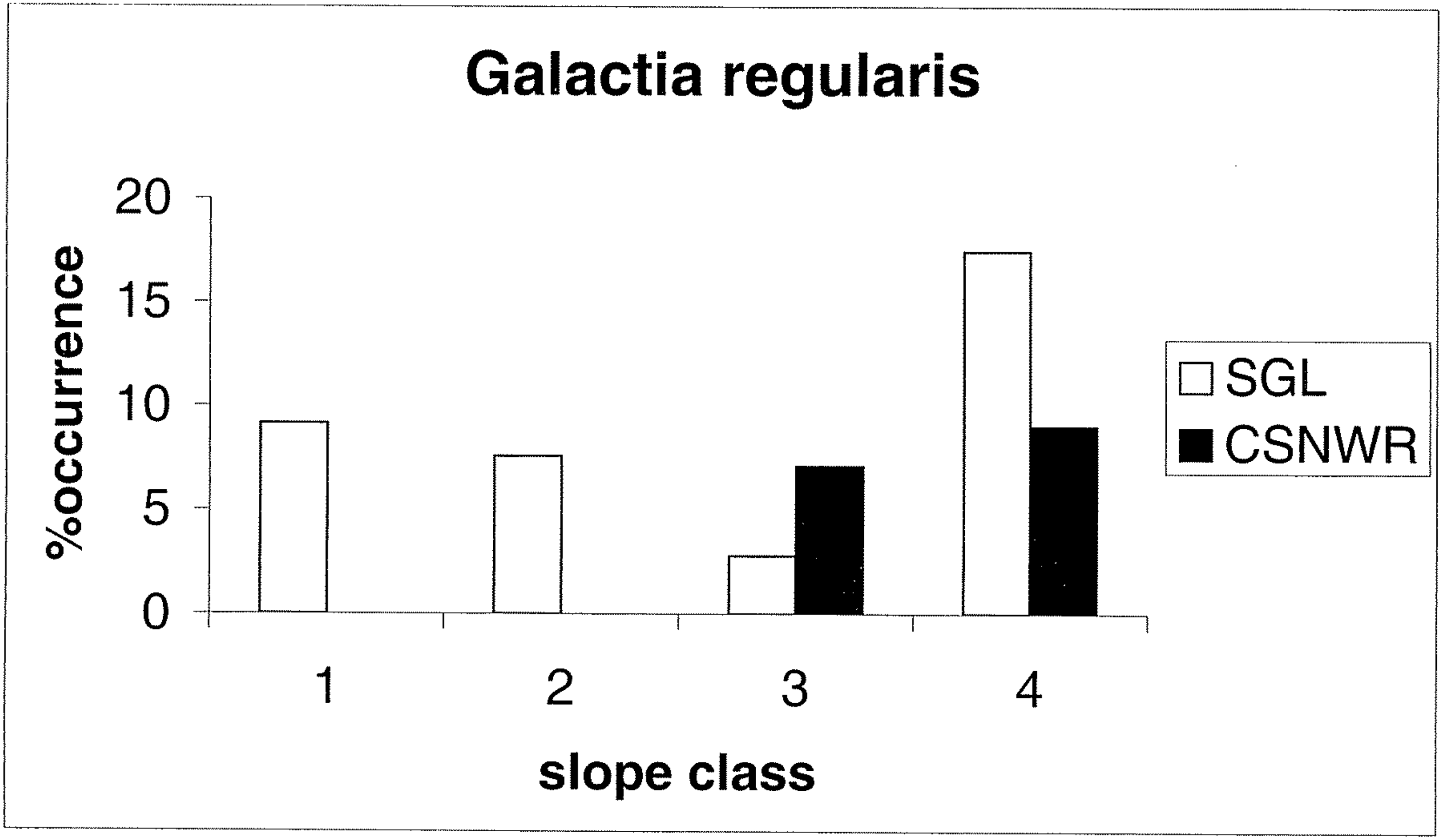


Fig. 3.15. Percent Occurrence of *Galactia volubilis* by Slope Class on the Refuge and Gamelands.

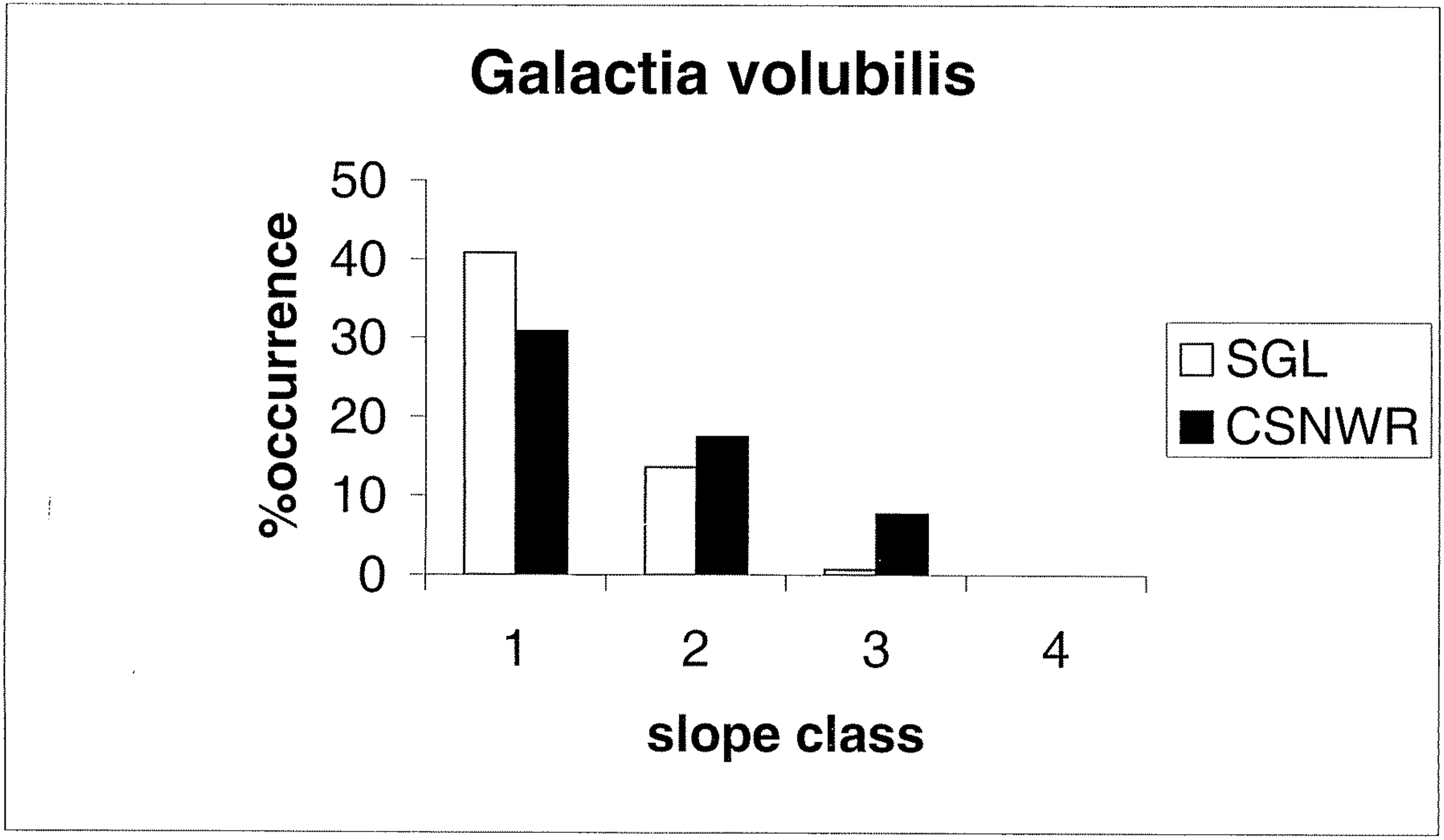


Fig. 3.16. Percent Occurrence of *Lespedeza procumbens* by Slope Class on the Refuge and Gamelands.

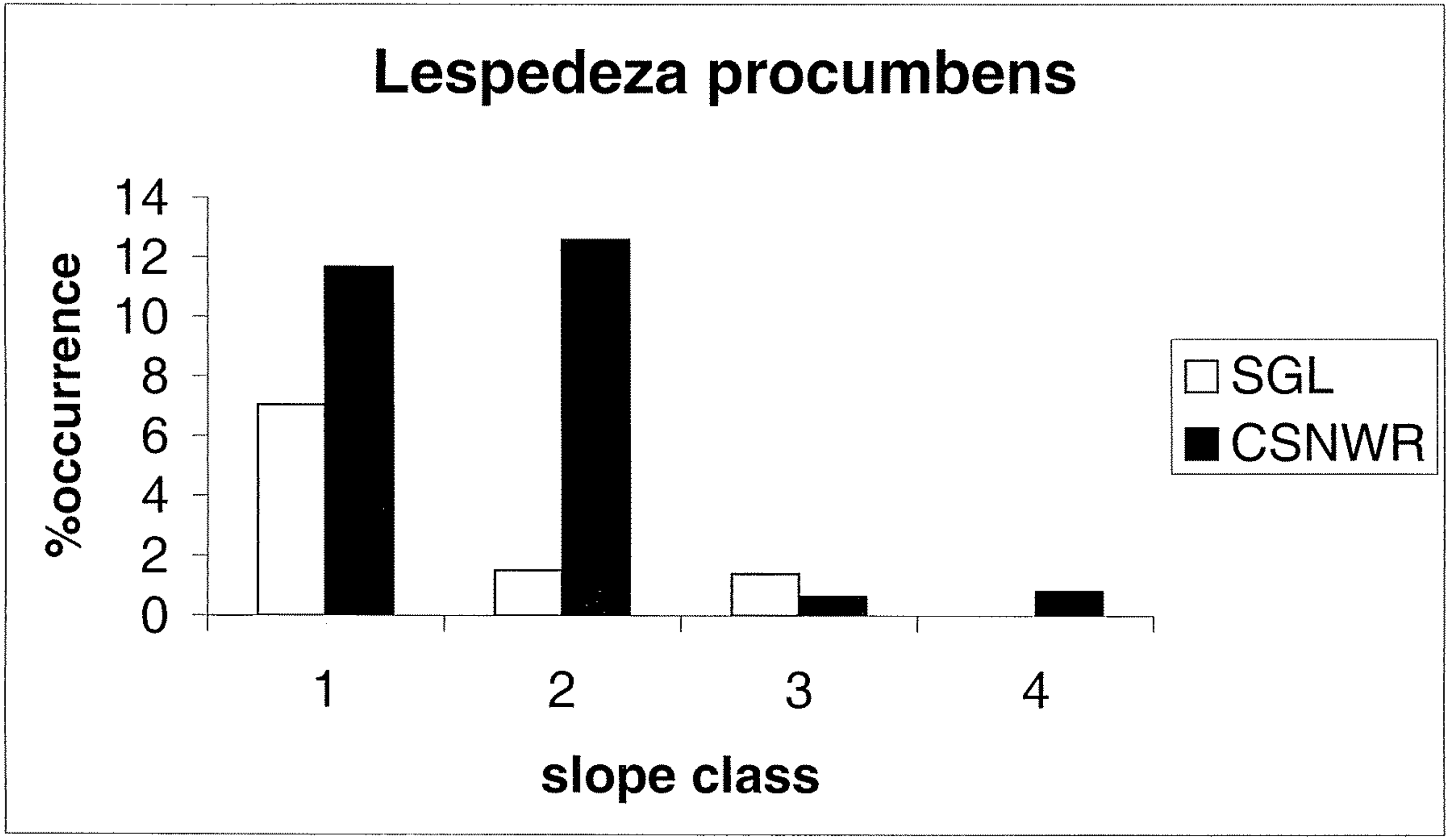


Fig. 3.17. Percent Occurrence of *Lespedeza repens* by Slope Class on the Refuge and Gamelands.

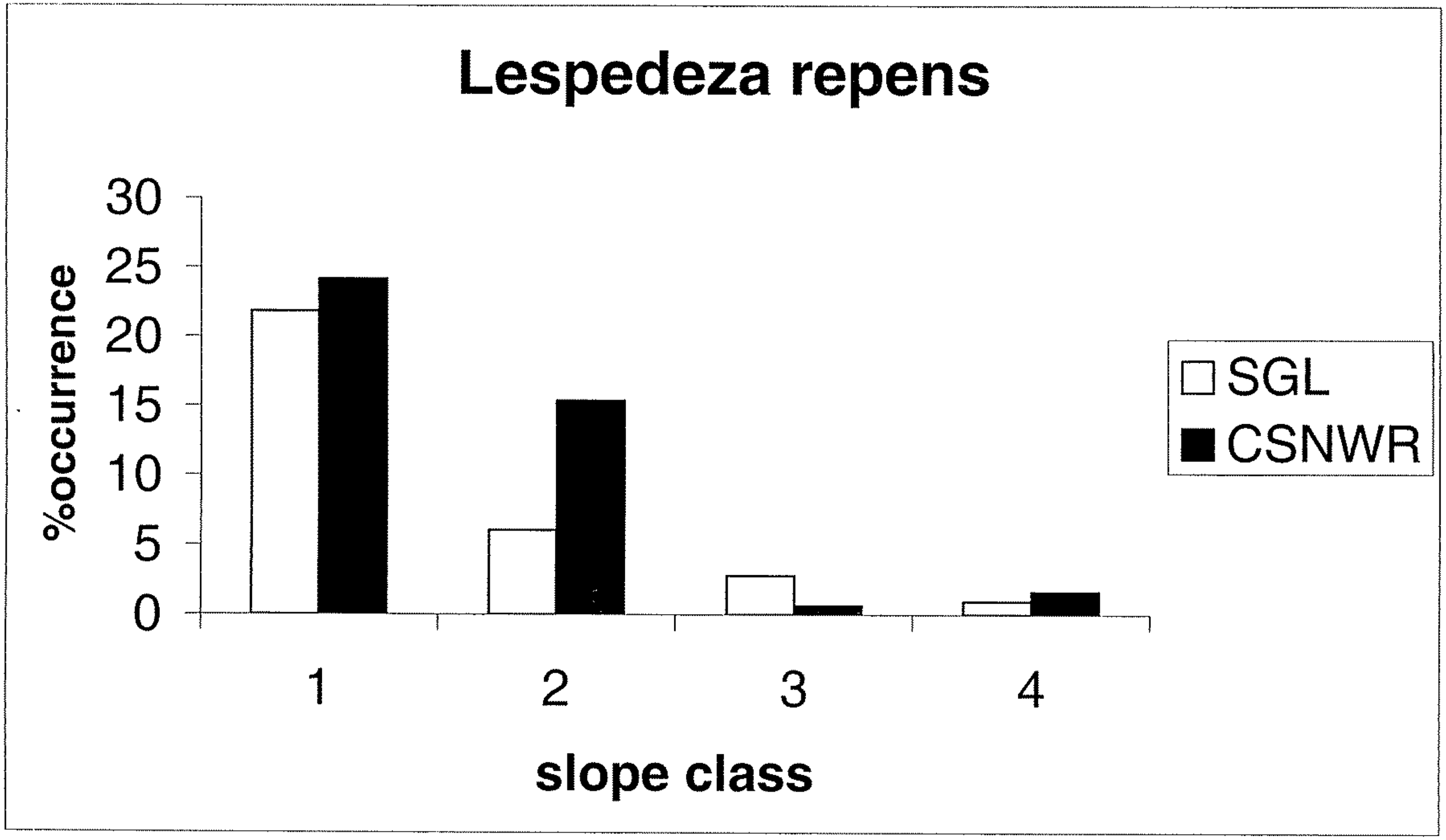


Fig. 3.18. Percent Occurrence of *Rhynchosia reniformis* by Slope Class on the Refuge and Gamelands.

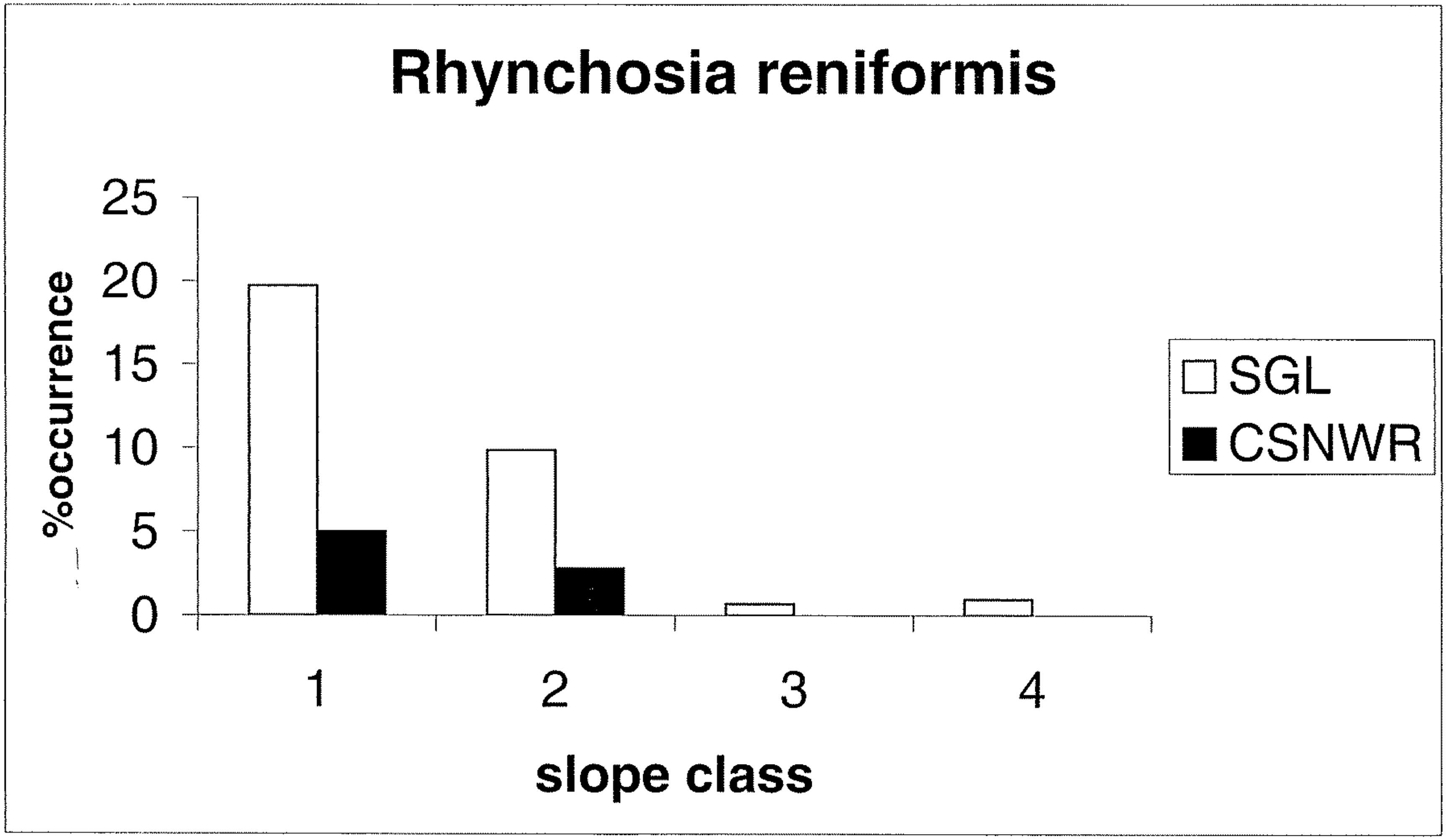


Fig. 3.19. Percent Occurrence of *Stylosanthes biflora* by Slope Class on the Refuge and Gamelands.

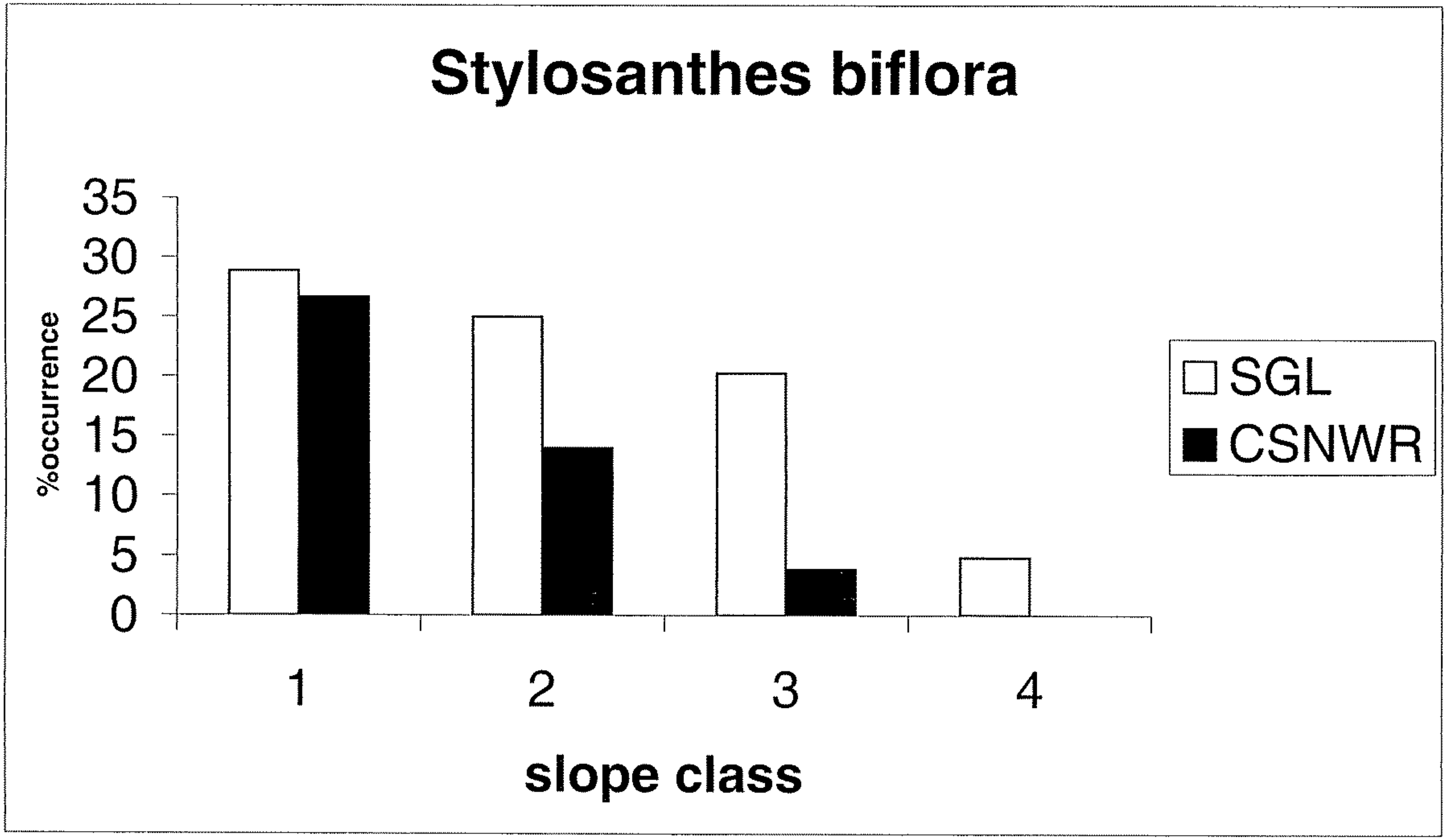


Fig. 3.20. Percent Occurrence of *Tephrosia virginiana* by Slope Class on the Refuge and Gamelands.

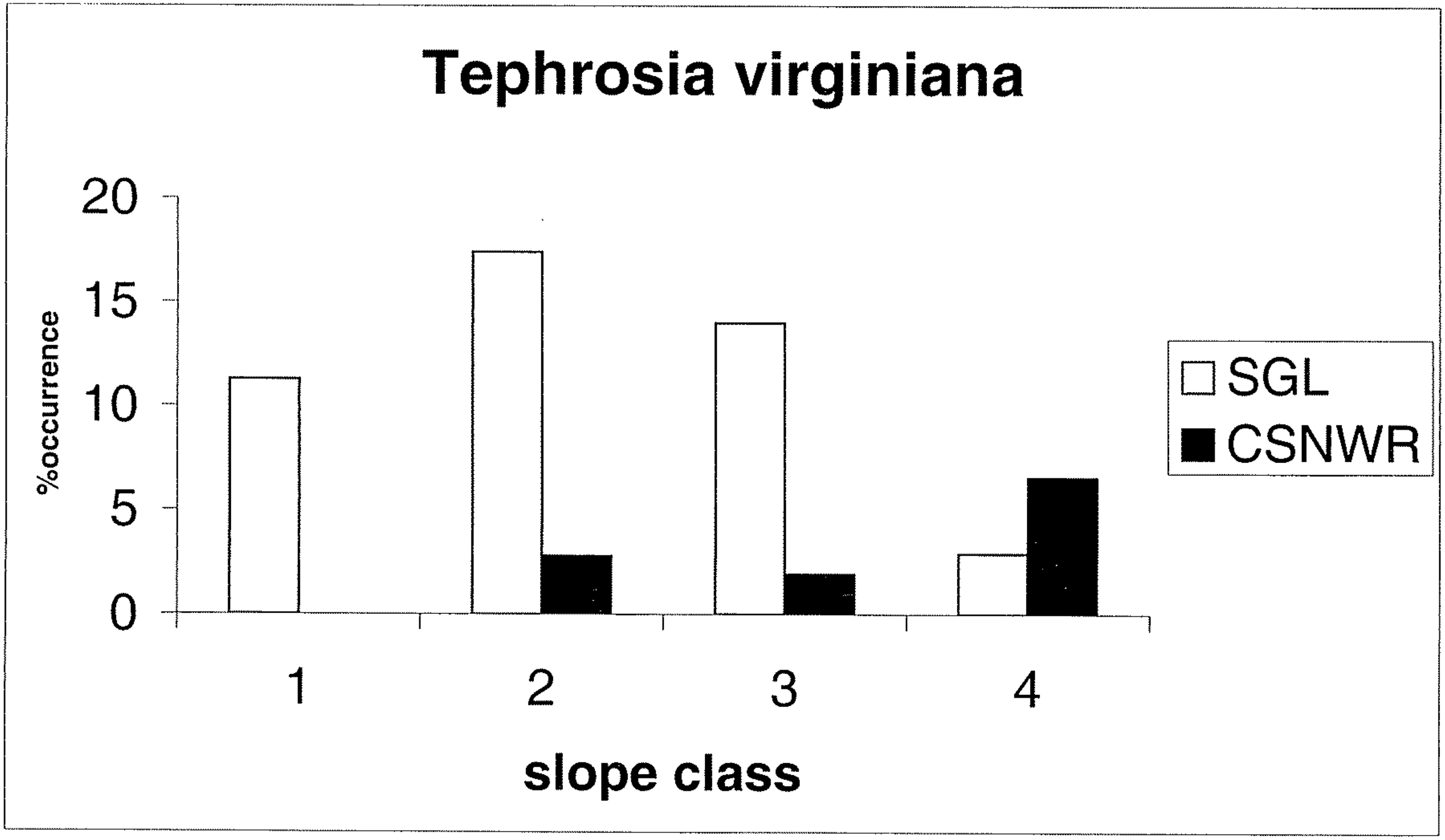


Fig. 3.21. Percent Occurrence of *Amorpha herbacea* var. *herbacea* by Slope Class on the Refuge.

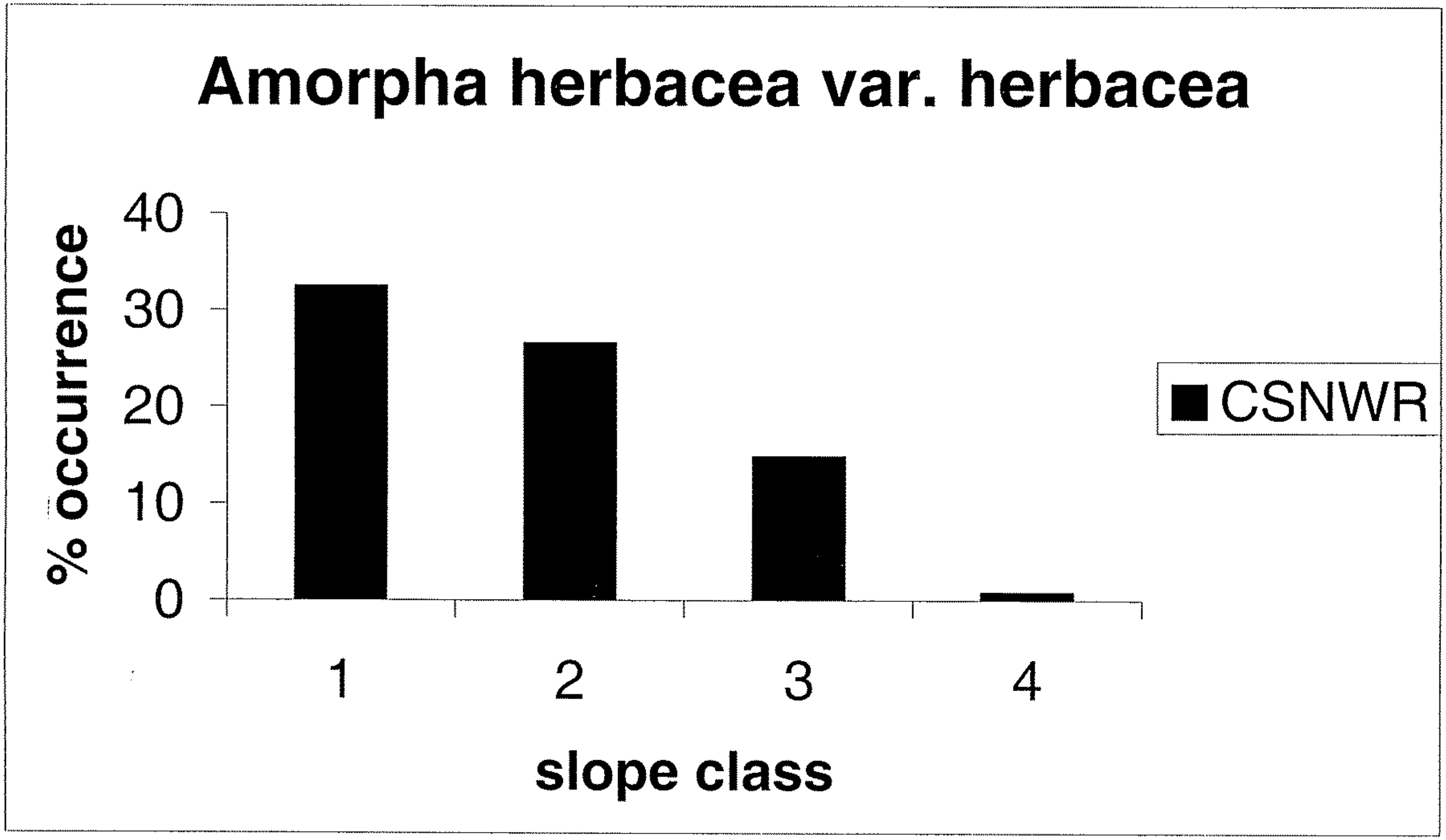


Fig. 3.22. Percent Occurrence of all *Desmodium* spp. (except *D. ciliare* and *obtusum*) by Slope Class on the Refuge and Gamelands.

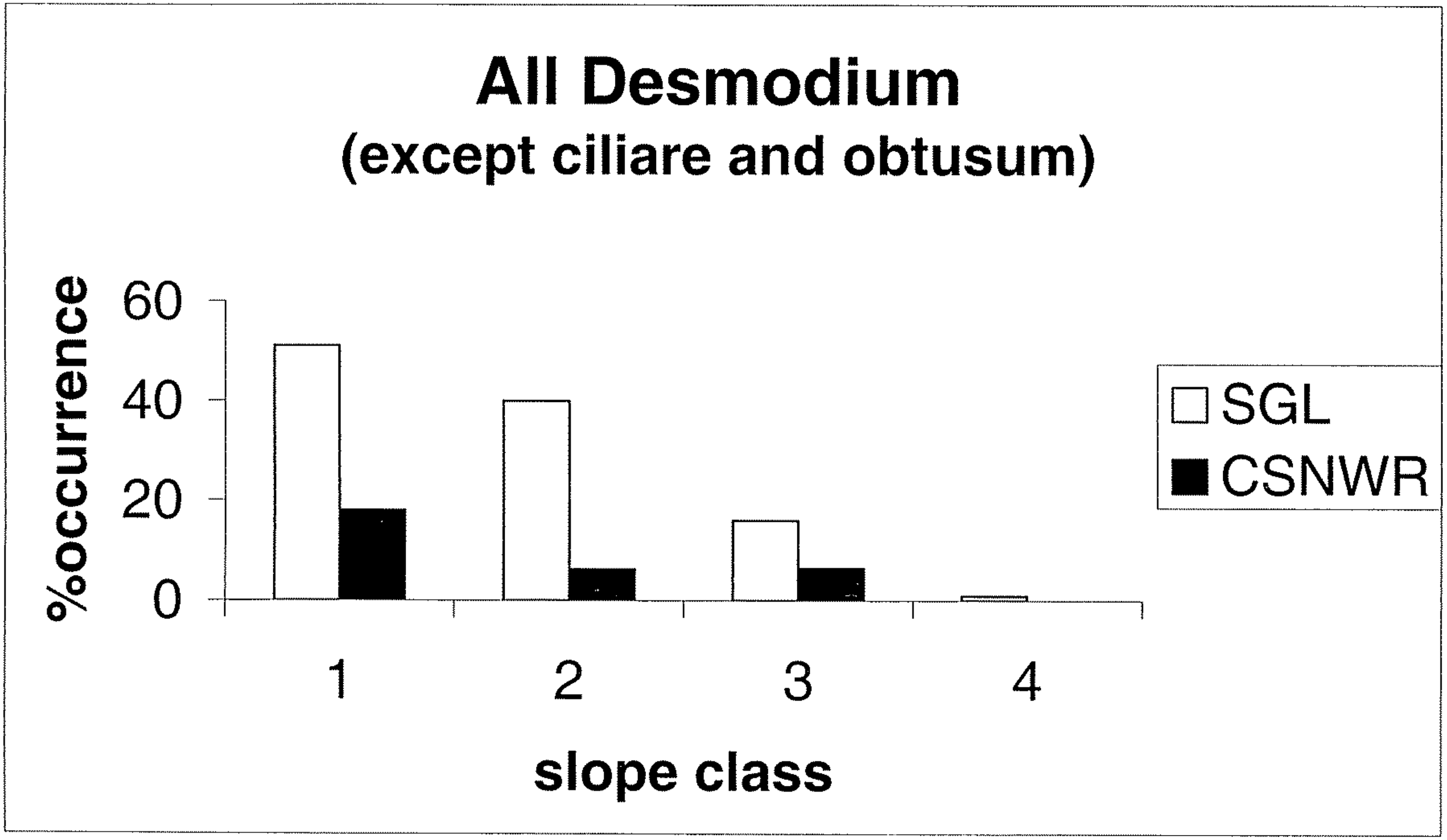
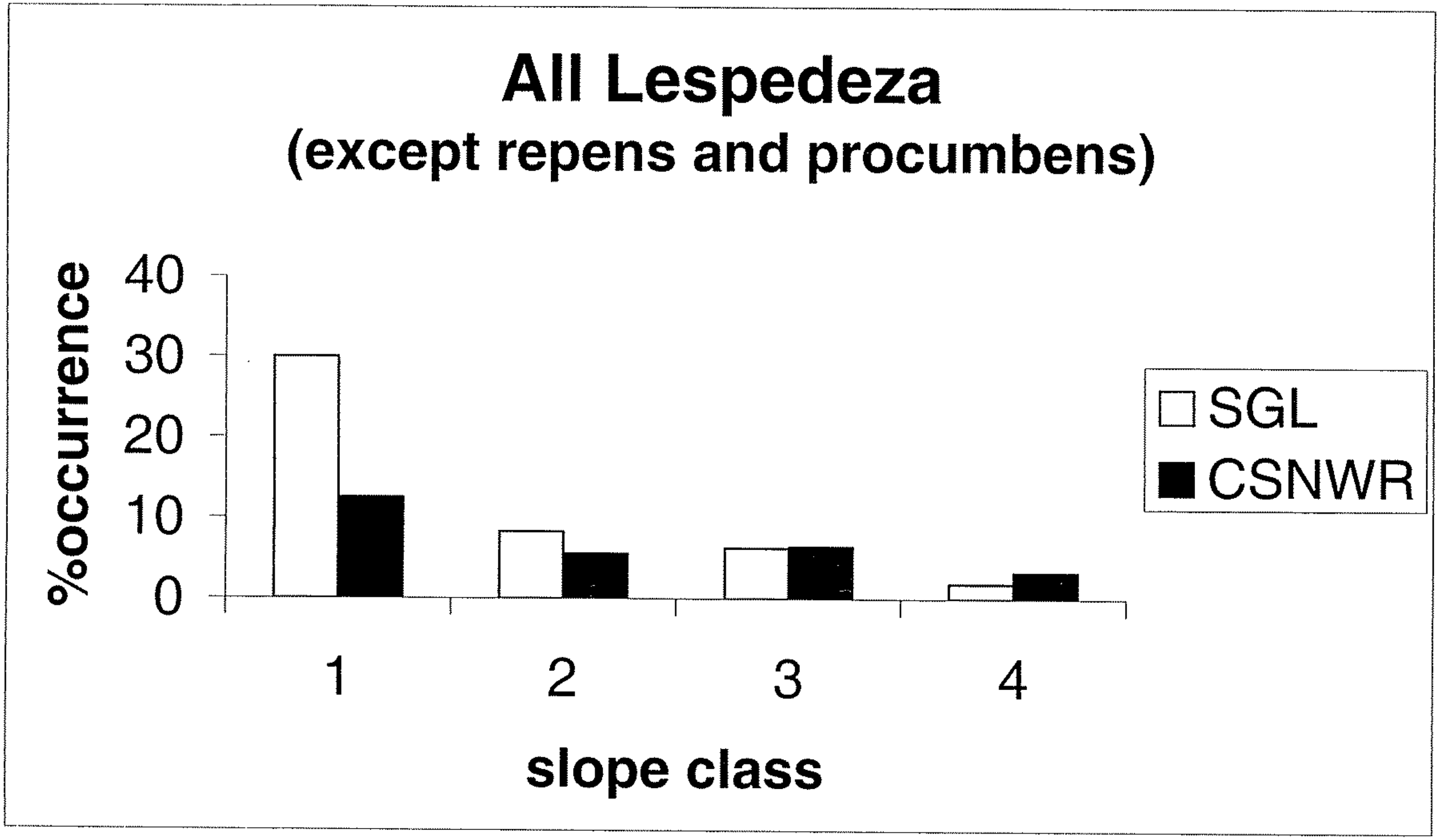


Fig. 3.23. Percent Occurrence of all *Lespedeza* spp. (except *L. repens* and *procumbens*) by Slope Class on the Refuge and Gamelands.



often in slope class 1. *Baptisia cinerea* and *Galactia regularis* were the only two species that occurred most frequently in slope class 4. Percent occurrence of *Baptisia cinerea* increased linearly from slope class 2 to 4, and it was never recorded in slope class 1. *Galactia regularis* did not exhibit this linear response, but it occurred nearly twice as frequently in class 4 as in all the other classes combined. Two species achieved their maximum distribution at intermediate slope classes. These were *Clitoria mariana* and *Tephrosia virginiana*, both of which occurred most often in slope class 2, and least often in class 4.

On the Refuge, ten species occurred less frequently as slope class increased. Those occurring most often in slope class 1 include: *Amorpha herbacea* var. *herbacea, Clitoria mariana, Desmodium ciliare, Desmodium obtusum, Galactia erecta, Galactia volubilis, Lespedeza repens, Rhynchosia reniformis,* and *Stylosanthes biflora*. Of these, *Desmodium ciliare, Galactia erecta, Galactia volubilis,* and *Stylosanthes biflora* never occurred in slope class 4. *Desmodium obtusum* and *Rhynchosia reniformis* were never present in classes 3 or 4. When all other *Desmodium* and *Lespedeza* species were combined, they also occurred most often in slope class 1. Three species showed the reverse trend: *Baptisia cinerea, Galactia regularis,* and *Tephrosia virginiana*. *Tephrosia virginiana* was never recorded in slope class 1, and *Galactia regularis* never occurred in classes 1 or 2. Only one species, *Lespedeza procumbens*, achieved maximum occurrence in an intermediate slope class. However, its presence was nearly as frequent in slope class 1.

Density data for these same species show a response that is similar to the presence data. Fig. 3.24 and 3.25 show density by slope class for both study sites, with species arranged in order of decreasing abundance. On the Gamelands, four species account for 57% of the total legume density in slope class 1. They are *Galactia volubilis, Desmodium*

Fig. 3.24. Legume Stem Density by Slope Class on the Gamelands.

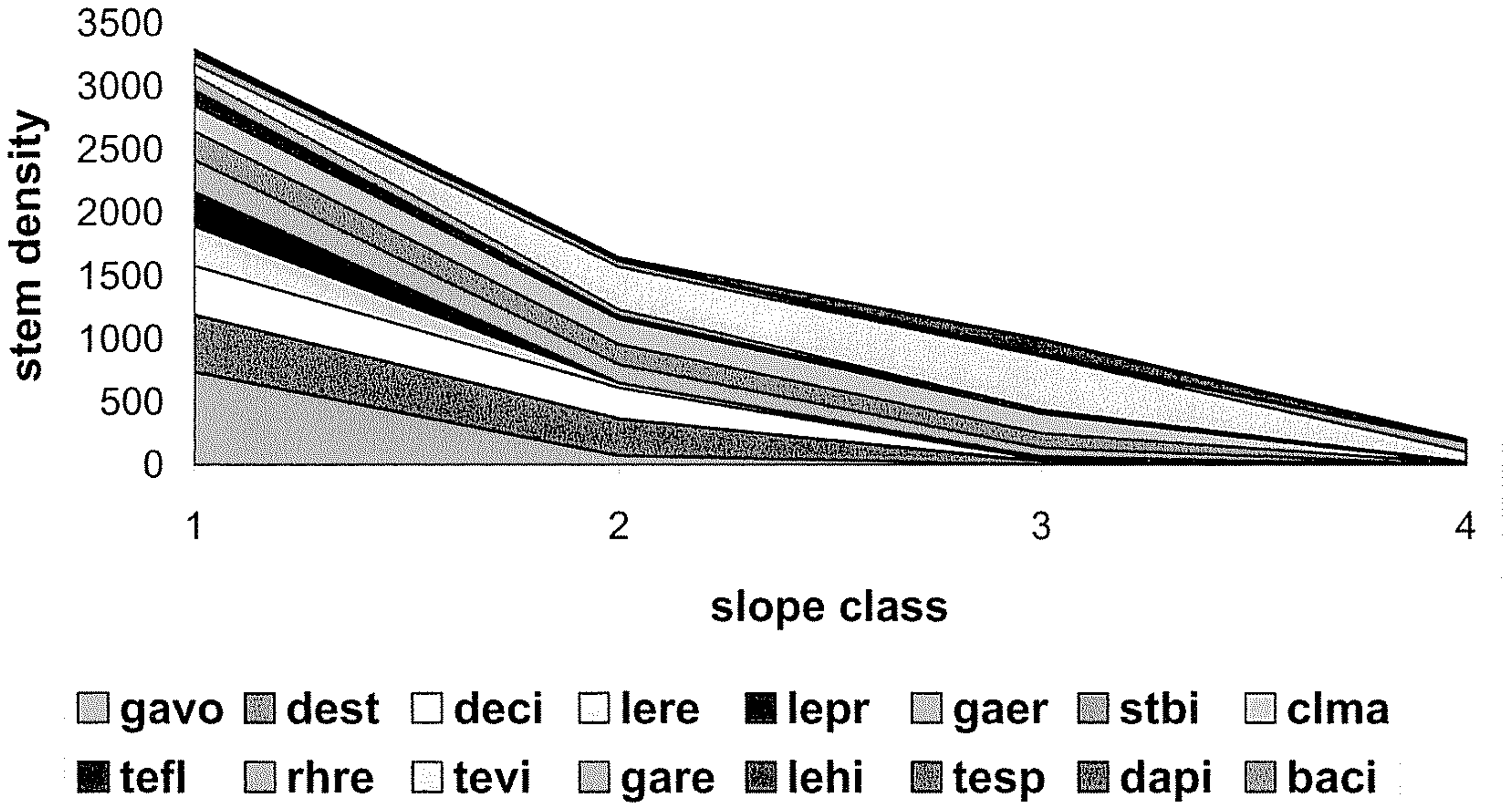
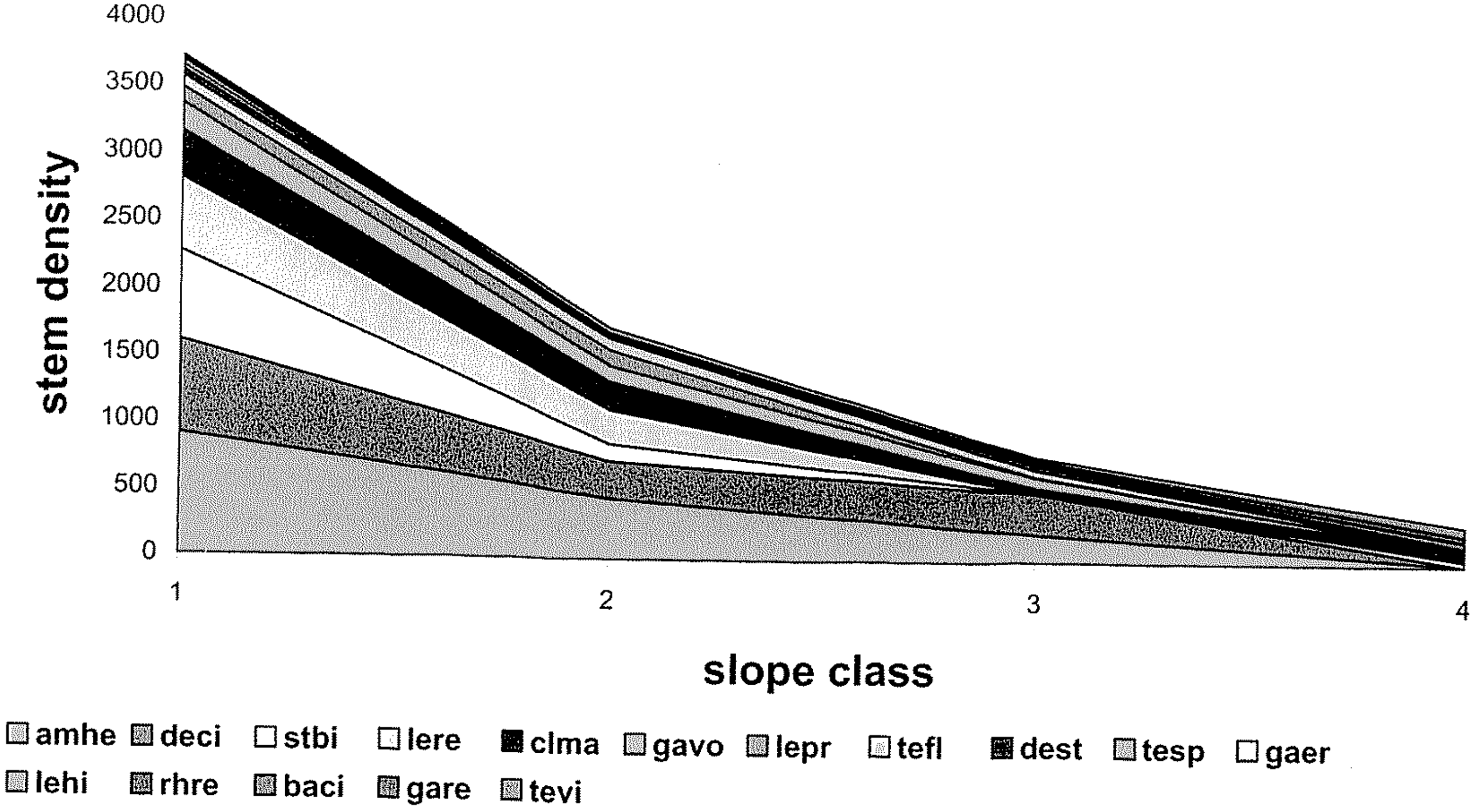


Fig. 3.25. Legume Stem Density by Slope Class on the Refuge.



strictum, D. ciliare, and *Lespedeza repens.* Four different species contribute 86% of the total legume density in slope class 4. In order of decreasing abundance they are *Tephrosia virginiana, Galactia regularis, Baptisia cinerea,* and *Stylosanthes biflora.* However, the first two alone account for 72% of the density. This graph also shows that total legume density decreased 50, 39, and 79% from slope classes 1 to 2, 2 to 3, and 3 to 4, respectively.

On the Refuge, *Amorpha herbacea* var. *herbacea, Desmodium ciliare, Stylosanthes biflora,* and *Lespedeza repens* account for 76% of the total legume density in slope class 1. In class 4, five other species account for 90% of the total legume density. In order of decreasing abundance, these are: *Clitoria mariana, Tephrosia virginiana, Baptisia cinerea, Galactia regularis,* and *Lespedeza repens.* The decrease in total density across slope classes is more regular than on the Gamelands. In the Refuge quadrats, total density declines 53, 55, 62% from slope class 1 to 2, 2 to 3, and 3 to 4. The 21 taxa that were rarely encountered, or taxa whose distributions did not exhibit a clear pattern, are shown with their abundance data by slope class in Table 3.2.

Individual legume distributions along the gradient indicate that there are essentially four groups encountered during this study: 1) species that occur most often in the bottoms, 2) species that occur most often on the upper slope/rim, 3) species that are widely distributed along the gradient (cosmopolitan species), and 4) rare species that occur so infrequently that their preferred location can not be adequately predicted by this sampling method. Most of the species encountered in this study show a strong preference for the conditions defined by slope class 1, although two species (*Baptisia cinerea* and *Galactia regularis*) occur most frequently in the extremely xeric conditions that typify slope class 4. *Clitoria mariana*, a sprawling pea, seems to be one of the more cosmopolitan legumes, occurring in all slope

Table 3.2. Number of Legume Stems Recorded on the Gamelands (NC) and the Refuge (SC) by Slope Class. Table includes species that were rarely encountered during sampling and/or species with arrhythmic distributions.

	SLOPE CLASS							SLOPE CLASS				
SPECIES	1	2	3	4	TOTAL		SPECIES	1	2	3	4	TOTAL
ASMI-SC	0	0	0	0	**0**		LEST-SC	0	0	0	0	**0**
ASMI-NC	0	0	0	1	**1**		LEST-NC	30	9	9	0	**48**
BATI-SC	0	86	0	0	**86**		LEVI-SC	17	6	20	0	**43**
BATI-NC	0	0	0	0	**0**		LEVI-NC	29	0	0	0	**29**
CEVI-SC	9	0	10	0	**19**		LUDI-SC	0	0	0	2	**2**
CEVI-NC	3	0	5	0	**8**		LUDI-NC	0	0	0	0	**0**
CHNI-SC	2	0	0	0	**2**		ORLU-SC	0	4	0	0	**4**
CHNI-NC	57	35	32	0	**124**		ORLU-NC	19	0	11	0	**30**
CRPU-SC	31	0	0	0	**31**		PECA-SC	0	0	0	0	**0**
CRPU-NC	0	0	6	0	**6**		PECA-NC	0	1	0	0	**1**
CRRO-SC	0	0	17	0	**17**		PHSI-SC	43	0	0	1	**44**
CRRO-NC	4	0	0	0	**4**		PHSI-NC	6	6	4	0	**16**
DAPI-SC	0	0	0	0	**0**		RHTO-SC	0	0	19	0	**19**
DAPI-NC	9	11	122	0	**142**		RHTO-NC	0	10	1	0	**11**
DELA-SC	1	0	0	0	**1**		SHMI-SC	21	19	26	5	**71**
DELA-NC	0	2	1	0	**3**		SHMI-NC	0	2	0	0	**2**
DELI-SC	8	1	1	1	**11**		DECIxST-SC	20	0	13	0	**33**
DELI-NC	44	6	0	0	**50**		DECIxST-NC	274	217	101	0	**592**
DENU-SC	1	13	0	0	**14**		Desm. spp.-SC	29	13	2	0	**44**
DENU-NC	10	11	9	0	**30**		Desm. spp.-NC	5	3	0	0	**8**
GAMO-SC	0	0	0	0	**0**		Lesp. Sp.-SC	3	1	0	0	**4**
GAMO-NC	40	0	0	0	**40**		Lesp. Sp.-NC	0	0	0	0	**0**
INCA-SC	0	1	0	0	**1**							
INCA-NC	0	0	0	0	**0**							

classes, but generally favoring the lower ones. *Tephrosia virginiana* displays this same tendency except that it was never encountered in Refuge slope class 1 plots. Apparently, there are no species that occur most frequently on the mid-slopes of the transects (slope class 3). Within these mid-slope positions, one finds the upper extent of mesophytes, the lower extent of xerophytes, and cosmopolitan species.

Soils

Correlations between Edaphic Variables

Spearman correlation coefficients between all soil variables on the Refuge show that K, Ca, Mg, Mn, B, CEC, %SILT, and %CLAY are positively and significantly correlated with each other (Fig. 3.26). %SAND is significantly and negatively correlated with all soil variables except P and Zn. It is positively correlated with P ($r=.26$, $p<.02$), but not with Zn. Zn is significantly correlated with K ($r=.38$, $p<.0004$). P is significantly and negatively correlated with Ca, Mg, Mn, B, CEC, and %CLAY.

On the Gamelands, the results of the correlations between soil variables are similar. Soil pH, Ca, Mg, Mn, B, Zn, CEC, and %CLAY were found to be significantly and positively correlated. K and Cu show the same relationship, except they are not significantly correlated with %CLAY. %SILT is positively correlated with K, Mg, Mn, Cu, B, and CEC. P appears significantly correlated with only three of the soil variables, two positively (K and %SAND) and one negatively (%CLAY). As on the Refuge, %SAND on the Gamelands is negatively correlated with all soil variables except P and Zn. Significant Zn correlations are with Mn, Cu, and CEC, all of which are positive.

Table 3.3. Spearman Correlation Coefficients between Soil Variables on the Refuge and the Gamelands.

****=p<.0001; ***=p<.001; **=p<.01.

CSNWR (n=84)

	soil pH	P	K	Ca	Mg	Zn	Mn	Cu	B	CEC	%CLAY	%SILT	%SAND
soil pH	1		.32***	.50****	.34***		.32***	.27**	.47****		.29***		-.20**
P		1		-.22**	-.33***		-.34***		-.20**	-.27**	-.39****		.26**
K			1	.68****	.66****	.38****	.65****	.46****	.66****	.61****	.47****	.44****	-.52****
Ca				1	.91****		.59****	.42****	.63****	.64****	.48****	.46****	-.53****
Mg					1		.60****	.45****	.60****	.58****	.49****	.39****	-.47****
Zn						1		.35***		.21**			
Mn							1	.48****	.68****	.66****	.59****	.39****	-.48****
Cu								1	.48****	.41****	.35***	.30***	-.36****
B									1	.60****	.61****	.50****	-.59****
CEC										1	.62****	.62****	-.69****

SGL (n=77)

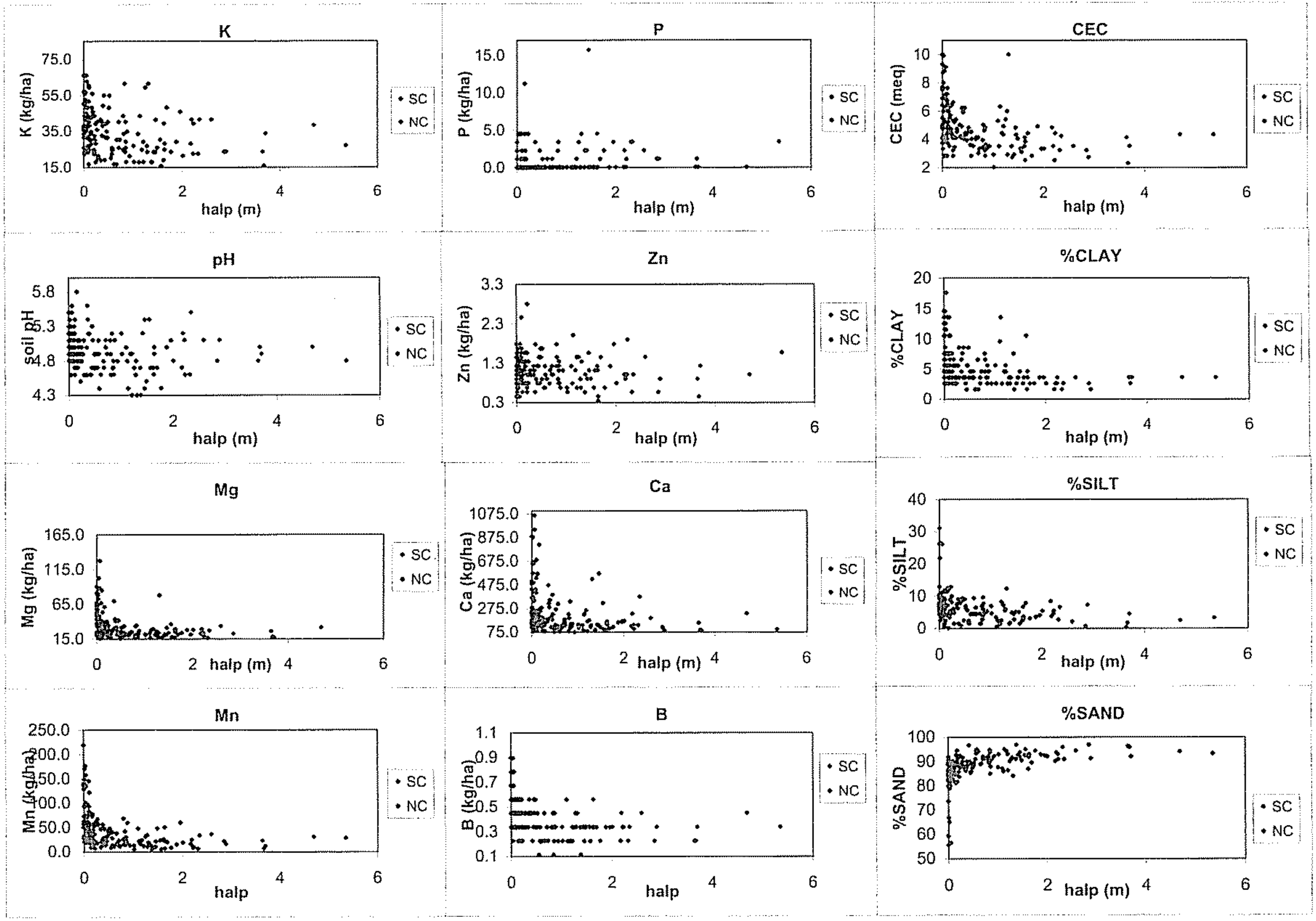
	soil pH	P	K	Ca	Mg	Zn	Mn	Cu	B	CEC	%CLAY	%SILT	%SAND
soil pH	1		.32***	.75****	.68****		.54****	.23**	.65****	.33***	.32***		-.29**
P		1	.40****								-.29**		.20**
K			1	.46****	.54****	.35***	.39****	.21**	.41****	.45****		.36***	-.26**
Ca				1	.95****	.21**	.40****	.29***	.64****	.59****	.21**		-.29***
Mg					1	.25**	.48****	.34***	.71****	.68****	.27**	.23**	-.38****
Zn						1	.22**	.44****		.25**			
Mn							1	.37****	.71****	.55****	.53****	.30***	-.58****
Cu								1	.38****	.32***		.22**	-.28**
B									1	.67****	.57****	.30***	-.64****
CEC										1	.37***	.44****	-.68****

In summary, nutrient and texture variables in both states exhibit pronounced collinearity, a majority of them strongly and positively correlated with each other. P, Zn, and %SAND are the major exceptions. Of these exceptions, Zn is positively correlated with CEC and Cu in both study areas, and Mn only on the Gamelands. P correlations are generally weak and few, but it is negatively correlated with %CLAY, and positively correlated with %SAND in both states. %SAND is negatively correlated with all other soil variables except Zn, with which it is uncorrelated. In this study, strongly and positively correlated soil variables are considered positive indices of fertility. Therefore, since %SAND is negatively correlated with these, it is regarded as a negative index of fertility.

Scatter plots of soil variables and relative elevation

In Fig. 3.26, a series of scatter plots effectively captures the edaphic variation that occurs with increasing height above lowest point (HALP). Six of these variables (Ca, Mg, Mn, B, CEC, %CLAY) show a strong L-shaped response to increasing elevation, such that most of the variation in these parameters occurs at elevations less than 0.3 m above the lowest point (ie. slope class 1). The change in soil pH, K, Zn, Cu, and %SILT with increasing elevation is more gradual. P levels are very low at all locations along the transects. %SAND shows the inverse of the dominant trend exhibited by the other soil variables. The bulk of the variation in %SAND also occurs at the lowest HALP, but the values of %SAND increase with increasing elevation. Between-state differences in soil texture and chemistry are also suggested in this diagram. The Gamelands sites usually appear higher on the y-axis than the Refuge.

Figure 3.26. Scatter plots showing soil texture and nutrients by relative elevation, measured as height above the lowest point (halp). NC=Gamelands; SC=Refuge.



Between-State Comparisons of Fertility

Comparisons of soil nutrient and texture levels between study sites indicate that Gamelands sites generally have higher nutrient values than sites on the Refuge. For slope class 1, soil pH, K, Ca, Mg, Zn, Mn, Cu, B, CEC, %CLAY, and %SILT were significantly higher on the Gamelands (Table 3.4). This trend was also true for Zn and CEC in slope classes 2, 3, and 4. %CLAY and Mn were higher on the Gamelands for slope classes 2 and 3, but no significant differences in soils were detected between study sites in slope class 4. Other significant examples of increased fertility on Gamelands sites include B in slope class 2 and Cu in slope class 3. No significant differences in %SAND or P were observed between study sites for any slope class.

Within-State Comparisons of Fertility

Comparisons of edaphic variables across slope classes show strong and consistent trends of decreasing fertility with increasing slope class in both states. On the Gamelands, differences in soil pH, Ca, Mg, Mn, B, CEC, %CLAY, and %SAND were highly significant among slope classes ($p<.0001$). Each of these decreased from class 1 to class 4, except %SAND, which increased. In all cases, the sharpest decrease or increase occurred between slope classes 1 and 2. %SILT also decreased across slope classes, but differences between classes were not as highly significant ($p<.0315$). Concentrations of P, K, and Zn were not significantly different across slope classes on the Gamelands.

On the Refuge, Ca, Mg, Mn, B, CEC, %CLAY, %SILT, and %SAND were significantly different among slope classes ($.0006<p<.0001$). Each of these variables decreased with increasing slope class with the exception of %SAND, which increased. K

Table 3.4. Edaphic Comparisons by Slope Class between the Refuge (SC) and the Gamelands (NC).

Variable	Slope Class	NC Mean	NC Std Dev	SC Mean	SC Std Dev	K-W test	df	Pr > Chi-Square	Z approx	One-sided Pr>Z	Two-sided Pr>|Z|
Soil pH	1	5.23	0.25	4.98	0.22	13.568	1	0.0002	3.676	0.0001	0.0002
	2	4.92	0.21	4.90	0.21	0.286	1	0.5929	-0.522	0.3009	0.6017
	3	4.82	0.26	4.91	0.25	0.453	1	0.5011	0.655	0.2564	0.5128
	4	4.72	0.29	4.80	0.23	1.527	1	0.2166	-1.212	0.1127	0.2254
p	1	1.17	2.59	1.23	2.80	0.364	1	0.5464	-0.593	0.2764	0.5529
	2	0.48	1.15	0.05	0.24	2.179	1	0.1399	-1.454	0.0730	0.1460
	3	0.66	1.38	1.11	1.42	1.798	1	0.1800	1.320	0.0934	0.1869
	4	1.64	4.34	0.97	1.27	0.502	1	0.4785	-0.683	0.2475	0.4949
k	1	45.78	13.94	34.57	8.96	9.950	1	0.0016	3.147	0.0008	0.0017
	2	37.79	12.87	30.95	10.40	2.973	1	0.0847	-1.712	0.0435	0.0870
	3	36.65	15.20	27.32	9.01	3.062	1	0.0802	-1.732	0.0417	0.0833
	4	32.75	11.88	25.62	5.78	1.988	1	0.1586	1.387	0.0828	0.1655
ca	1	560.44	519.24	262.13	129.91	9.012	1	0.0027	2.994	0.0014	0.0028
	2	208.62	143.37	160.64	54.06	0.412	1	0.5211	-0.629	0.2647	0.5293
	3	189.15	114.39	165.18	74.15	0.083	1	0.7732	-0.270	0.3935	0.7870
	4	157.26	131.67	121.95	35.76	0.090	1	0.7644	0.277	0.3910	0.7821
mg	1	66.99	48.53	35.14	15.43	12.442	1	0.0004	3.520	0.0002	0.0004
	2	29.78	14.80	26.20	6.35	0.414	1	0.5202	-0.630	0.2642	0.5284
	3	28.09	15.03	24.16	5.46	0.000	1	0.9856	0.000	0.5000	1.0000
	4	20.69	4.72	20.91	4.87	0.335	1	0.5628	-0.556	0.2893	0.5785
zn	1	1.28	0.33	0.94	0.48	14.917	1	0.0001	3.854	0.0001	0.0001
	2	1.26	0.38	0.89	0.28	13.007	1	0.0003	-3.594	0.0002	0.0003
	3	1.28	0.34	0.96	0.24	7.203	1	0.0073	-2.666	0.0038	0.0077
	4	1.38	0.40	0.87	0.33	10.696	1	0.0011	3.247	0.0006	0.0012
mn	1	95.68	51.70	43.81	37.85	22.309	1	0.0000	4.715	0.0000	0.0000
	2	60.46	38.89	32.77	20.03	8.015	1	0.0046	-2.818	0.0024	0.0048
	3	35.07	16.79	19.40	8.89	8.115	1	0.0044	-2.831	0.0023	0.0047
	4	21.64	15.37	13.29	8.00	2.995	1	0.0835	1.707	0.0439	0.0877
cu	1	1.18	0.29	0.99	0.26	6.729	1	0.0095	2.586	0.0049	0.0097
	2	1.01	0.24	0.94	0.21	0.889	1	0.3457	-0.930	0.1761	0.3522
	3	1.05	0.15	0.91	0.26	4.953	1	0.0260	-2.207	0.0136	0.0273
	4	1.03	0.22	0.89	0.20	3.301	1	0.0693	1.794	0.0365	0.0729

Variable	Slope Class	NC Mean	NC Std Dev	SC Mean	SC Std Dev	K-W test	df	Pr > Chi-Square	Z approx	One-sided Pr>Z	Two-sided Pr>|Z|
b	1	0.65	0.20	0.44	0.20	13.003	1	0.0003	3.598	0.0002	0.0003
	2	0.41	0.12	0.31	0.08	6.292	1	0.0121	-2.495	0.0063	0.0126
	3	0.35	0.09	0.29	0.11	3.646	1	0.0562	-1.890	0.0294	0.0587
	4	0.25	0.05	0.25	0.07	0.112	1	0.7379	0.309	0.3787	0.7574
cec	1	6.75	2.06	5.42	2.46	10.285	1	0.0013	3.199	0.0007	0.0014
	2	5.41	1.01	4.12	1.10	12.690	1	0.0004	-3.550	0.0002	0.0004
	3	4.89	1.49	3.66	0.95	8.757	1	0.0031	-2.941	0.0016	0.0033
	4	4.09	0.89	3.27	0.77	6.817	1	0.0090	2.588	0.0048	0.0097
clay	1	8.48	3.26	6.06	3.71	9.061	1	0.0026	3.002	0.0013	0.0027
	2	5.89	2.73	4.27	1.45	3.812	1	0.0509	-1.940	0.0262	0.0524
	3	5.56	2.83	2.94	1.15	12.240	1	0.0005	-3.480	0.0003	0.0005
	4	4.25	2.29	2.69	1.06	5.619	1	0.0178	2.347	0.0095	0.0190
silt	1	6.97	2.97	11.50	6.92	10.583	1	0.0011	-3.245	0.0006	0.0012
	2	5.68	3.54	6.95	2.25	1.778	1	0.1824	1.321	0.0933	0.1865
	3	4.62	3.11	4.35	2.55	0.016	1	0.8996	-0.108	0.4569	0.9139
	4	4.23	2.41	4.14	2.55	0.002	1	0.9632	-0.023	0.4908	0.9816
sand	1	84.55	4.27	82.44	10.16	0.041	1	0.8388	-0.196	0.4225	0.8449
	2	88.43	3.08	88.78	3.02	0.445	1	0.5047	0.655	0.2564	0.5128
	3	89.82	2.60	92.71	2.49	9.610	1	0.0019	3.082	0.0010	0.0021
	4	91.52	2.51	93.17	2.40	2.530	1	0.1117	-1.568	0.0585	0.1170

levels also decreased from slope class 1 to 4, but the differences among slope classes were not as highly significant ($p<.0037$). As with soil parameters on the Gamelands, the greatest variation in levels occurred between slope classes 1 and 2, except for Mn, which declined most precipitously from class 2 to 3. Among Refuge soils, soil pH, P, Zn, and Cu did not differ significantly among slope classes.

Both states showed significant differences in Ca, Mg, Mn, and B among slope classes. Since each of these elements is expressed in kg/ha, it is possible to compare their sum across slope classes as shown in Fig. 3.27. The four trends illustrated here are generally true for the other soil variables that are not expressed in compatible units or are not significantly different among slope classes in both states. These trends are: 1) decreasing fertility with increasing slope class 2) Gameland sites more fertile than Refuge sites, 3) sharpest declines in fertility occurring between slope classes 1 and 2, and 4) the differences in fertility between slope classes 1 and 2 are more pronounced on the Gamelands.

K/Ca Ratios

The K/Ca ratio has been identified as a major determinant of plant distribution in cases where P levels are so low that variation in concentration does not significantly affect vegetation (Albrecht, 1940). In these cases, low K/Ca ratios are generally associated with mesophytic morphological traits and high ratios are indicative of xerophytic morphological traits. Since my study sites met the low P criterion, the ratio of K to Ca by slope class was calculated (Fig. 3.28). Within each study site, the K/Ca ratio is positively related with slope class, but nearly 80% of the total change occurs between slope classes 1 and 2 for both the

Fig. 3.27. Sum of Mean Ca, Mg, Mn, and B Concentrations by Slope Class.

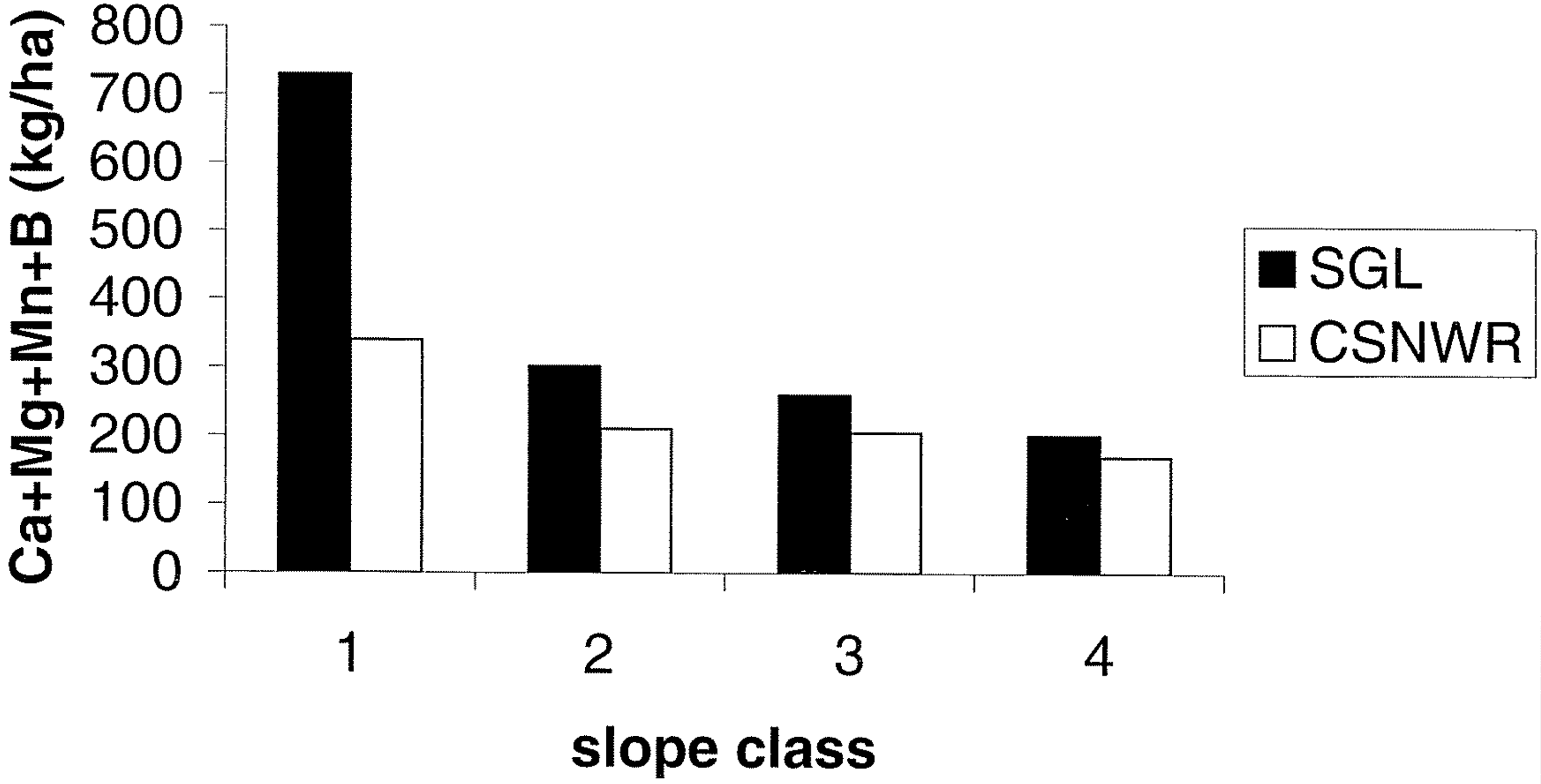
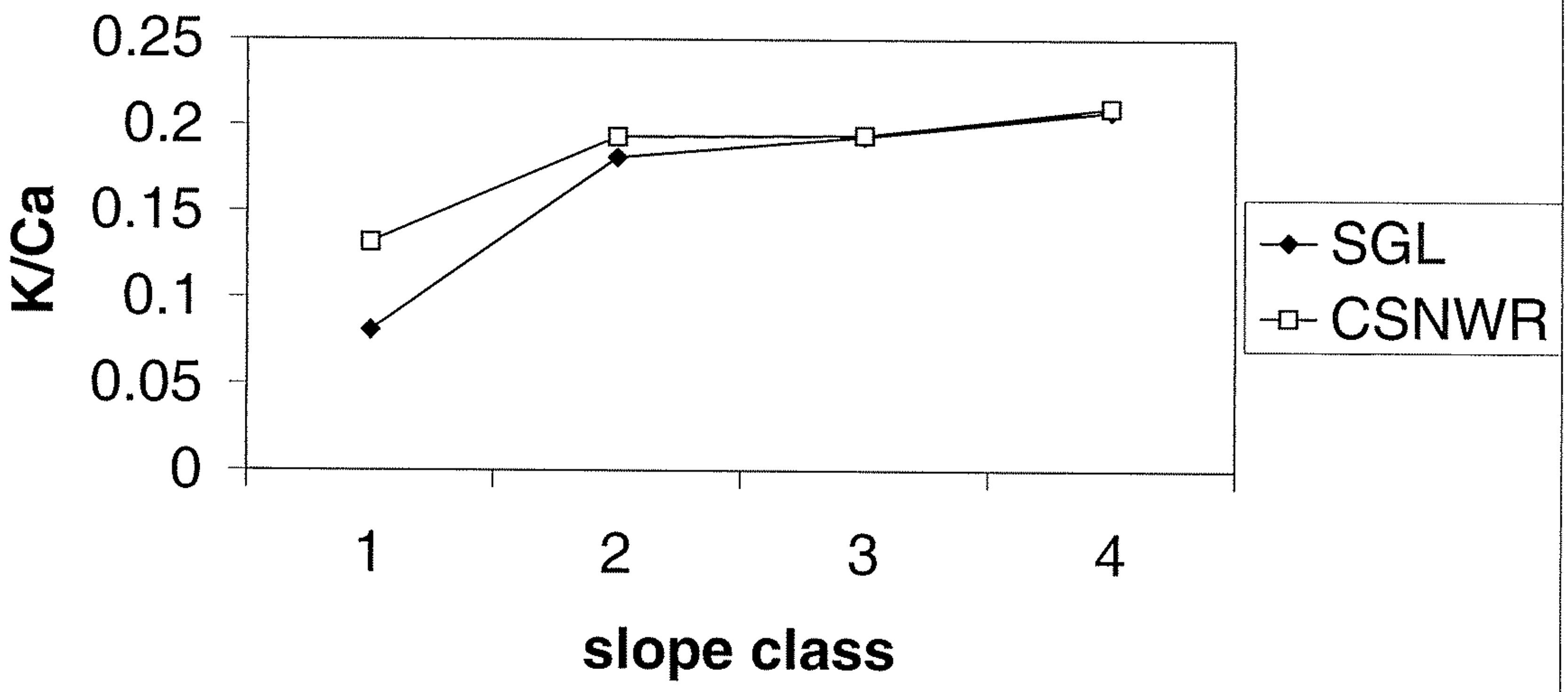


Fig. 3.28. Mean K:Ca Ratios by Slope Class on the Refuge and Gamelands.



Refuge and the Gamelands. It is also apparent that the K/Ca ratio is higher on the Refuge at slope classes 1 and 2, but converges with the Gamelands at slope classes 3 and 4.

Discussion

Landscape Patterns

By examining legume distribution patterns in loamy soil communities of the Carolina Sandhills, this study has achieved several objectives. The first question I sought to answer was whether or not perceived differences in topography between study sites were manifested in bean dip size, frequency, and elevation differences. I found that although bean dips occur at similar frequencies in both study locations, they are larger and occur at lower elevations on the Gamelands in North Carolina. This result implies that conditions for bean dip development were generally more favorable on the Gamelands during the Pleistocene when these eolian deflation basins were probably formed (See Chapter 2). This interpretation is consistent with my preliminary observation that Gamelands interstream divides have more flat area than those on the Refuge. In a global review of eolian deflation basins similar to bean dips, Goudie & Wells (1995) recognized that basin development was enhanced in flatter areas due to the lack of topographic interference with wind velocity.

In the Sandhills, topographic variation is primarily governed by the morphology of the underlying, indurated, and irregularly-weathered Cretaceous clays of the Middendorf Formation. Upon this layer, younger surficial sands of various origins are deposited at varying thicknesses. The depth of this sand:clay contact is believed to have a strong effect on soil moisture, and, therefore, plant productivity. In addition, the slope of this contact is expected to influence productivity due to the effect on the mean residency time of sub-surface water that it would have, since precipitation in the Sandhills generally percolates rapidly downward until reaching this impermeable horizon. In flatter Sandhills terrain, the velocity of horizontal, sub-surface waterflow along the sand:clay contact would be slower than would be expected in more broken Sandhill topography, allowing more time for assimilation by plants. It is probably due to these basically geological reasons that, even to the casual eye, the North Carolina Gamelands appear to be more mesic than the South Carolina Refuge. These broad landscape differences are vital for understanding fundamental differences in plant productivity, composition, species richness, and overall aspect between study sites. They should be explored further.

Legume Patterns Along the Gradient

A second objective of this study was to describe the patterns in legume distribution that occur along the slopes of loamy soil communities. It has been shown that both legume species richness and stem density decreased with increasing slope class in both study areas. In addition, legume density and richness were consistently higher at Gameland sites, except on the upper slopes and rims (slope class 4) where no differences were detected. The decline in abundance and diversity across slope classes was also more gradual on the Gamelands. As for individual legumes species, nearly all of the species occurred most frequently and abundantly in the bottoms of bean dips and pea swales. Only two species, *Baptisia cinerea* and *Galactia regularis*, both relatively common in the Sandhills, occurred most frequently on the upper slopes. *Tephrosia virginiana, Clitoria mariana,* and *Lespedeza procumbens* tended to have broader distributions along the gradient in one or both study sites. These results indicate that the bottoms and slopes of pea swales and bean dips provide a unique and insular growth environment for mesophytic plants that, otherwise, would not persist in the predominantly xeric conditions of the Sandhills. They also suggest that a strong and complex environmental gradient is driving patterns in legume species sorting.

Edaphic Patterns Along the Gradient

This study characterized fundamental changes in soil texture and nutrient status that occur along the slopes of bean dips and pea swales. Most indices of fertility decreased with increasing slope class, with the notable exception of P, which was low at all points along the transects. The bulk of the variation in edaphic conditions that occurred was encountered in the bottoms (slope class 1+2) of bean dips and pea swales. Soil comparisons between study sites indicated that Gamelands sites generally had higher indices of fertility than sites on the Refuge. Between-state differences in fertility were most extreme in the bottoms of bean dips and pea swales, where soil pH, K, Ca, Mg, Zn, Mn, Cu, B, CEC, %CLAY, and %SILT were significantly higher on the Gamelands. On the upper slopes and rims of bean dips and pea swales, where %SAND was highest, no differences between study sites were detected.

Soil:Plant Interactions Along the Gradient

The combined effect of the legume and soil results suggests that these variables are strongly associated. Legume species richness, density, and abundance were all highest in the bottoms of bean dips and pea swales where soils had the highest indices of productivity. Although soil moisture was not measured directly in this study, patterns can be inferred based on soil texture and nutrients using the results of other studies in the coastal plain that found these variables to be strongly associated. In Hainds (1999) review of legume distributions in the longleaf pine forest of southwest Georgia, he determined that %SAND was inversely related to moisture, and Christensen (1987) found soil moisture and nutrients to be positively related in the Carolina Coastal Plain. These relationships are also probably true in the Sandhills, therefore, it is presumed that soil moisture is also maximized in the bottoms of bean dips and pea swales since nutrients are higher and %SAND is lower there. On a local scale, the lowest points also represent the area with maximum upstream watershed and minimum depth to impermeable substrate. I hypothesize that the interaction between these three variables (soil texture, depth to impermeable layer, and area of upstream watershed) is the primary determinant of moisture availability in the coastal plain on both large and small scales.

My study of legume distributions in the Sandhills provides an interesting contrast to studies that have addressed legume distributions in other longleaf pine-dominated ecosytems. As in the Green Swamp of North Carolina (Walker & Peet, 1983; Taggart, 1990) and in southwest Georgia (Hainds, 1999), legume distribution in the Sandhills are strongly influenced by soil moisture, represented by texture, nutrients, and slope position in this study. However, unlike the Green Swamp, where legumes proliferated on relatively xeric convex islands, legume density and species richness in the Sandhills was maximized in the comparatively mesic, concave depressions of bean dips and pea swales. This contrast suggests that landform, in and of itself, does not explain legume variation in longleaf pine forests. Rather, it brings attention to the importance of considering the regional context in which landforms such as islands and depressions occur. Depressions in the Sandhills offer a more mesic refuge for plants that are unable to persist in the surrounding xeric matrix, whereas, islands in the Green Swamp provide a drier alternative to the dominantly waterlogged surroundings. Peet & Allard (1993) circumvented these irregularities in their classification of longleaf pine communities across the entire range of this great southeastern forest. Their review identified four major series, also defined by a soil moisture gradient—xeric, subxeric, mesic, and seasonally wet. Based on this classification, legumes were most prominent in the subxeric series, a term that encompasses bean dips in the Sandhills and bean "mounds" in the Green Swamp.

In the longleaf pine forest of southwest Georgia, Hainds (1999) also found an abundance of legumes. However, patterns in legume species sorting were not pronounced when quantified across landform classes. Only one species was distinctly associated with the hydric-pond margin, and two with the xeric sand ridge extreme. In the Sandhills, I found legume attenuation to be high, particularly between the bottoms and mid-slopes of bean dips and pea swales. The incongruities between these studies are probably explained by differences in sampling strategies. In the Sandhills, I recognized a strong legume response to topography, and therefore, established transects along a topographic gradient. In the Hainds study, sampling was stratified based on landform. 37 plots were established on high flats, whereas no more than 12 plots represented other landforms. Presumably, topographic variation is low on "high flats," so one would also expect legume turnover to be low. The differences in legume sorting results may also be explained by the fact that the Hainds study spanned a broader ecological amplitude, from dry sand ridges to saturated pond margins. The present study sampled a narrower range more intensely (e.g. no hydric sites).

Although soil moisture explained most of the 27% of legume species variation along the gradients that Hainds studied, Ca was the second most important variable associated with that variation. Legumes require substantial amounts of Ca for the N-fixation process, especially in acidic soils (Lowther & Lonerogan, 1968), and nodulation of legume roots by *Rhizobium* spp. is enhanced when Ca levels are increased (Munns, 1968). This may be one of the important factors limiting legumes on the upper slopes and rims of bean dips and pea swales. The high concentration of %SAND at these locations precludes the retention of this base cation due to the low CEC characteristic of very sandy soils. However, in the bottoms of bean dips and pea swales I studied, Ca levels were exceptionally high for Sandhill soils. These elevated Ca levels are probably attributable to increased %CLAY and organic matter, both of which are recognized as having a high CEC. Clay and organic matter are also regarded as having a much higher water-holding capacity than sand. These relationships between soil texture, soil nutrients, and soil moisture ultimately determine productivity in frequently burned longleaf pine forests where light is seldom limiting. Productivity, in turn, affects the amount of organic matter in the soil, and, therefore, to some degree, Ca levels. Positive feedback mechanisms such as these are responsible for maintaining the fertility of loamy soil communities.

Wells (1942) suggested that K:Ca ratios may explain plant distribution in the Sandhills. When P is low and evenly distributed, as it was in this study, an increase in K or Ca respectively results in the production of more carbonaceous or more proteinaceous plant tissue (Albrecht, 1940). The domination of wiregrass (*Aristida stricta*) in the Sandhills, a species renowned for its high lignin content and unpalatability, points to a high K:Ca ratio in the area (Wells, 1942). In the bottoms of bean dips and pea swales, however, proteinaceous plants appear to dominate, and the K:Ca ratios are comparatively low. Xerophyllous species such as *Baptisia cinerea* and *Galactia regularis* occur most frequently on the upper slopes and rims, where %SAND values are higher, and the K domination over Ca is increased.

Wiregrass also appears to be more abundant on the upper slopes than in the bottoms of loamy soil communities. In the bottoms and on lower slopes, the graminoid component is usually more diverse and mesophytic (James, pers. obs.), and may include species of *Andropogon, Dichanthelium, Sorghastrum, Muhlenbergia, and Gymnopogon*, and/or *Schizachyrium scoparium, Anthaenantia villosa, Paspalum bifidum*, and *Tridens caroliniana*. The effect of this shift in the palatability and digestibility of leaf-tissue are probably important to local herbivores. Therefore, it is expected that the bottoms of bean dips and pea swales provide important feeding sites for many faunal species, especially quail, deer, turkey, rabbits, and insects, due to the higher nutrient content of the vegetation. The role that these herbivores play in the distribution of legume seeds and the regulation of biomass should be investigated further.

Fire in Loamy Soil Communities

A number of unmeasured variables, both biotic and abiotic, likely change along the slopes of bean dips and pea swales, and affect soil and plant interactions. Although no direct evidence exists to compare differences in fire frequency and intensity between slope classes in bean dips and pea swales, the increased fuel load in the bottoms of these depressions suggests that intensity and frequency would be maximized there. Increases in the amount and intensity of fires could be beneficial to legumes in multiple ways. Since fire intensity is positively related with the amount of N lost to volatilization (Davidson & Davidson, 1993), N deficiencies may be maximized at the lower slope classes immediately following fire, giving N-fixing legumes a competitive advantage. In addition, fire stimulates microbial populations, including the legume-inoculating *Rhizobium* spp., in all but the most intense fire regimes (Cochrane, 1968), which are seldom seen on the uplands in the Sandhills. The mobility and availability of Ca, an essential element in N-fixation, is also maximized following fire due to ash inputs (Christensen, 1987). Furthermore, heat, particularly moist heat, increases the germination of legume seeds, most of which are encapsulated by an otherwise resistant waxy cuticle (Martin & Cushwa, 1966). These issues should be experimentally evaluated in the context of loamy soil communities in the Carolina Sandhills. Restoration and maintenance of these unique communities will require an understanding of their responses to fire regimes that differ in frequency, intensity, and season of burn.

Related to fire are two other related and unmeasured variables that are expected to vary along the gradient—light and succession. As mentioned above, it is expected that higher productivity in the bottoms of loamy soil communities translates to higher fire intensity and frequency. Under these conditions, increased fire intensity would serve to keep the mid-story scrub oak cover in the bottoms to a minimum, leaving only the thin longleaf pine canopy to interfere with light interception at ground level. Increased fire frequency would maintain this open mid-story. On the upper slopes and rims, however, decreased fire intensities and frequencies due to decreased productivity are expected to enable succession to a fire-suppressed oak-dominated system. Once established, the low combustibility of oak leaves, and the detrimental shading effect that they have on other-wise combustible ground cover, have a negative impact on fuel quality, that serves only to perpetuate low fire intensity and frequency in these areas. Although quantification of these dynamics was outside the scope of this research, my field observations suggest that these relationships between productivity, plant biomass, and fire frequency and intensity are worthy of further exploration.

The Importance of Rooting Depth

Differences in rooting morphology between legume species may also help explain the patterns in sorting that were observed along the gradient. In the deep, porous, infertile sands that dominate the Upper Coastal Plain, rooting strategies are especially critical. Although the Sandhills receive a generous annual supply of precipitation, "the rain disappears as fast as it falls" (Wells, 1932) in most places, and successful xerophytes must develop mechanisms to cope with the prevailing moisture deficit. During the course of this study several root excavations were made. Mesophytic legumes inhabiting the bottoms of bean dips and pea swales tended to have finer, shallower root systems than their xerophytic relatives inhabiting the upper slopes and rims of these landforms, presumably because there is less need for deep foraging where resources (nutrients+moisture) are relatively close and plentiful (Weaver, 1919). The increased surface area and decreased root thickness characteristic of bottom-dwelling species also probably enhances the chances of inoculation by N-fixing bacteria (Davidson & Davidson, 1993). However, during times of drought stress, these fine-rooted, mesophytic species are potentially more vulnerable. Consequently, extreme drought periods are probably important in limiting the establishment of mesophytic legumes to the bottoms and lower slopes of loamy soil communities.

Regional Gradients: NC vs. SC Sandhills

Variation in edaphic factors and legume distributions between study areas suggest that the North and South Carolina Sandhills are not identical. Just as a productivity gradient was found from the bottoms to the tops of bean dip and pea swale slopes, a similar gradient seems to exist between study areas, with the Gamelands representing the more favorable site for nutrient availability and legume species richness and abundance. These differences are probably related to differences in general topography and geologic history, rather than management styles. During the course of this study, only one paper was found that compared the geology of the North and South Carolina coastal plains. Soller's (1989) monumental contribution to the understanding of subtle differences between these areas was made via an exhaustive study of the Lower Cape Fear River Valley in southeastern North Carolina.

The Lower Cape Fear River Valley is unique among Atlantic Coastal Plain river valleys in that it sits astride the largest of a series of temporarily-persistent, northwest-southeast-trending tectonic flexures that resulted from compressive forces beginning 750,000 ka (Soller, 1989). This particular flexure is known as the Cape Fear Arch, and it is flanked by the Albemarle Embayment to the north and the Charleston Embayment to the south. Periodic uplift along the Cape Fear Arch has caused the Cape Fear River to migrate towards its southeastern valley wall, thereby eroding one side of a series of paired terraces associated with elevated shorelines. This behavior contrasts dramatically with equivalent sections of the Pee Dee River in South Carolina, which flows along the southeastern flank of the Cape Fear Arch, and also approximates the mid-point between my study sites on the Gamelands and Refuge. Paired, symmetrical terraces and high sinuosity values typify the upper reaches of the Pee Dee River Valley, indicating that the effects of uplift on valley entrenchment and subsequent erosion have been minimal here compared to the upper Cape Fear River Valley, and that differences are related to position relative to the Arch axis.

Although there is still some debate about the nature of these tectonic features in the Coastal Plain (Marple & Talwani, 2000), other anomalies seem to support its existence. Soller (1989) and Nifong (1999) noted that the area with the greatest concentration of large Carolina Bays occurred within the Cape Fear River Valley in an area known as "Bladen Lakes," and that bays were relatively scarce and small in adjacent embayed regions. This study has confirmed that larger bean dips also tend to occur on the North Carolina Gamelands which are closer to the Cape River Valley, and, therefore, closer to the Arch axis. Since both bean dips and Carolina Bays are classified as eolian deflation features known as pans (Goudie & Wells, 1995) that were probably formed by the same processes operating at the same time in different substrates (See Chapter 2), the overlap of their maximum development along the Cape Fear Arch suggests that this tectonic feature has dramatically affected the nature of the current landscape. In addition, some meteorological phenomena also correspond to the location of the Cape Fear Arch. Church et al (1993) presented a summary of all very strong-violent tornados (F3-5) in the southeast between 1950-1988. In the Carolinas, the most conspicuous belt of tornados trended northeast-southwest, approximately along the crest of the Carolina Sandhills (Church, Fig. 2, p.446). The Middle and Lower Coastal Plain were devoid of tornado tracks, with the notable exception of a northwest-southeast trending belt that precisely overlaps the Cape Fear Arch axis as mapped by Soller (1989).

Ecological Implications

The regional decline of high-quality longleaf pine-dominated vegetation calls for rapid identification and characterization of community types that are in danger of permanent extirpation. Communities such as the Loamy Soil Variant of the Pine/Scrub Oak Sandhills, that are naturally infrequent across the landscape, are particularly vulnerable and worthy of preservation. Despite their small coverage area, these communities support a significant amount of the total plant diversity in the Sandhills, and harbor an unusual number of rare taxa (Sorrie, 1998). The enhanced fertility of loamy soil communities also appears to positively affect the quality of wildlife habitat, as many quail, deer, rabbits, turkeys, and insects were encountered during the course of this study despite the relatively small area of these isolated communities. This perceived faunal response is probably attributable to both the improved abundance and nutritive status of vegetation for forage in the bottoms of these communities, and the improved physical environment in the form of dense nesting and bedding grounds for many species. In the xeric context of the Sandhills, where a majority of the vegetation is lignin-rich and sparsely distributed, these advantages are both rare and important.

Ironically, the destruction of loamy soil communities has been accelerated by the same features that make them distinctive. Agricultural activities are often concentrated in these fertile soils, and many bean dips have been converted to a form that no longer resembles their former species diversity and composition. Of the bean dips that have been converted on public lands, most have been planted as wildlife food plots, although row-cropping, on a small-scale, is occasionally practiced. In either case, the fields generally mimic the shape of the depression and remnants of the original community are relegated to the unplowed margins. However, due to the decreasing popularity of wildlife food plots, many of these fields have been abandoned over the last several decades. Unfortunately, they do not appear to recover toward the original composition of the Loamy Soil Variant, though observations are limited. In view of the contributions they make to regional diversity, restoration of degraded bean dips and pea swales is a worthy pursuit towards the greater goal of perpetuating the entire longleaf pine ecosystem. This study has provided valuable baseline information regarding the soil characteristics and the distribution of native legumes in these habitats. These contributions should facilitate future restoration activities by identifying appropriate targets and clarifying regional differences.

CHAPTER IV.

LEGUME SEED AND SEEDLING PERFORMANCE ALONG SOIL AND TOPOGRAPHIC GRADIENTS IN BEAN DIPS AND PEA SWALES

Introduction

The Loamy Soil Variant of the Pine/Scrub Oak Sandhill Community is a distinctive habitat within the predominantly xeric matrix of the Carolina Sandhills (Schafale & Weakley, 1990). This community includes bean dips and pea swales, two types of topographic depressions that have relatively high levels of moisture and nutrients compared to adjacent uplands. The higher fertility in these small, shallow pockets is correlated with legume (Leguminosae) species richness and density, both of which decrease with increasing slope position. Legume species composition also changes along these complex topographic gradients (See Chapter 3). Diversity of grasses, composites, and oaks is also notably higher within the depressions (Sorrie, 1998), and at least eighteen rare taxa have been recorded (See Chapter 1). Variation among loamy soil communities in composition and productivity is probably most strongly associated with moisture availability (Peet & Allard, 1993; Hainds, 1999). In the Sandhills, this limiting resource may be largely determined by geomorphology, depth to impermeable layer, and area of upstream watershed.

The uniqueness and scarcity of the Loamy Soil Variant is sufficient grounds for it to be given conservation priority in land management decisions. In the past, a disproportionate number of bean dips and pea swales have been converted from their natural state for agriculture, wildlife food plots, and pine plantations because of their fertility and productivity. However, I hypothesize that the short-term gains they provide through any form of land conversion are small compared to the long-term contributions they make to ecosystem diversity. Legume seeds and leaves are also known to be attractive to many wildlife species because of their greater nutrient content and higher C:N ratio. Numerous quail, deer, rabbits, and turkeys were sited in loamy soil communities throughout the course of this study, and insect diversity also appeared higher than in the surrounding upland communities.

Loamy soil communities represent some of the most species-rich areas in the Sandhills (Sorrie, 1998), and because of their value to native wildlife, restoration of degraded examples should be a high priority for land managers. Restoration efforts must be guided by an understanding of species composition and factors affecting species distributions within these communities. Partial fulfillment of this initial requirement was met in 1998, when legume populations were sampled along edaphic and topographic gradients in high-quality examples of bean dips and pea swales (See Chapter 3). Once restoration targets have been identified, practitioners must determine the best method for establishing the correct species assemblage. The present study addresses this second need. In 1999, I introduced legume seeds and seedlings, in reciprocal-transplant fashion, to five of the bean dip and pea swale gradients in the Carolina Sandhills Wildlife Refuge sampled in 1998. The performance of these treatments was evaluated at the end of one growing season, and the following questions were addressed: 1) Does first year seed and seedling performance reflect the adult legume distribution patterns observed in 1998? 2) Do seeds and seedlings perform with equal vigor across the gradient?

Field Methods

Study Area

This experiment was conducted on the Carolina Sandhills National Wildlife Refuge in Chesterfield County, South Carolina. Elevations here range from 70 m in the Black Creek Valley to 180 m on the highest interfluves. The topography is dominated by a series northeast-southwest trending ridges, most of which are capped by deep and highly-weathered sands. Approximately 70% of the soils on the Refuge are mapped as the Alpin-Candor series. These excessively-drained sands are classified as thermic, coated Typic Quartzipsamments and sandy, siliceous, thermic, Arenic Paleudults, respectively (Morton, 1995). They are ideally suited to the xeric, longleaf pine-turkey oak association that is the dominant natural vegetation association in the area. Loamy soil communities such as bean dips and pea swales occur sporadically within the mainly xeric fabric of the Refuge.

Seed Collection and Storage

Propagules were collected between June and October, 1998, from various populations on the Refuge. Seeds were cleaned, labeled, and stored in Ziploc® bags in a frost-free freezer as quickly as possible following collection. In December, 1998, seeds were removed from the freezer, and each species was immersed separately in cool water. Seeds that floated on the surface were skimmed and discarded. The remaining ones were air-dried and counted by groups of 100 using a pharmaceutical pill-counting tray and a letter opener. After each species was counted, the seeds were again placed in the freezer until time of sowing.

The number of available seeds was an important factor in selecting the legume species to be used in this experiment. A minimum of 1,500 seeds and 150 plants per species was desired to accommodate the experimental design. It was also necessary that the species represent different portions of the topographic gradient observed in 1998 sampling. Because no information was available regarding the percent germination of these species, a minimum of 25% was assumed in planning the sowing density, and more species were planted than would eventually be used.

Initial Seed Sowing and Greenhouse Growth

In late January, 1999, a total of eighteen, 98-cell trays were filled with potting medium. Each cell was approximately 3x3x10 cm, and the potting medium consisted of a 2:1 Promix®:Sand ratio. Twelve quarts of Promix® (w/o Pearlite®) were combined in a cement mixer with six quarts of sand. Four of the six parts were collected from the Refuge, and two were of sterile, commercial origin. Three trays were allocated to each of the following six species: *Amorpha herbacea* var. *herbacea, Baptisia cinerea, Galactia regularis, Galactia volubilis, Stylosanthes biflora,* and *Tephrosia virginiana*. These species were selected because of available seed supply and their tendency to occupy different portions of the gradient (See Chapter 3). *Baptisia cinerea* and *Galactia regularis* represented the xeric species, due to their maximum frequency of occurrence on the upper slopes and rims of bean dips and pea swales. *Tephrosia virginiana* is more widely distributed across the gradient, but shows a slight preference for the drier portion of the gradient. All others were classified as mesic species, occurring more frequently in the bottoms and on lower slopes of these landforms.

On the evening of January 30, 1999, boiling water was allowed to cool two minutes before it was poured over seeds designated for production of seedlings in the greenhouse. The seeds were soaked for approximately twelve hours to facilitate germination since many legumes in fire adapted systems have a moist heat requirement (Martin & Cushwa, 1966). The following day, seeds were sown at an average density of three seeds per cell. Each seed was individually drilled to a depth of approximately 1 cm into the potting medium using a blunt, pointed object. Trays were placed on a greenhouse bench, and monitored at least three times per week. Trays were watered as needed, and fertilized sparingly with a 20-20-20 fertilizer on two occasions during the four and one-half months of observation.

Selection of Experimental Sites

Of the ten Refuge transects sampled during 1998, five were selected for introduction of legume seeds and seedlings. These transects were 50 to 60 m in length and extended in the direction of maximum slope gradient from the lowest point to the surrounding rims of the depressions. A combination of slope position, soil texture and soil nutrient attributes was used to select three quadrats from each of these five transects to serve as the experimental plots. These fifteen quadrats were originally chosen to represent one of four %SAND classes with the following parameters: Class 1=81-83% (n=4); Class 2=87-89% (n=4); Class 3=90-91% (n=3); Class 4=93-97% (n=4). In all but three quadrats, the %SAND class corresponded exactly with the following slope classes that were used for the 1998 analysis: 1=bottoms; 2=lower slope; 3=mid-slope; and 4=upper slope/rim. Each of the exceptions was either a discrepancy between sand class 2 and slope class 1, or sand class 3 and slope class 4.

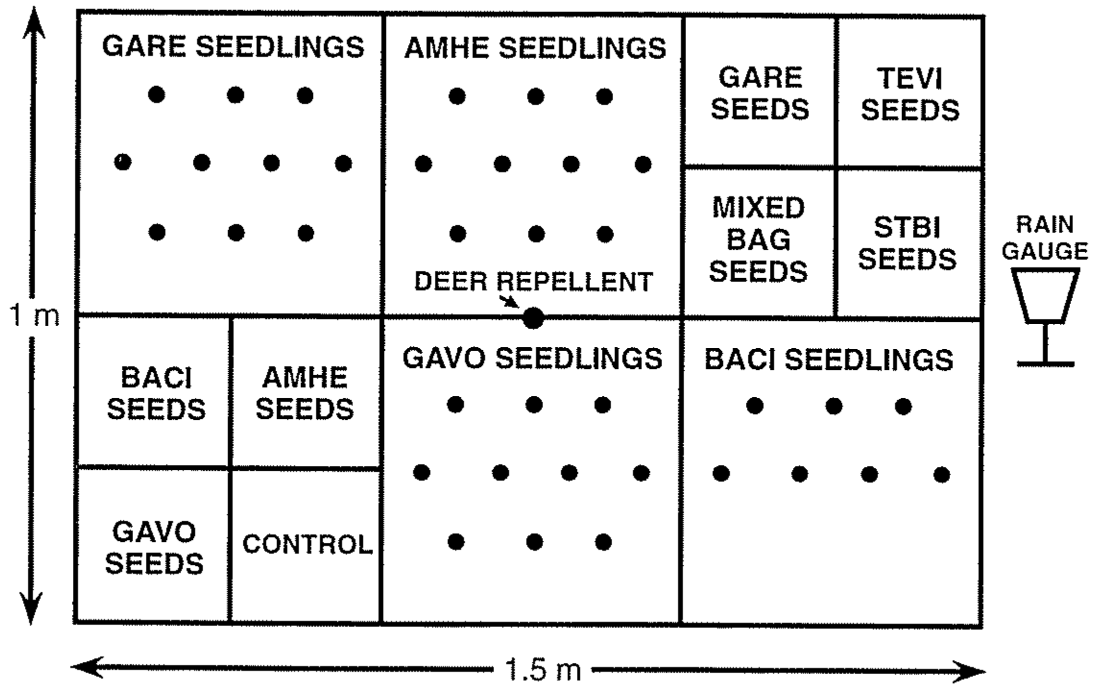
All plots were located in the southeastern corner of the Refuge between 98-115 m above sea level. None were more than 38 m above or 3 km away from Black Creek.

Plot Establishment

The fifteen 0.5 x 1.0 m quadrats with known edaphic conditions selected for plot establishment were prepared for seedling transplant and seed sowing in early June, 1999. Plot preparation involved the expansion of the original quadrat by a factor of three, resulting in a 1.5 m^2 plot that was centered over the original quadrat. Within this area, all above- and below-ground competition was removed to a depth of approximately 0.3 m using shovels, rakes, and other implements of destruction. All practical efforts were made to remove undecomposed litter from the plots, and shake loose soil from the root masses before they were discarded. Once all plant material had been removed, the soil within the plot was turned repeatedly with a shovel to achieve maximum homogeneity.

The plot design is shown in Fig. 4.1, although individual sub-plots were randomly assigned at each location. This diagram does not show the 0.5 m buffer zone that surrounded the 1.0 x 1.5 m planting and sowing area, but the plot preparation procedures were identical for each. Throughout this manuscript, references to the "plot(s)" will imply the central 1.0 x 1.5 m area where selected legume seeds and seedlings were introduced. Each plot was divided into six 0.5 x 0.5 m sub-plots. Four of these were designated for seedling transplant, and two for seed sowing. The two seed sub-plots were further divided into 0.25 x 0.25 m blocks to accommodate eight seed treatments. The corners of all sub-plots and blocks were marked with wooden stakes and boundaries by a tautly-strung strand of synthetic fiber about

Figure 4.1. Experimental Plot Design. 0.5 m buffer zone not shown. AMHE=*Amorpha herbacea* var. *herbacea*; BACI=*Baptisia cinerea;* GARE=*Galactia regularis*; GAVO=*Galactia volubilis*; TEVI=*Tephrosia virginiana*; and STBI=*Stylosanthes biflora.*


GARE SEEDLINGS
AMHE SEEDLINGS
GARE SEEDS
TEVI SEEDS
MIXED BAG SEEDS
STBI SEEDS
RAIN GAUGE
DEER REPELLENT
1 m
BACI SEEDS
AMHE SEEDS
GAVO SEEDLINGS
BACI SEEDLINGS
GAVO SEEDS
CONTROL
1.5 m

10 cm above the ground surface. This fiber effectively minimized interference between *Galactia volubilis*, a twining-trailing species, and adjacent subplots.

A rain gage was installed at each of the five transect locations, adjacent to the plot that had the least interference from the longleaf pine overstory. This was intended to provide a rough estimate of the variance in precipitation that may occur across relatively small spatial scales in the Sandhills. A locally popular form of deer retardant was also installed in the center of each plot to discourage browsing and trampling. This method consisted of a human hair-kneehigh pantyhose unit that was suspended in the air to encourage circulation of the presumably displeasing aroma. Whether the method is effective or not is not known, but no deer interference was noted during the experiment.

Legume Introductions to the Plot: Seeds

On June 11, seeds of the following legumes were removed from the freezer: *Amorpha herbacea* var. *herbacea, Baptisia cinerea, Galactia regularis, Galactia volubilis, Stylosanthes biflora,* and *Tephrosia virginiana.* Each species was pre-counted into fifteen groups of 100 seeds, corresponding to the fifteen experimental plots. The 100-seed groups were wrapped in fine cheesecloth prior to their immersion in ~90° C H_20. They were left to soak and cool to room temperature for sixteen hours. A seventh "Mixed Bag" seed treatment, containing eleven legume species, was treated similarly. Although the exact number of seeds was unknown in this treatment, nearly equal volumes were allocated to each of the fifteen plots. The approximate recipe for the Mixed Bag treatment is recorded as Fig. 4.2.

Fig. 4.2. Mixed Bag Recipe. Per bag contents.

Crotolaria rotundifolia	20 seeds
Crotolaria purshii	40 seeds
Desmodium nuttallii	3 seeds
Galactia erecta	¼ tsp
Lespedeza hirta var. *hirta*	½ tsp
Lupinus diffusus	¼ tsp
Orbexilum lupinellum	20 seeds
Orbexilum pedunculatum var. *gracile*	100 seeds
Pediomelum canescens	25 seeds
Rhynchosia reniformis	10 seeds
Tephrosia spicata	5 seeds

Total volume of each mixed bag=approximately 1 Tablespoon (n=15)

While the seeds were soaking, it rained for the first time in four weeks. The recently-installed rain gages recorded 1.5 +/- 2.5 cm, demonstrating the extent of variability in precipitation that occurs across small spatial scales in the Sandhills. In the hot, humid daylight hours of June 12, all seeds were sown in their designated sub-plots by the following method: 1) each seed treatment block was massaged by hand to a depth of ~15 cm and smoothed, 2) a circular depression was rounded out in proportion to the width of the treatment block without exceeding a depth of 3 cm, 3) 100 seeds of each species were evenly scattered within the prepared seedbed, and 4) seeds were covered with ~2 cm of soil, and the entire block was packed firmly. A control block was prepared in an identical fashion (except no seeds were introduced) to assess the degree of influence from the native seed bank. When all seeds were sown, a light layer of pine straw litter (~380 g/m^2) was evenly distributed over the surface of each sub-plot.

Legume Introductions to the Plot: Seedlings

Seedlings were allowed to acclimate to ambient Sandhill conditions in their trays beneath the shade of a large *Prunus caroliniana* for one week following transport from greenhouse facilities in Chapel Hill, North Carolina. In the two days after seed-sowing was completed, all seedlings were transplanted to their respective sub-plots. Ten individuals of similar size and vigor were planted equidistant from each other for the following three species: *Amorpha herbacea* var. *herbacea, Galactia regularis,* and *Galactia volubilis.* Only seven individuals were available for each *Baptisia cinerea* sub-plot, but these were also planted at regular spacing intervals. The planting procedure consisted of 1) each seed treatment block was massaged by hand to a depth of ~15 cm and smoothed, 2) a 6 x 10 cm hole was dug by hand for each seedling, 3) seedling plugs were carefully removed from their cells and centered within the hole, and 4) holes were back-filled with soil and packed firmly. When all seedlings were planted, a light layer of pine straw litter (~380 g/m^2) was evenly distributed over the surface of each sub-plot.

By June 14, all legume seeds and seedlings had been successfully introduced to each of the fifteen plots. Each sub-plot was then immediately irrigated at the rate of 1.0 gallon/m^2 using water from the closest natural source (i.e. lakes & creeks on the Refuge). Following this initial irrigation, only one other watering episode (June 25) was deemed necessary to ameliorate the shock to the transplanted seedlings.

Monitoring & Data Collection

During the first month, all plots were monitored two times per week. At each visit, the number of germinated seeds/species and the number of leaves/seedling sub-plot were counted. After the first month, the monitoring frequency decreased to once per week, and, again, to two times per month in the third and final month. However, only data from the final census and harvest were used in the final analysis due to the inability to track survivorship of individual germinules and leaves. Germinated seeds in the mixed bag and control treatment blocks were identified to species as early as possible. Rainfall was recorded for all sites each time the plots were monitored.

Final Count and Harvest

The last census of the experimental plots was conducted on September 19 and 20, 1999. At this time, a final count of the germinated seeds was made. Within the seedling sub-plots, roots and shoots of all individuals were harvested and bagged separately by sub-plot. Although 100% extraction of fine roots was impractical, approximately 90% of the root biomass was successfully retrieved. Roots and shoots were dried in a 70° C oven for 48 hrs, and weighed separately using a Mettler Model PN-1210 balance.

Analytical Methods

All analyses of the experimental data were performed using SAS 7.0. The General Linear Model procedure (PROC GLM) was used to test for the effect of either one or two independent variables on biomass, shoot mass, root mass, and root:shoot ratio. This parametric analysis was used to compare between-group biomass, shoot mass, root mass, and root:shoot ratios, each of which approximated a normal distribution. When only one independent variable was being tested (species or sand/slope class), a one-way ANOVA was used. In testing for the effects of possible interactions among biotic and abiotic variables on biomass, etc. a two-way ANOVA was used. The Type III Sum of Squares was always used for reporting F Ratios and probabilities of significant differences between classes.

A non-parametric equivalent of 1-way ANOVA (PROC NPAR1WAY) was used to test for the effects of either sand/slope class or species on the number of germinules alive at the last census. A non-parametric method was used because this data was binomially distributed since germination and survival was between 0-100 in all plots. Wilcoxon scores were generated and compared using the Kruskal-Wallis test (Kruskal & Wallis, 1952). Effects of possible interactions between independent variables on the number of surviving germinules were tested using a Generalized Linear Model (PROC GENMOD).

Results

Seedlings

Survivorship of the transplanted seedlings was generally high for all four species: *Amorpha herbacea* var. *herbacea* (97%), *Baptisia cinerea* (68%), *Galactia regularis* (95%), and *Galactia volubilis* (96%). Mortality by sand class is shown for each species in Fig. 4.3. No clear trends in survivorship can be deduced for *Amorpha herbacea* var. *herbacea,* but twice as many *Baptisia cinerea* seedlings died in sand classes 1 and 2 as did in classes 3 and 4. The two *Galactia* species experienced their highest mortality in sand class 4. No *Galactia volubilis* seedlings died in sand class 1, and mortality increased linearly from classes 2 to 4. 71% of the total mortality of *Galactia regularis* seedlings occurred in sand class 4.

The results of the 2-way ANOVA indicate that both species and sand class had a significant effect on the average biomass that was harvested from the plots in September. However, no significant interactions between species and sand class were detected. When the effect of species was held constant, biomass differed significantly between sand classes ($p<.01$). In sand class 1 and 2 plots, average final biomass was nearly twice as great as in sand class 3 and 4 plots (Fig. 4.4). A coarser comparison between bottoms (sand class 1+2) and slopes (sand class 3+4) verified this trend (Fig. 4.5), and the differences were highly significant ($p<.0004$). When the effects of sand class were held constant, differences in biomass were also significantly different among species ($p<.0008$). Average biomass of *Galactia volubilis* was almost three times greater than *Baptisia cinerea*, apparently the least productive of the species tested. *Amorpha herbacea* var. *herbacea* and *Galactia regularis* occupied the middle range of productivity, and differences between these two species are probably not significant (Fig. 4.6). Biomass was almost twice as high in bottom plots as in

Fig. 4.3. Seedling Mortality by Sand Class.

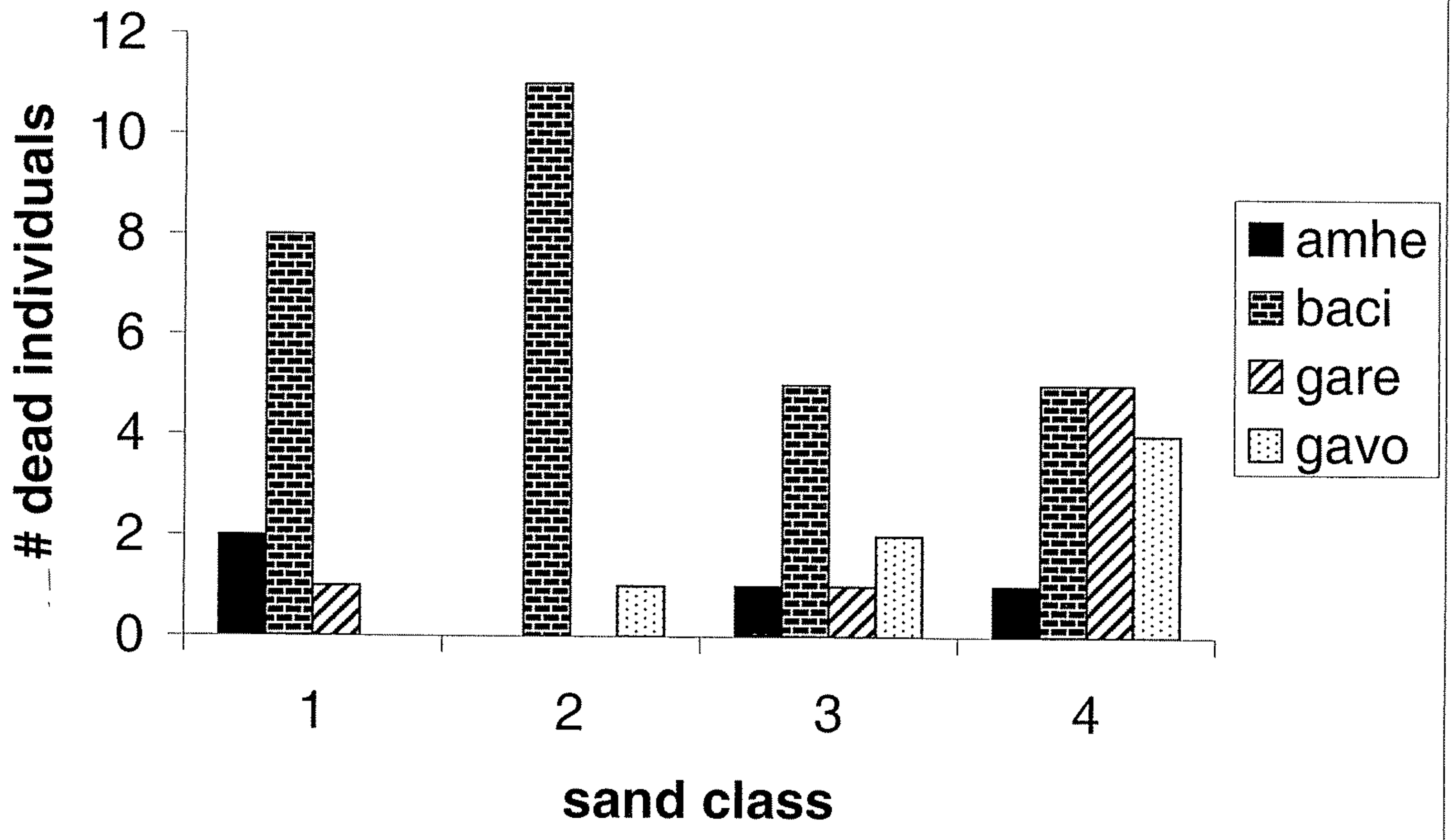


Fig. 4.4. Average Biomass by Sand Class

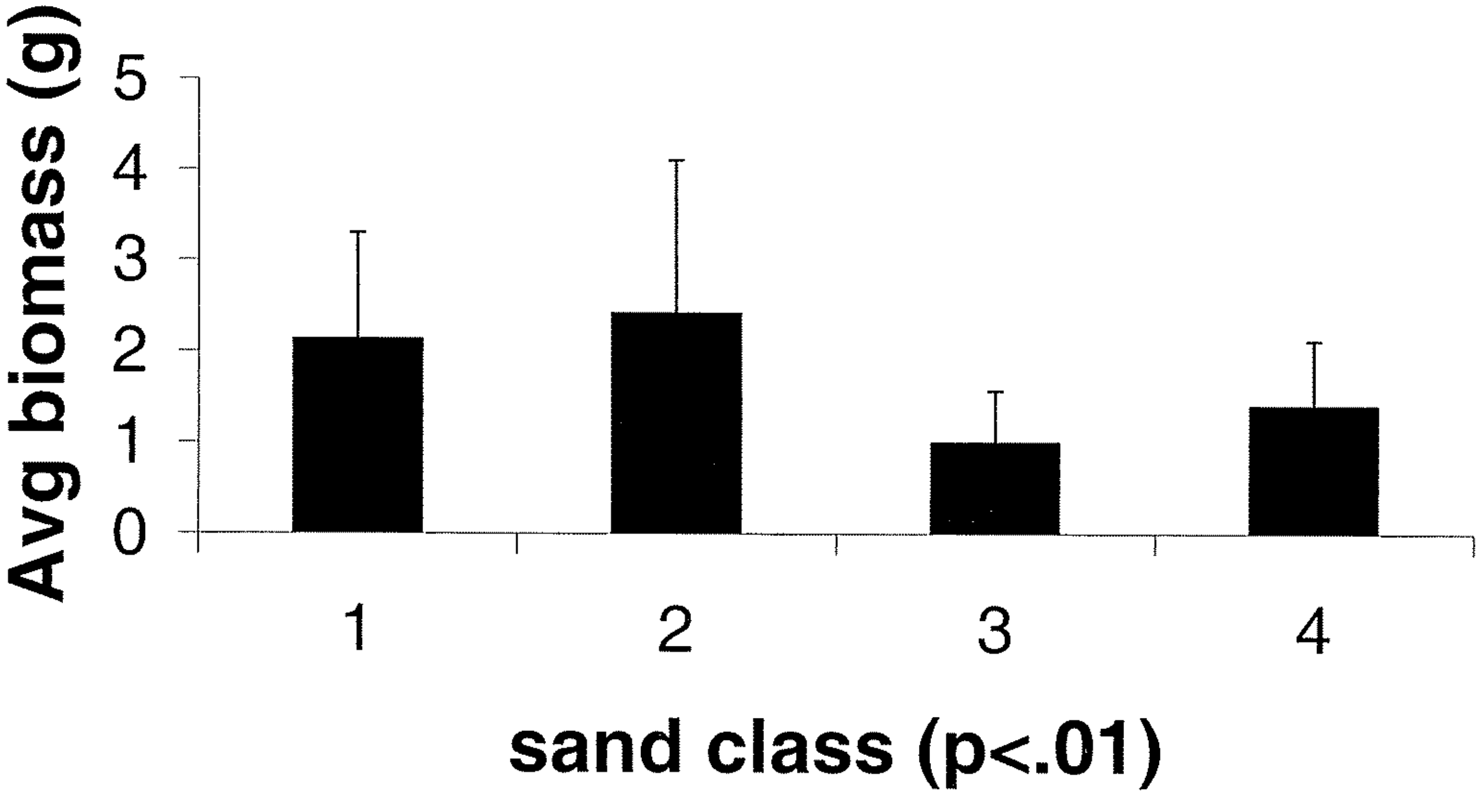
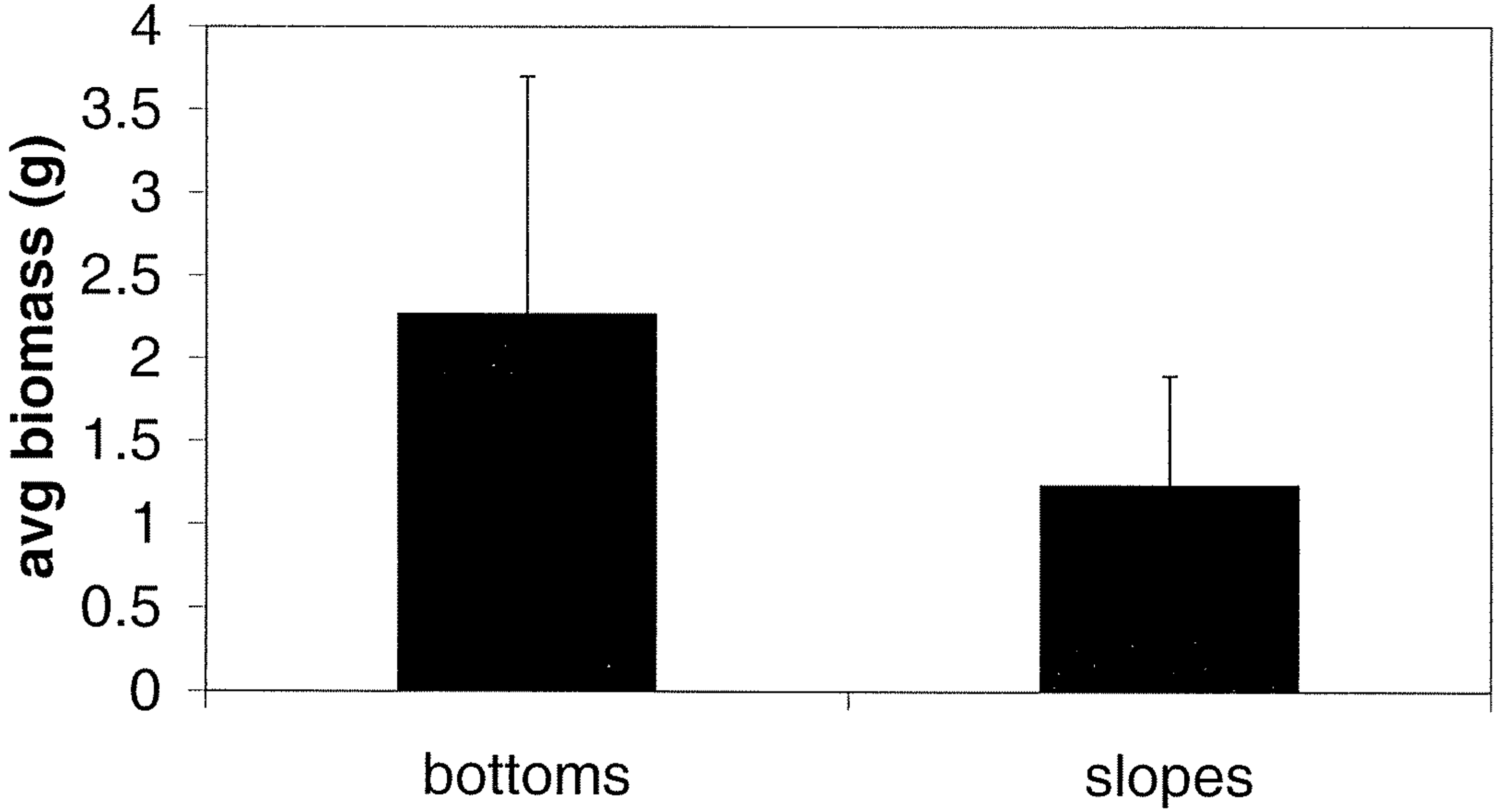
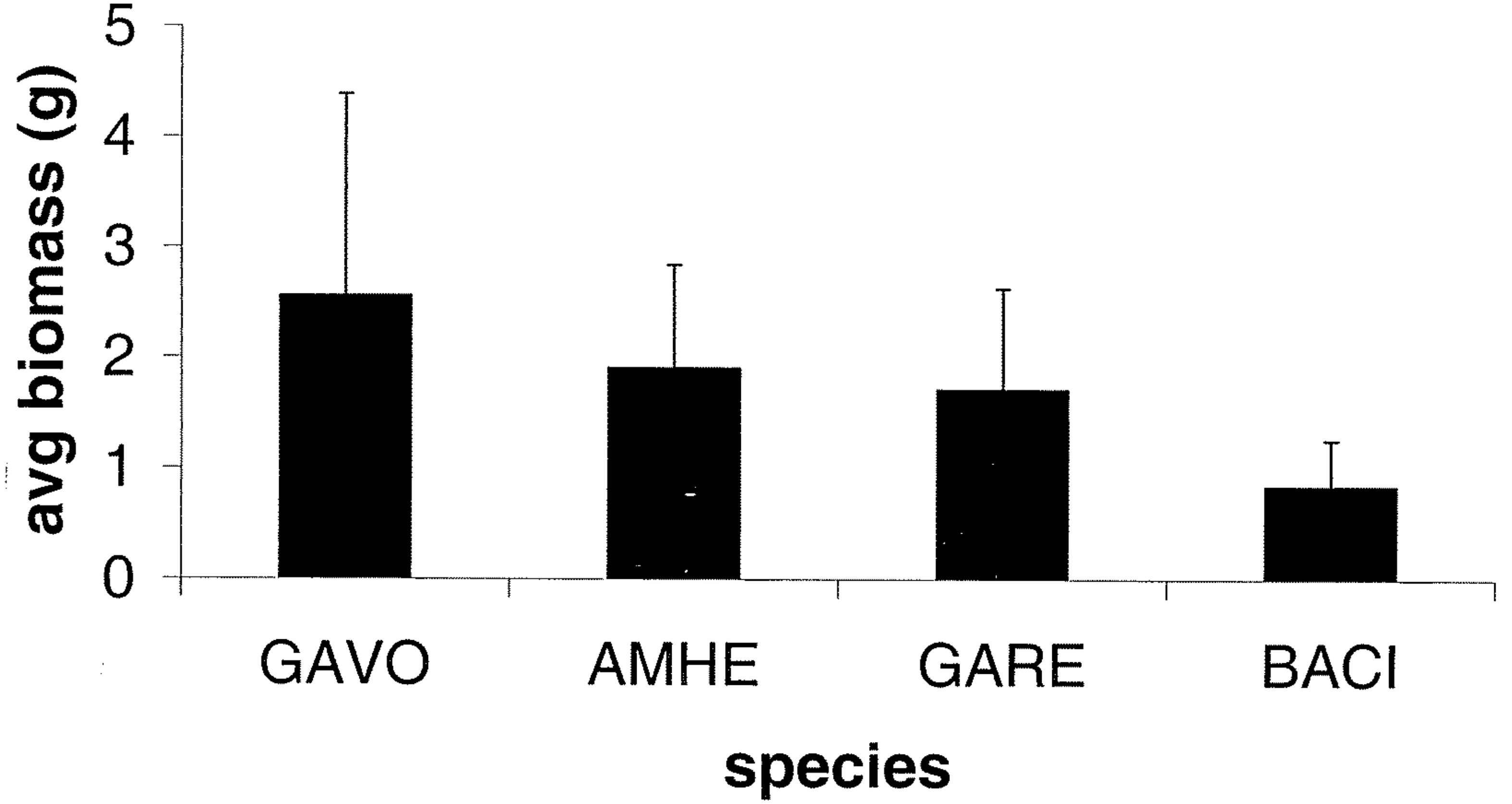


Fig. 4.5. Average Biomass in Bottoms vs. Slopes.



p<.0004

Fig. 4.6. Average Individual Biomass by Species.

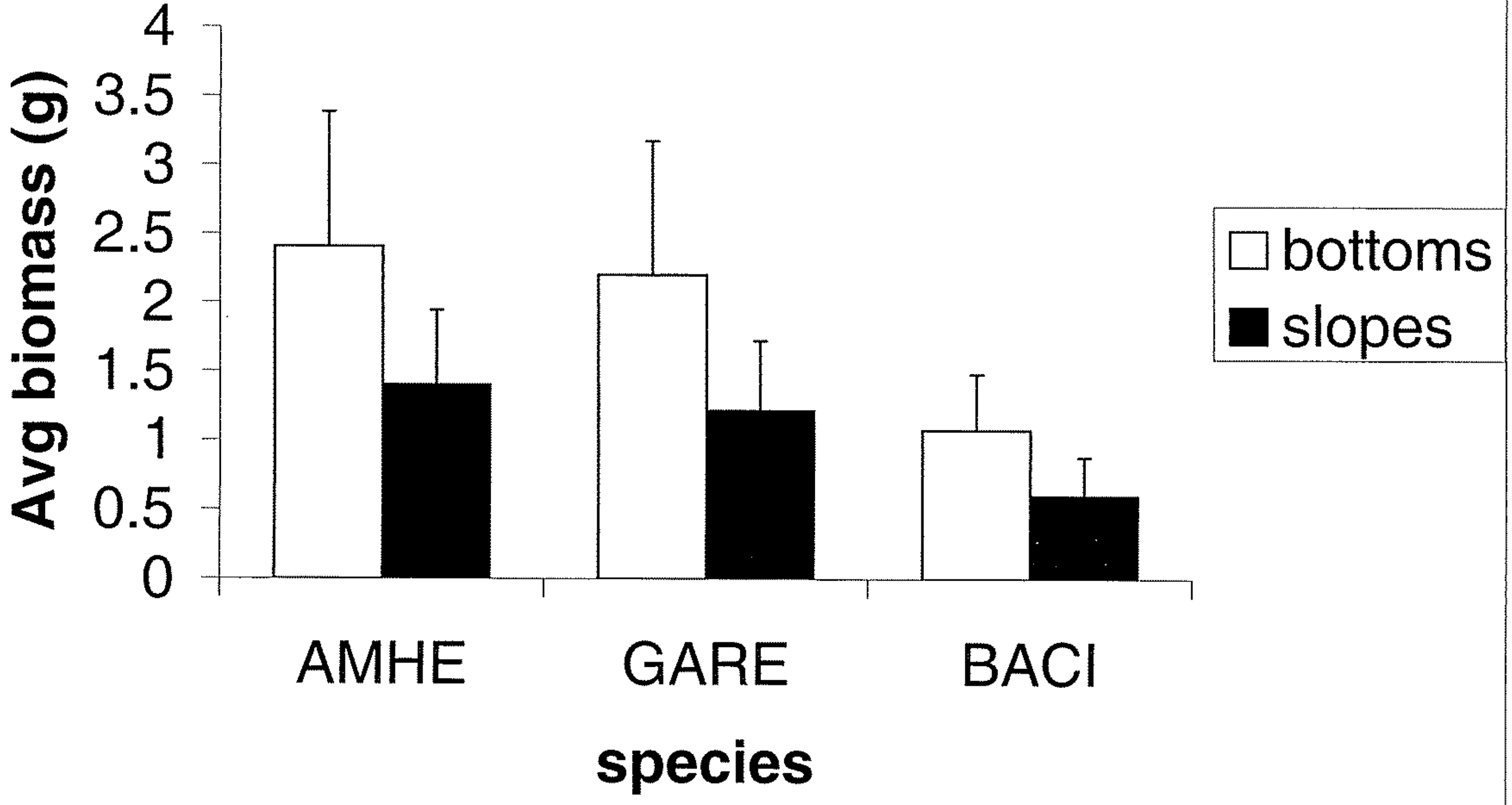


slope plots for *Amorpha herbacea* var. *herbacea* (p<.03), *Galactia regularis* (p<.03), and *Baptisia cinerea* (p<.02), but no significant differences were detected for *Galactia volubilis* (Fig. 4.7).

Average shoot mass was also significantly affected by species (p<.0004) and sand class (p<.04) when variation in the other was accounted for. Like biomass, shoot mass was generally highest in sand classes 1 and 2 (Fig. 4.8), and *Galactia volubilis* and *Baptisia cinerea* represented the highest and lowest shoot mass, respectively (Fig. 4.9). Average shoot mass in bottom plots was two times greater than in slope plots (p<.003), but only two species, *Baptisia cinerea* (p<.03) and *Galactia regularis* (p<.05) had significantly more shoot production in bottom plots (Fig. 4.10 & 4.11).

Average root mass was found to be significantly different among sand classes (p<.0004) when the intervening effect of species was held constant. Fig. 4.12 indicates that average root mass is generally highest in sand classes 1 and 2, as it was for shoot mass and total biomass. The effect of species on average root mass was also highly significant (p<.0001), but the rankings implied by least-square means are slightly different than for total biomass and shoot mass (Fig. 4.13). *Galactia volubilis* did not have the highest average root mass as it did for shoots and total biomass. Instead, root productivity was highest among the intermediate species, *Amorpha herbacea* var. *herbacea* and *Galactia regularis*. Differences between average root mass in bottom vs. slope plots were highly significant (p<.0001), again, with productivity nearly twice as high in bottom plots (Fig. 4.14). This trend was significantly supported by three of the four seedling species: *Amorpha herbacea* var. *herbacea* (p<.01), *Galactia regularis* (p<.02), and *Baptisia cinerea* (p<.03) (Fig. 4.15).

Fig. 4.7. Average Biomass by Species in Bottoms vs. Slopes.



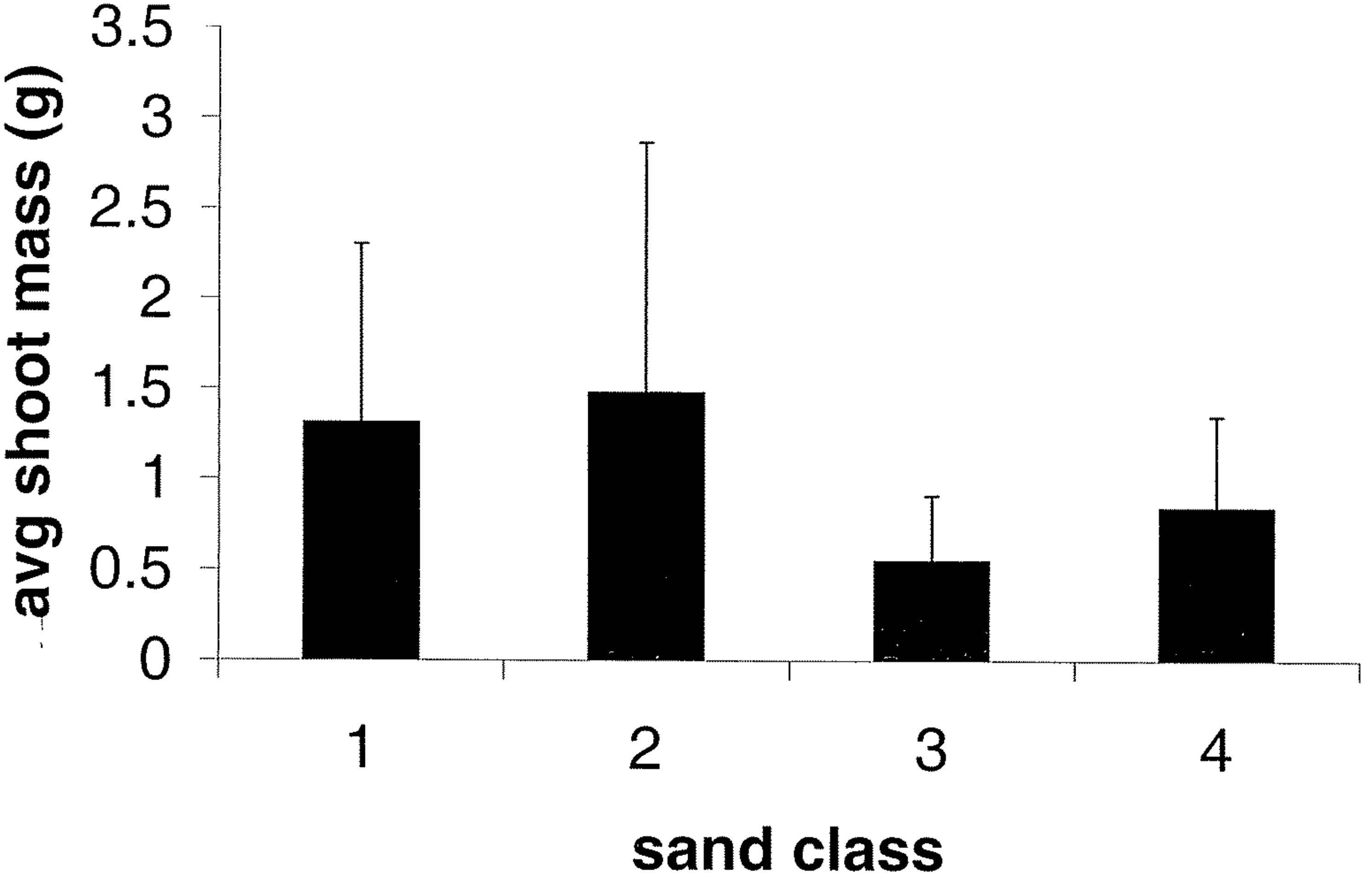


Fig. 4.8. Average Shoot Mass by Sand Class.

Fig. 4.9. Average Shoot Mass by Species.

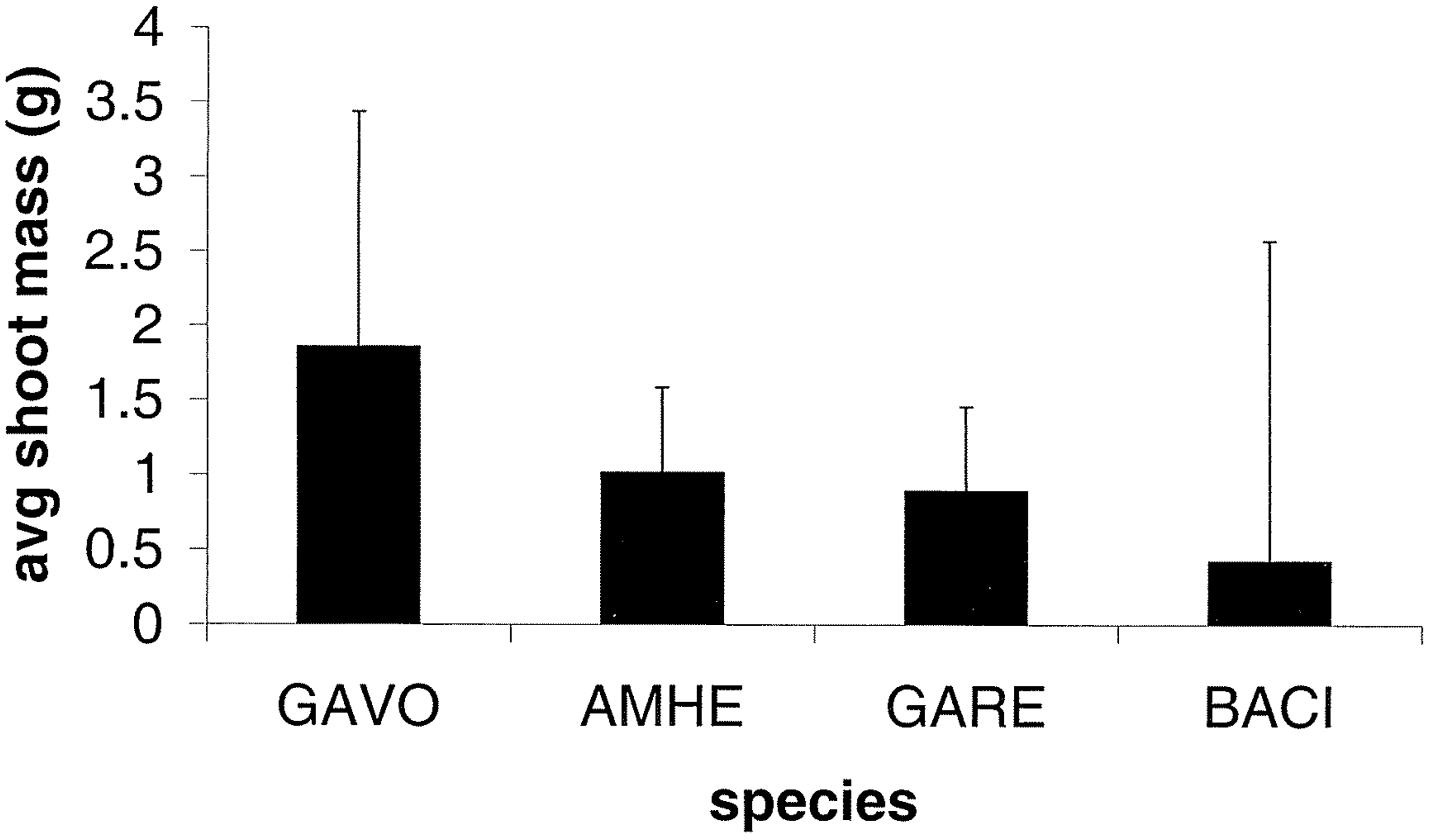


Fig. 4.10. Average Shoot Mass in Bottoms vs. Slopes.

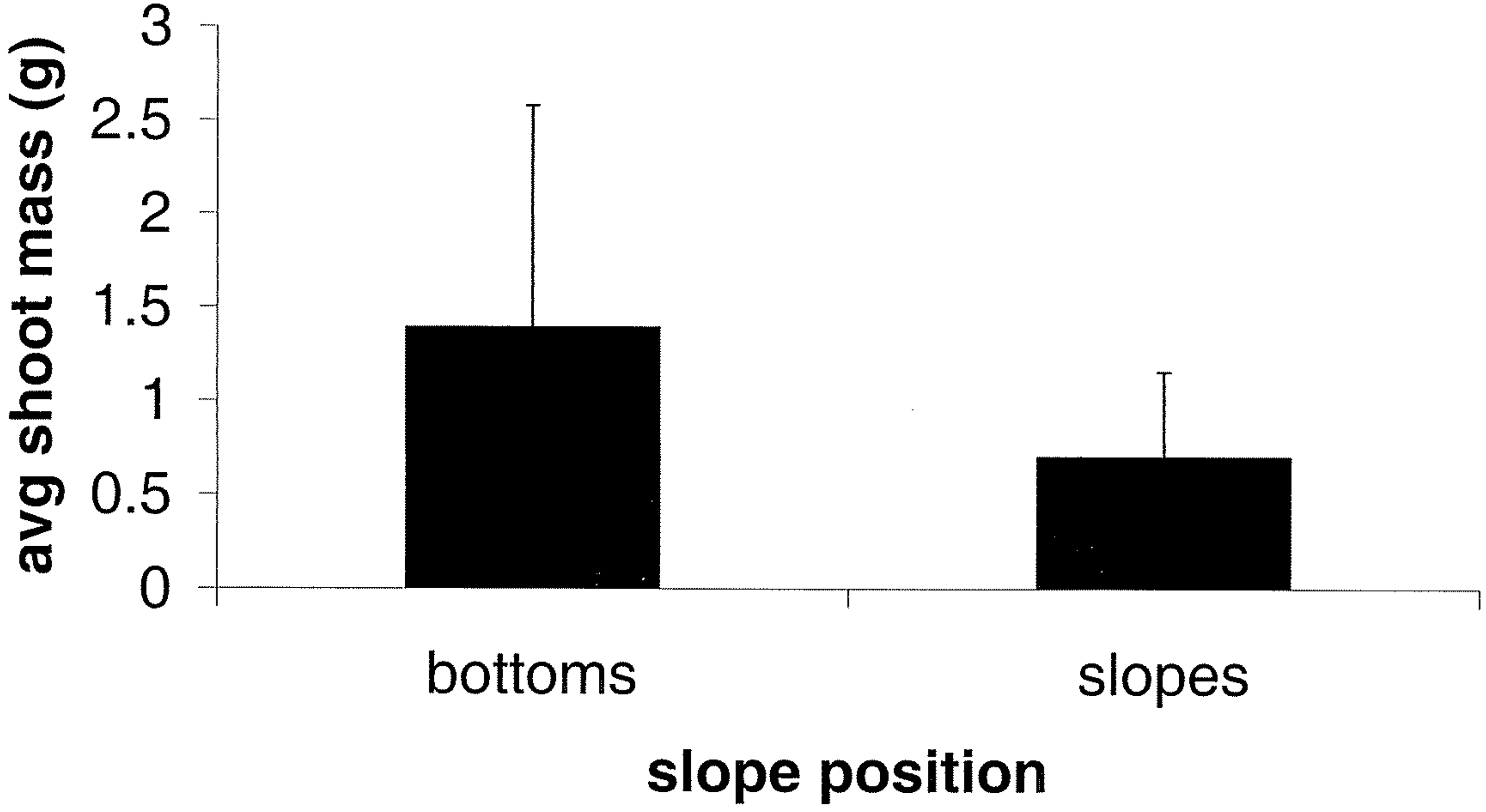


Fig. 4.11. Average Shoot Mass by Species in Bottoms vs. Slopes.

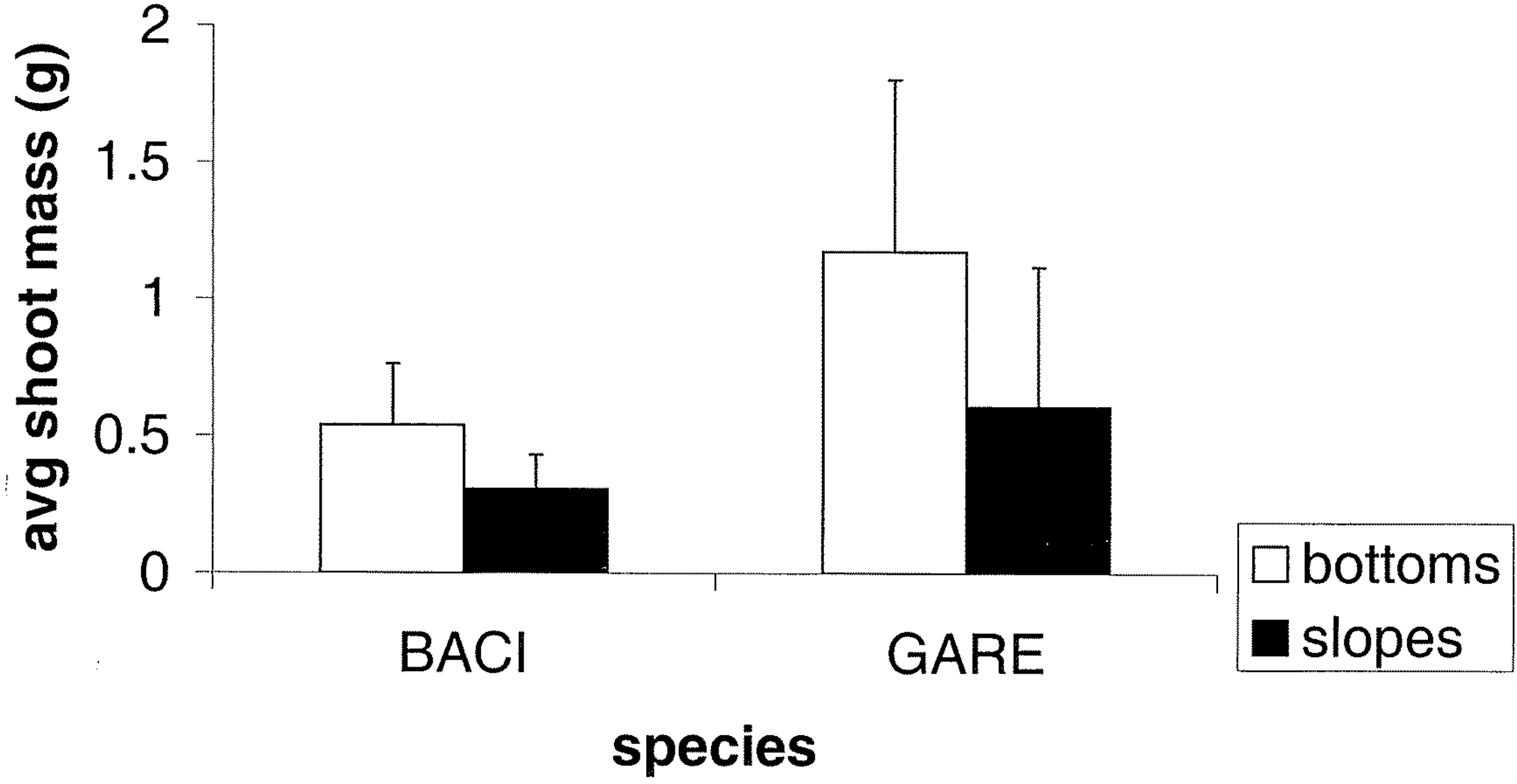


Fig. 4.12. Average Root Mass by Sand Class.

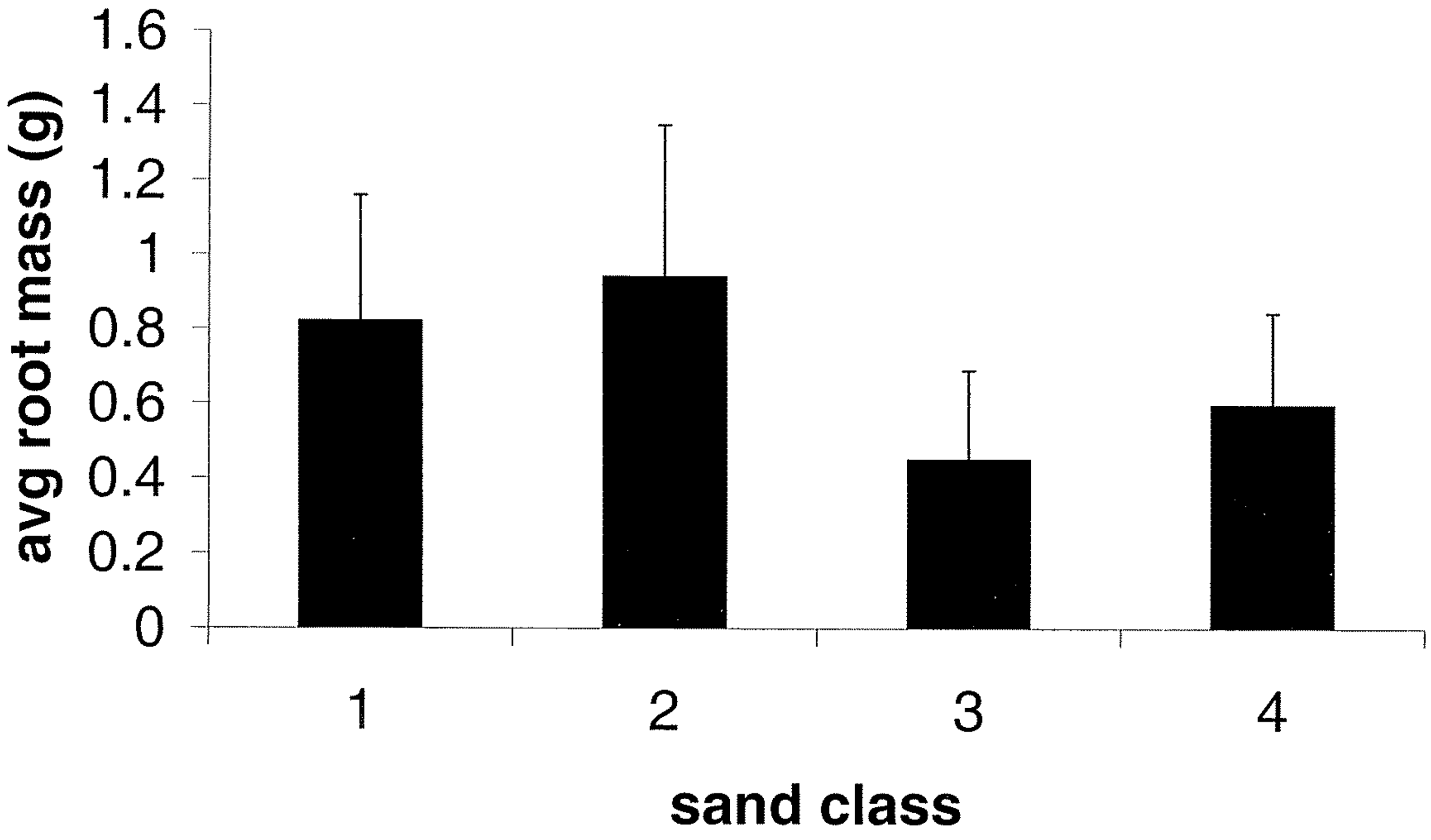


Fig. 4.13. Average Root Mass by Species.

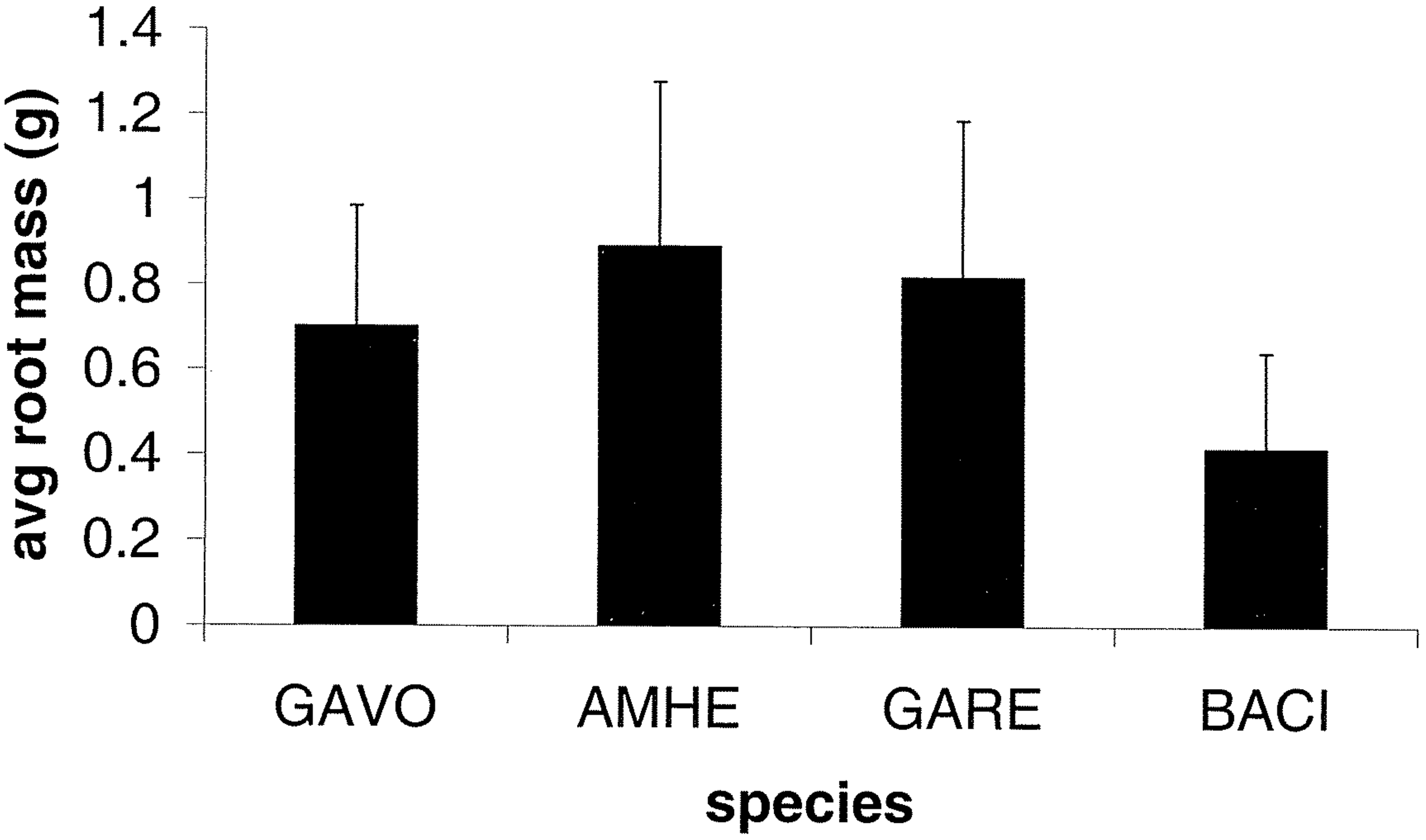


Fig. 4.14. Average Root Mass in Bottoms vs. Slopes

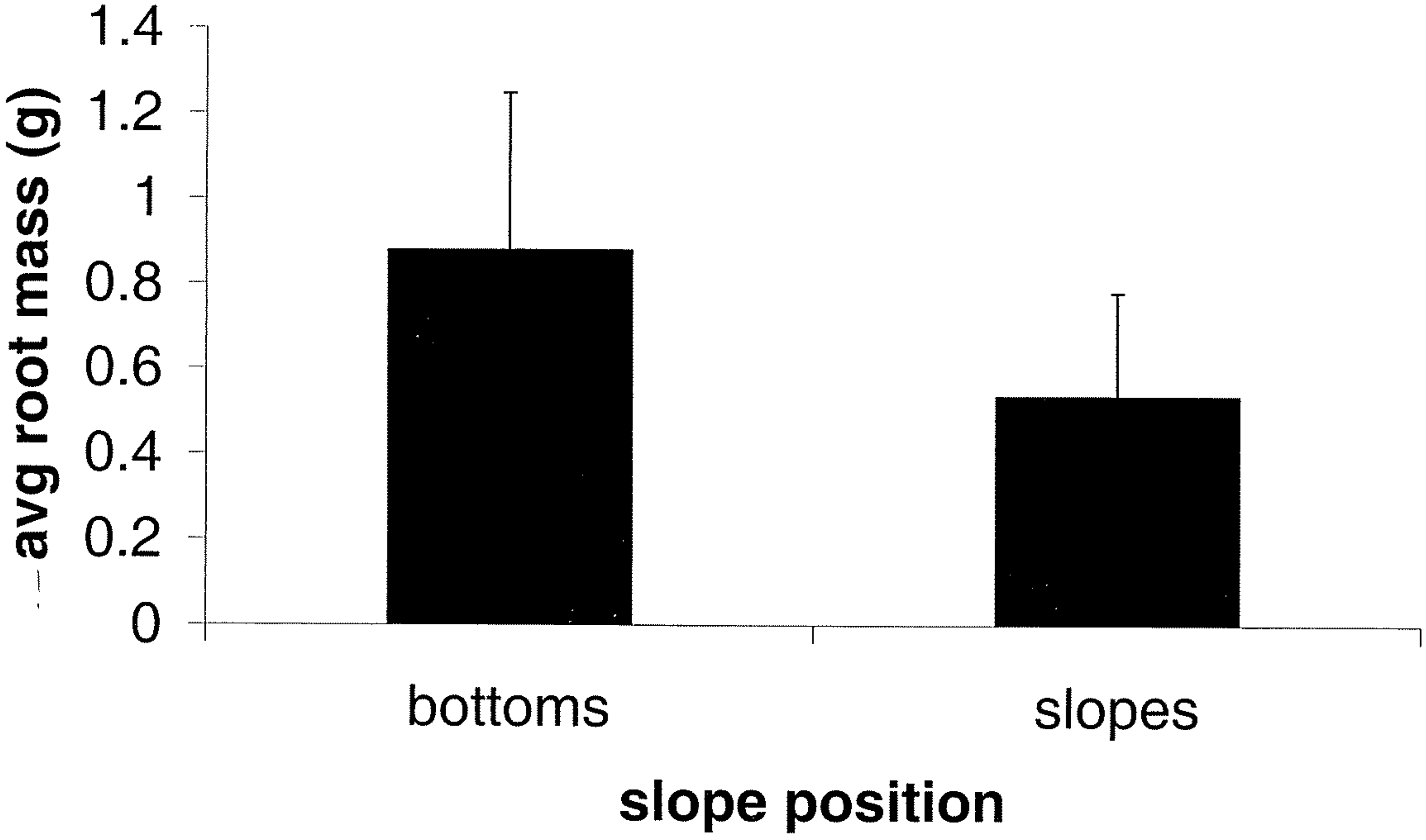
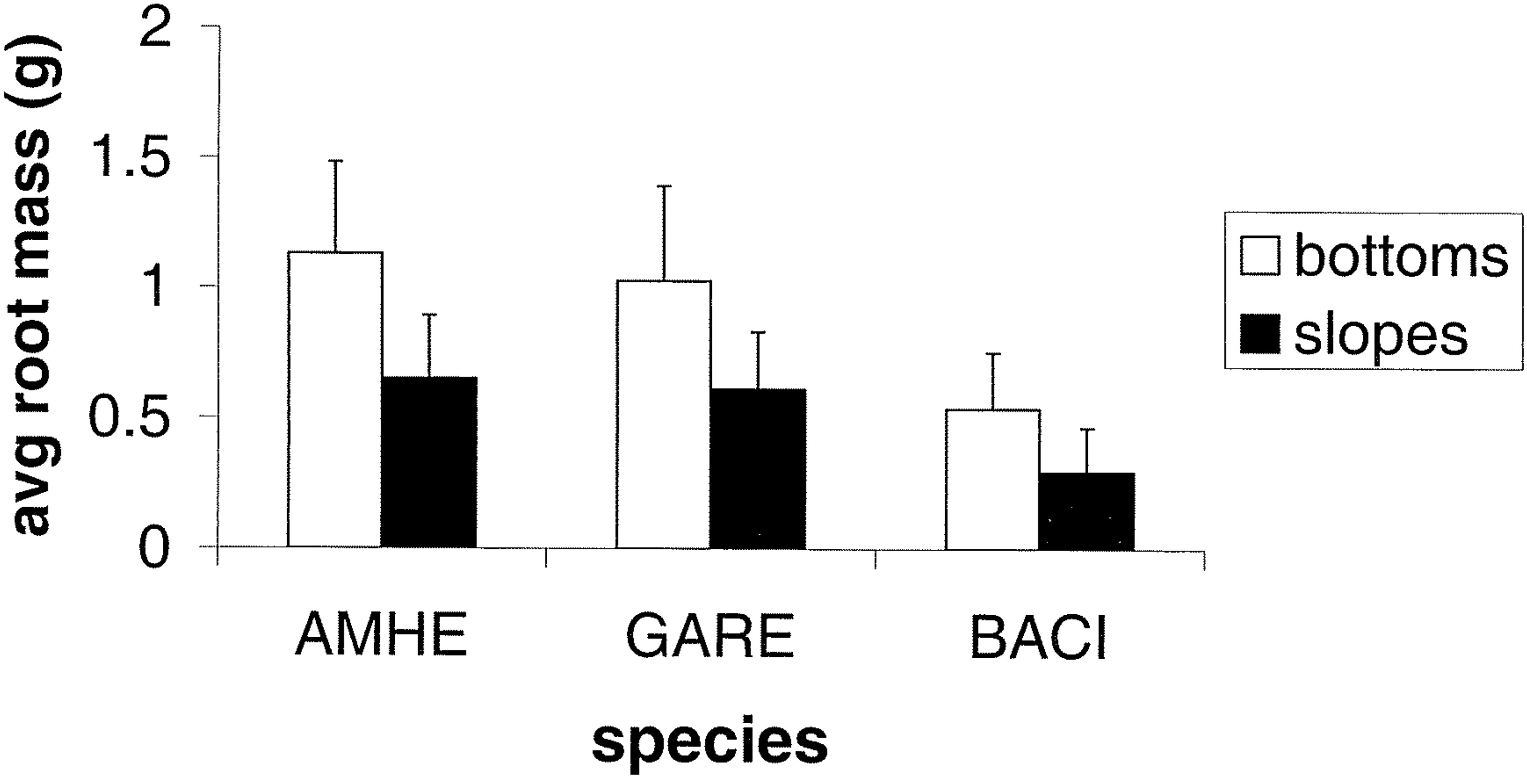


Fig. 4.15. Average Root Mass by Species in Bottoms vs. Slopes.



Only species was found to have a significant effect on average root:shoot ratios ($p<.01$). Although variances in the means of individual species make comparative rankings difficult, the trend suggests that *Galactia volubilis* has a lower root:shoot ratio than the other species (Fig. 4.16).

Seeds

The number of seeds that germinated and survived until the final census did not differ significantly among sand classes for any of the species that were sown. However, germination and survival differed significantly between species when the effect of sand class was held constant ($p<.0001$). Fig. 4.17 shows the mean number of surviving germinules for the four species that achieved some measurable success. The effect of sand class was also significant when variation in species was accounted for ($p<.0001$). Average germination and survivorship for classes 1 through 4 was 21.3, 18.0, 19.1, and 17.5%, respectively. However, large standard deviations are associated with these means due to differences among individual species. Species also had a significant effect on the number of surviving germinules in bottoms vs. slopes ($p<.0001$), but there was no significant interactions between species and slope class. Performances of individual species are discussed in greater detail below.

Amorpha herbacea var. *herbacea:* Although this species was a successful germinator under greenhouse conditions, its performance in the experimental plots was comparatively poor. Only three germinules survived to the final census, and all of these occurred in

Fig. 4.16. Average Root:Shoot Ratio by Species.

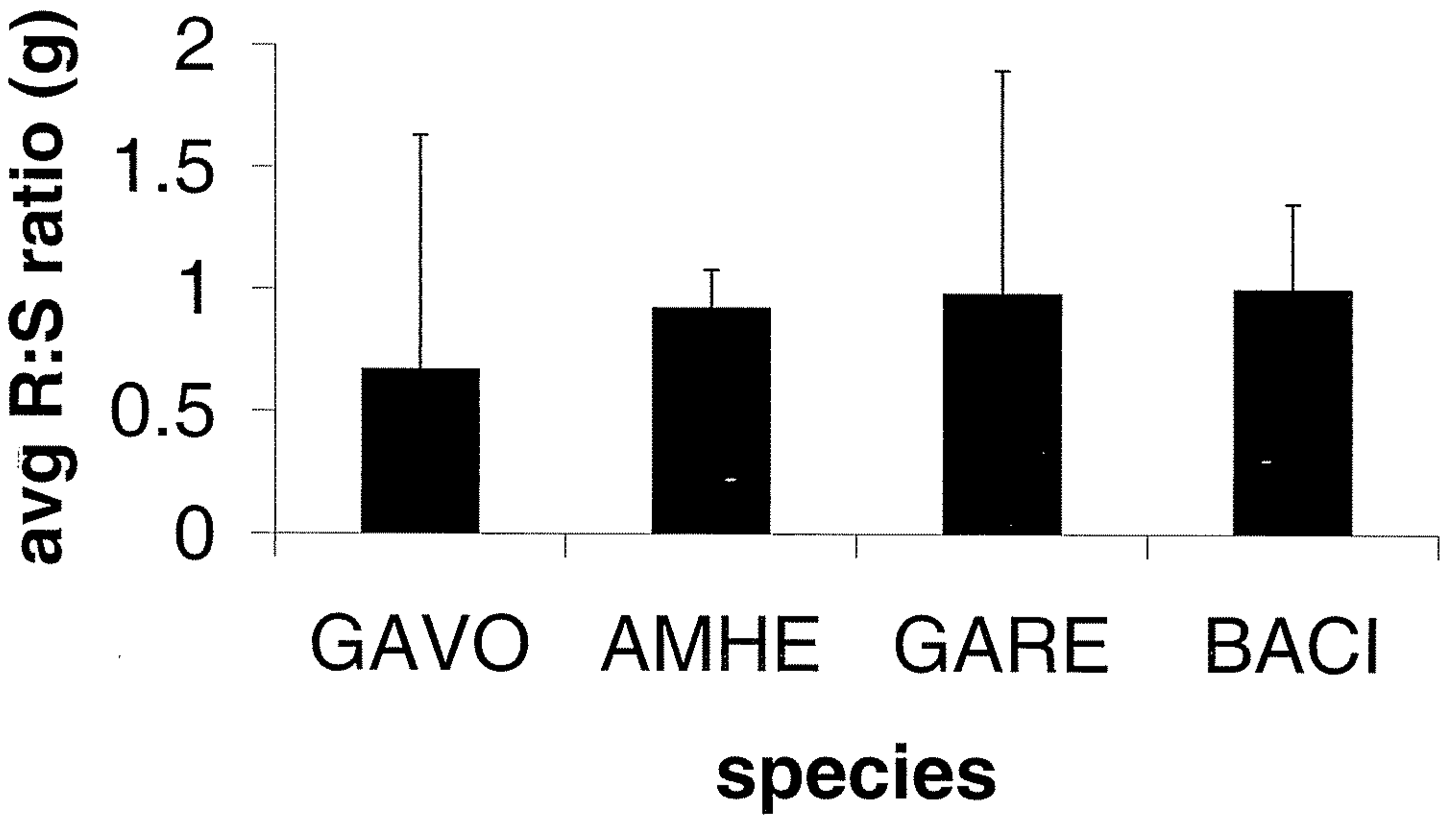
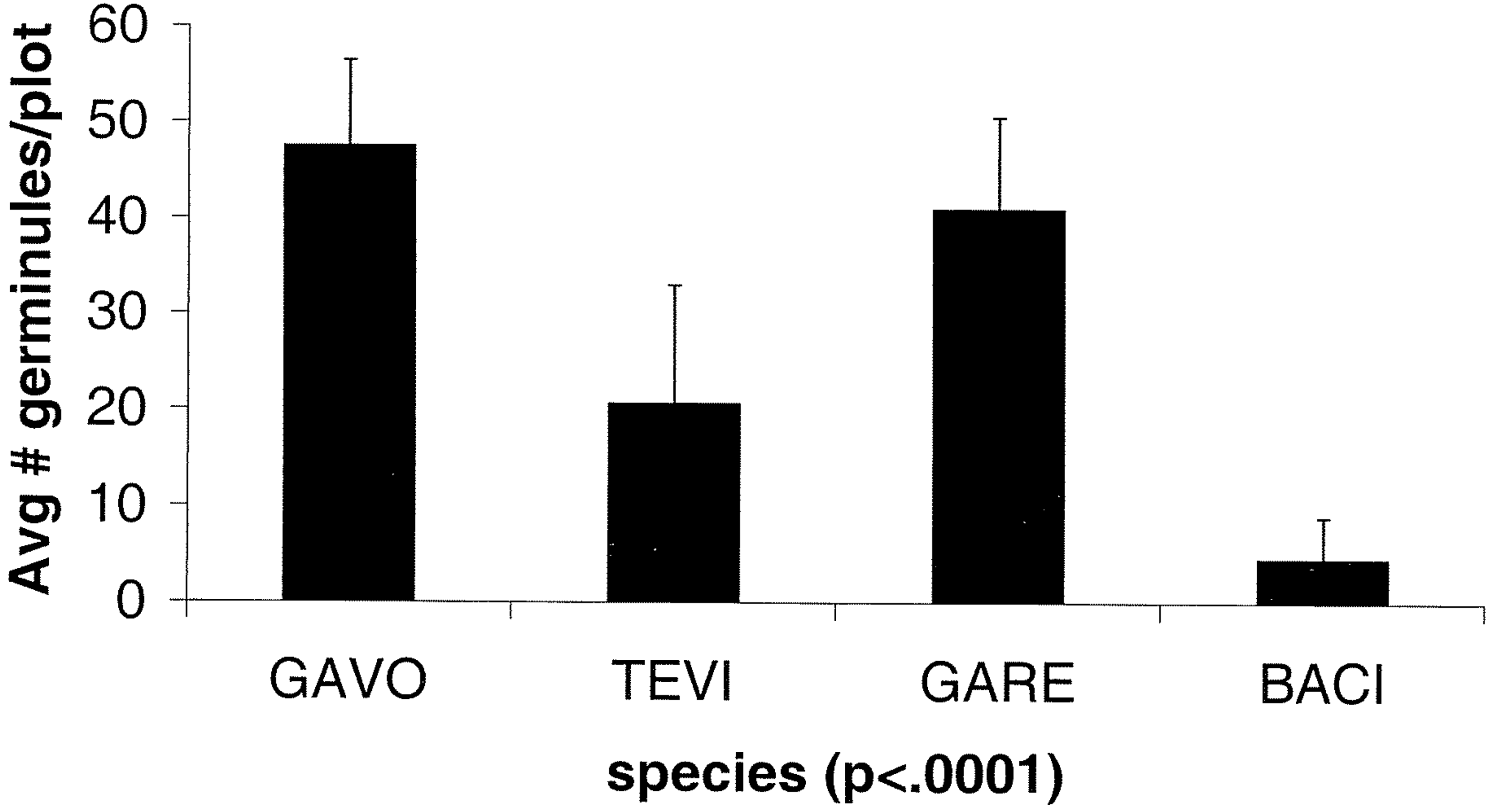


Fig. 4.17. Average Number of Germinules per plot Alive at Final Census.



sand/slope class 1 plots. The maximum germination that occurred within any plot was also three, and this was reached in only two plots (class 1 and 4).

Baptisia cinerea averaged 4.5 (SD=4.4) germinules across all plots at final census, but there were no significant differences in survivorship among plots or slope classes. Maximum germination in any one plot was 18%. At final census, the number of germinules ranged from 0 to 14 across all plots.

Galactia regularis: At final count, germination and survivorship of this species ranged from 19 to 54%, but performance was unrelated to sand class or slope class. Averaged across all slope plots, this species had the second highest number of surviving germinules (x=40.9; SD=9.7).

Galactia volubilis had the highest average percent germination and survivorship (x=47.5; SD=8.5) of all species that were sown. At final census, the range was from 35 to 60, but there were no significant differences between sand classes or slope classes.

Tephrosia virginiana germination and survivorship ranged from 3 to 42% at final census, and neither sand class or slope class had a significant effect on its performance. An average of 20.6 (SD=12.3) germinules survived the experimental period.

Stylosanthes biflora: No germination was observed for this species in any of the experimental plots although 60% of the cells sown in the greenhouse had successful germination.

Control: Only one legume seedling (*Galactia regularis*) emerged from the fifteen control plots, suggesting that inputs from the native seed bank have not significantly affected the results of this experiment. The maximum number of germinules never exceeded six in the control plots, and *Bulbostylis* spp. and *Dichanthelium* spp. were the most frequently encountered species.

Mixed Bag: The results of the Mixed Bag treatment generally mimic the trends in legume density and species richness that were described in Chapter 3. Specifically, average density and species richness decreased with increasing sand and slope classes (Fig. 4.18). The effect of sand class on density in the Mixed Bag treatment was highly significant (p<.0001), but its relationship with species richness was less predictable (p<.14). However, when richness was regressed on the continuous variables %SAND and slope (measured as the height about the lowest point in 1998; See Chapter 3), the significance of the relationship improved (p<.01, p<.07). Maximum density and species richness levels were both attained in sand class 1 plots (six species/32 stems).

The final species composition of all Mixed Bag plots consisted of various combinations of seven species. In order of decreasing percent occurrence they are: *Crotolaria rotundifolia*, *Crotolaria purshii*, *Galactia erecta*, *Rhynchosia reniformis*, *Lespedeza hirta* var. *hirta*, *Lupinus diffusus*, and *Orbexilum pedunculatum* var. *gracile*. In

Fig. 4.18. Stem Density and Species Richness in Mixed Bag Plots by Sand Class.

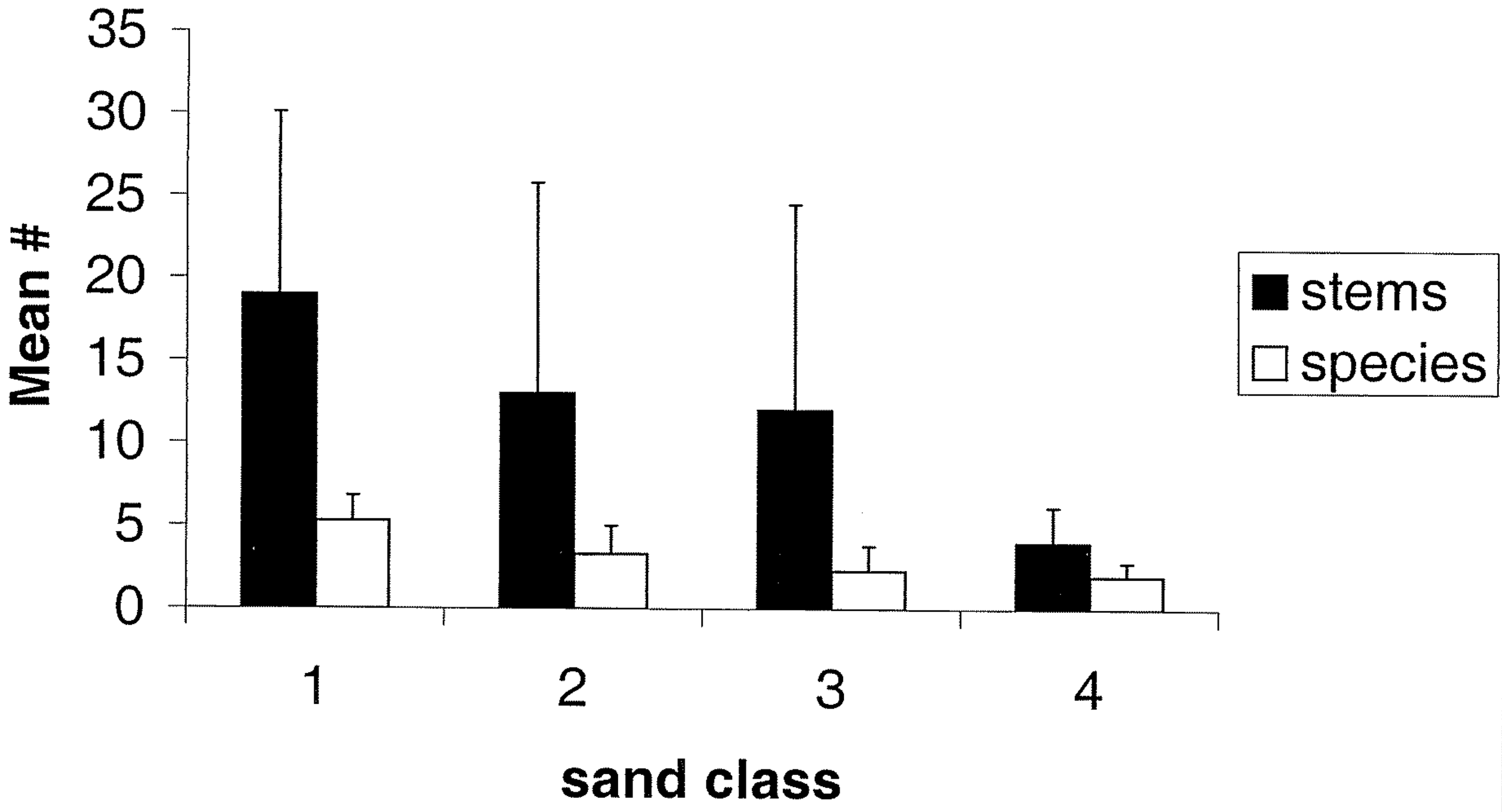


Table 4.1, these species are arranged horizontally in order of decreasing frequency, and experimental plots are arranged vertically by decreasing species richness. A strong nested effect is implicit in this arrangement. Plots that had high species richness were more likely to contain the less frequently-encountered species, *Rhynchosia reniformis*, *Lespedeza hirta* var. *hirta*, *Lupinus diffusus*, and *Orbexilum pedunculatum* var. *gracile.* Conversely, plots that had low species richness usually contained *Crotolaria rotundifolia*, *Crotolaria purshii*, *Galactia erecta.* *Crotolaria rotundifolia* was the only species that occurred in all fifteen plots. It flowered and produced seven fruits in the sand class 1, bean dip plot. *Crotolaria purshii* was the second most frequent component of Mixed Bag plots, occurring in all but two at the time of final census. Interestingly, *Crotolaria rotundifolia* and *Crotolaria purshii* were encountered in only five and eight plots (n=1060), respectively, throughout the entire 1998 census.

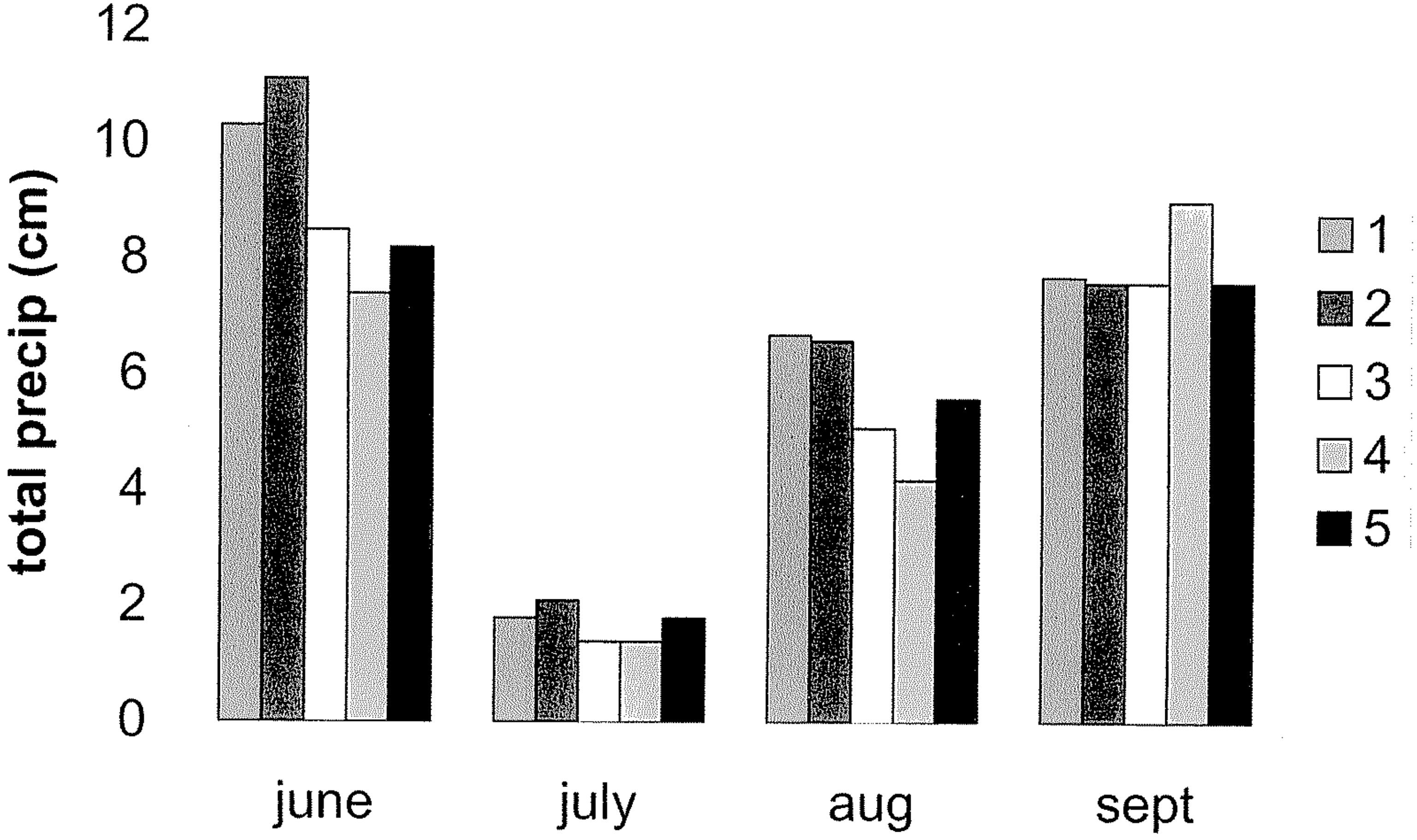
Precipitation

The total monthly precipitation recorded at each experimental site is shown in Fig. 4.19. However, the September data only reflects rainfall patterns up until the nineteenth day, including precipitation associated with Hurricanes Dennis and Floyd. Rainfall was extremely low at all sites in July. Variability in rainfall between sites was highest in June, July, and August, and lowest in September.

Table 4.1. Number of Seedlings Alive at Final Census in "Mixed Bag" Seed Treatment Blocks. Plots are sorted vertically by decreasing species richness and species are sorted horizontally by frequency of presence.

Slope Class	# Stems	Species Richness	CRAN	CRPU	GAER	RHRE	LEHI	LUDI	ORPEG
1	20	6	3	6	4	0	2	1	3
1	32	5	11	13	4	1	0	0	2
2	20	5	5	1	12	1	0	1	0
1	5	4	2	1	0	1	1	0	0
1	18	4	3	1	13	1	0	0	0
3	26	4	8	4	12	2	0	0	0
2	27	4	2	0	23	1	1	0	0
4	5	3	3	1	0	1	0	0	0
2	3	3	1	1	1	0	0	0	0
4	4	2	2	2	0	0	0	0	0
3	6	2	4	2	0	0	0	0	0
4	6	2	1	3	0	0	0	0	0
4	1	1	0	0	0	1	0	0	0
2	1	1	0	0	1	0	0	0	0
3	3	1	3	0	0	0	0	0	0
SUM			**48**	**35**	**70**	**9**	**4**	**2**	**5**

Fig. 4.19. Monthly Precipitation Recorded at Experimental Sites.



Discussion

In this experiment, legume seed and seedling performance reveal several patterns that reflect adult distribution trends observed in 1998 sampling of unaltered bean dips and pea swales. These patterns are summarized below, separately for seeds and seedlings, and the implications for restoration of loamy soil communities are then discussed.

Seedlings

Mortality was generally low among the transplanted seedlings. Less than 4% mortality was observed for both mesic species (*Galactia volubilis* and *Amorpha herbacea* var. *herbacea*), and *Galactia regularis*, a xeric species, was similarly successful. *Baptisia cinerea*, the other xeric species, experienced the highest mortality, with 68% of the transplanted individuals surviving the experimental period. Two species, one xeric and one mesic, showed survivorship trends that mimicked adult distribution patterns observed the previous season. Twice as many *Baptisia cinerea* seedlings survived on the upper slopes, and *Galactia volubilis* survivorship decreased systematically with increasing sand class.

The productivity comparison between species strengthens and clarifies the slope position classifications assigned in 1998 (Chapter 3). For average shoot mass and total biomass, *Galactia volubilis* was shown to be the most productive and *Baptisia cinerea* the least productive, an outcome compatible with their ranks as the most mesic and most xeric seedling species tested. *Amorpha herbacea* var. *herbacea* and *Galactia regularis* consistently occupied the middle range between the two extremes, and differences between them are probably not significant. Although *Amorpha herbacea* var. *herbacea* and *Galactia regularis* occurred most frequently in slope class 1 and 4, respectively, in 1998, they also occurred with appreciable frequencies in the middle slope classes, and may be more widely tolerant across the gradient than the other seedling species tested.

There was no evidence to suggest that xeric species performed better on xeric sites as indicated in the 1998 sampling of adult legumes where *Baptisia cinerea* and *Galactia regularis* occurred most frequently on the upper slopes and rims. In fact, productivity of both xeric species was nearly twice as great in bottom plots than in slope plots. This suggests that edaphic conditions in the bottoms are not inherently unfavorable for growth of species that occur most frequently on the upper slopes and rims. Other factors, such as interspecific competition and seed dispersal, may explain the natural exclusion of xeric species from the mesic sites. One of the mesic species, *Amorpha herbacea* var. *herbacea,* also performed better in the comparatively mesic bottom plots, but the other, *Galactia volubilis,* showed no significant differences in biomass between bottoms and slopes in this first season of growth. Differences in species productivity between slope classes would probably increase if the experiment were continued over multiple growing seasons.

Seeds

Seed germination and survivorship of seedlings was high for three of the six species tested. *Galactia volubilis* and *Galactia regularis* had the highest germination and survivorship, averaging between 40 to 50% in all plots. The similarities in performance are probably related to their similarities in seed morphology. The boiling water treatment may have been especially effective for stimulating the germination of these hard, waxy *Galactia* seeds. *Tephrosia virginiana* ranked third in average number of surviving germinules (21%). Though widely distributed in the Sandhills, this species never occurred in slope class 1 plots and reached its maximum percent occurrence (53%) in slope class 4 plots during the Refuge portion of the 1998 census. *Baptisia cinerea*, a slow-growing, conservative species most frequently encountered in slope class 4, averaged only four germinules per plot.

Surprisingly, very poor to no germination was observed with *Amorpha herbacea* var. *herbacea* and *Stylosanthes biflora*, species most frequently encountered in the lower slope classes in the 1998 census. However, both germinated well under greenhouse conditions in February (>33 and 20%, respectively). Although there are many possible explanations for this variability in performance, similarities in seed morphology between *Amorpha* and *Stylosanthes*, and the effects of this morphology on seed longevity, may help explain this finding. These species have softer, smaller, more permeable seed coats than any of the other individual species that were tested. Seed respiration is generally enhanced by these characters, so it is possible that *Stylosanthes* and *Amorpha* exhausted their dormancy period during the four and one-half months between greenhouse-sowing and plot-sowing. It is also possible that their increased susceptibility to fluctuations in moisture may have inhibited germination under field conditions where these fluctuations are larger than in the greenhouse.

Germination and survivorship did not differ between sand or slope classes for any individual species, indicating that some factor other than first-year seed performance is driving the patterns observed among mature plants. The cumulative effects of year-to-year variation in the timing and amount of rainfall (and the concomitant effects upon interspecific competition) probably play a large role in producing the legume species sorting patterns documented in 1998. Over the long-term, climatic fluctuations would tend to narrow individual distributions, as individuals are exposed to a wider array of selective forces. If this experiment had been continued for more than one growing season, it is likely that differences in species performance would have been perceptible.

The results of the Mixed Bag seeds mimic the trends that were observed for total legume species richness and density in 1998. Both richness and density decreased with increasing %SAND and slope class in this treatment. Surprisingly, the two native *Crotolaria* species were the most frequently encountered in the Mixed Bag plots, yet they rarely appeared in the 1998 sampling. Although the factors inhibiting the distribution of these species in natural populations cannot be isolated, limited dispersal, seed predation, and inadequate moist heat to stimulate germination are possible causes.

The contributions from the native seed bank were surprisingly small in this experiment with only one legume emerging from the control plots. It is possible that a vast majority of the seed bank was removed during the plot preparation procedure. However, May (1981) reported a similarly small seed bank for longleaf forests on the Sandhill Gamelands. The poor response could also be related to the fact that seeds in these plots were not subjected to a boiling water treatment. Martin & Cushwa (1966) demonstrated that moist heat dramatically improved the germination of legume seeds, although separate heat and moisture treatments did not. They also proposed that seeds would more likely encounter moist heat conditions during growing season burns, which are considered similar to the natural fire regime under which species of the southeastern longleaf pine forest evolved.

Implications for Restoration

The results of this experiment, coupled with the 1998 study, provide baseline information for the restoration of legumes in species-rich loamy soil communities of the

Carolina Sandhills. This work has shown that many legumes can be established by either the seed or seedling method, and that success over one growing season is related to variation in %SAND and slope position for some species. Although only a small subset of the total legume flora was investigated in this experiment, taxa were carefully selected to represent the range of habitat preferences (and corresponding life-history traits) observed near bean dips and pea swales during the 1998 sampling initiative.

The question of whether to use seeds or seedlings in community restoration deserves careful consideration and cost-benefit analysis. In general, introduction of seeds is considered the least costly method because seedling care and transplant require substantially higher initial investments of time and labor. However, hidden future costs, such as weed control, may be more closely associated with the seed method, and should be considered in relation to the task. The seed method is also often favored because of the greater degree of filtering and selection of genotypes that occurs under ambient germination and early seedling growth conditions. Although the unilateral pre-treatment of seeds with a hot-water soak in this experiment may have weakened the natural filtering effect, this is a method readily available to restoration practitioners that generally enhances legume germination. Finally, the efficacy of either method must be evaluated in terms of successful establishment and persistence of the species. In most ecosystems, these success measures can only be made through long-term monitoring.

When the seed and seedling performance results are considered simultaneously, it appears that both methods produced relatively high success, at least over the course of one growing season. These results bode well for the restoration of legumes to the loamy soil communities. Each of the species tested performed with vigor at these stages except

Amorpha herbacea var. *herbacea* and *Stylosanthes biflora*. Further study is needed to understand the discrepancies between greenhouse germination and field germination for these species.

Because both seed and seedling addition appear reliable, I recommend restoration by seeds until further research suggests otherwise as it is the less costly method and allows for natural filtering of genotypes. Supplemental transplants of seedlings may be necessary for establishing rare species and species that have low germination/survival in the field. Transplants may also be preferable when weed competition is severe. If seed supply is a limiting factor, it may also be more efficient to concentrate restoration efforts on the bottom and lower slope classes, as overall productivity is greater here. Bottoms also have higher species richness, and, in general, contain the most distinctive features of the loamy soil communities. Upper slopes and rims of bean dips and pea swales are typically occupied by legume species that are more widely distributed in the Sandhills, and their populations are more likely to recover through natural regeneration methods.

This experiment was conducted only in high-quality examples of bean dips and pea swales; results may differ dramatically in the disturbed examples of these communities that are more likely to be of restoration interest. Altered soil chemistry due to fertilizer additions is likely to be a significant impediment to the restoration of degraded examples. Highly immobile elements, such as phosphorus, may be elevated in cultivated loamy soil communities, and remain so long after cultivation has ceased. The effects of high phosphorus levels on Sandhill legume distributions have not been investigated yet, but innovative methods may be needed to accelerate leaching of this element. Advances in soil restoration could also expedite the reestablishment of native soil microbial populations and simplify the control of aggressive exotic species. These are also expected to present substantial challenges to the restoration of loamy soil communities in the Carolina Sandhills.

CHAPTER V.

SUMMARY

This thesis is the first work to focus exclusively on legume distributions in the longleaf pine forests of the Carolina Sandhills. In doing so, it has brought much-needed attention to a unique plant community known as the Loamy Soil Variant of the Pine/Scrub Oak Sandhills Community (Schafale & Weakley, 1990). The following findings contribute to the understanding, preservation, and restoration of these communities.

1. At least eighteen "special status" plants occur in the Loamy Soil Variant of the Pine/Scrub Oak Community although this community occurs on only a small portion of the total land area in the Sandhills. The Loamy Soil Variant also supports a greater diversity of legumes, grasses, and composites than found in the prevailing xeric communities of the Sandhills, leading some to conclude that they are the most species rich communities in this region (Sorrie, 1998; James, this thesis).

2) Three types of landforms were associated with the occurrence of loamy soil communities: 1) bean dips—small, closed depressions of eolian origin, 2) pea swales—the upper troughs of streamheads with a distinct inlet and outlet, and 3) loamy flats—topographically unbounded areas where the depth to impermeable layer is relatively shallow. Although differing in geomorphology, each of these landforms promote the accumulation and retention of moisture and nutrients, thus producing a

distinctive subxeric habitat within the general matrix of upland xeric communities. Soil moisture has been identified as a major determinant of legume distributions patterns in other parts of the longleaf pine range (Hainds, 1999; Taggart, 1990; Walker & Peet, 1983), and my results confirm the importance of this factor.

3) A review of the geologic history of the Carolina Sandhills was included in order to describe the probable origin of bean dips. The Carolina Sandhills have been subjected to dramatic alternations in climate during the Pleistocene and Holocene, and abundant sand has accumulated in this region associated with transgressions and regressions of the Atlantic Ocean and vigorous incisement of major Peidmont-draining rivers. These surficial sands were deposited unconformably on an irregularly-eroded, relatively impermeable Cretaceous horizon. Preliminary mapping on the Gamelands indicates that bean dips occur at the same approximate elevation as this sand:clay contact, leading me and several geologists that I contacted to hypothesize that bean dips are eolian deflation basins of interdune and intradune swales whose downward deflation limits were determined by this impermeable horizon (Farrell, Nystrom, Markewich, and Dennison, pers. comm.). A similar origin has been proposed for closed depressions in other parts of the world, and these geomorphological entities are collectively known as pans (Goudie & Wells, 1995). Carolina Bays, the closed, oriented basins that occur on the flatter terraces of the Middle and Lower Coastal Plain, are also classified as pans. It was proposed that bean dips and Carolina Bays were both created by similar processes, and that their differences in shape and alignment are explained by differences in water-holding

capacity and topographic interference with wind velocity between the regions in which they were formed.

3. 37 native legume taxa were encountered along twenty transects, sampled with a total of 1,060 quadrats (1.0 x 0.5 m^2), established in bottoms and along slopes of bean dips and pea swales on the Carolina Sandhills National Wildlife Refuge in South Carolina and the Sandhills Gameland in North Carolina. The legumes that were encountered represent 67% and 57% of all native legume taxa at these sites, respectively, although less than one thousandth of one percent of the total land area at either site was sampled.

4. A strong and complex ecological gradient was recognized along the slopes of bean dips and pea swales. At both study sites, legume density and species richness decreased with increasing topographic position, measured as height above the lowest point and slope classes in this study. Many legumes also showed patterns of species sorting. On the Gamelands, twelve of the sixteen legume species analyzed (75%) occurred more frequently as slope class decreased. *Baptisia cinerea* and *Galactia regularis* were the only species that occurred more frequently as slope class increased. Similarly, on the Refuge, ten of fourteen legumes (71%) showed a preference for the bottoms of loamy soil communities, and only three occurred more frequently on the upper slopes and rims: *Baptisia cinerea, Galactia regularis,* and *Tephrosia virginiana.*

5) Soil texture and nutrients also varied along the slopes of bean dips and pea swales in a pattern that corresponded with measured changes in legume species richness and density. Most positive indices of productivity (Ca, Mg, Mn, B, CEC, and %CLAY) also decreased with increasing slope class in both study areas. %SAND, the only negative index of productivity that was measured, was higher on the upper slopes and rims of bean dips and pea swales. Extractable P levels were consistently low along the transects, and variation between slope classes was not significant. No significant variation in K was detected along Gamelands transects, although it decreased with increasing slope class on the Refuge (p<.0037).

6) Comparisons between study sites revealed that there were significant differences in average bean dip size, bean dip elevation, legume density, legume species richness, and edaphic indices of productivity. On the Gamelands, bean dips are larger and occur at lower elevations than those on the Refuge. Legume density, legume species richness, and general productivity are also higher on the Gamelands. It was proposed that these differences are associated with broad topographic differences between the two study areas. Specifically, it was noted that interstream divides on the Gamelands are typified by more flat area, whereas, on the Refuge, the topography is generally more broken. Due to the rapid percolation of precipitation through the surficial sands in the Sandhills, and the subsequent effect that the shape of the underlying clay horizon has on the mean residency time of soil moisture, the flatter Gamelands interfluves are expected to have a positive effect on overall productivity. In addition, since bean dips are found more frequently on flatter landscapes, more susceptible

areas for development of these loamy soil communities can be found on the Gamelands. It is believed that the higher legume density and legume richness found on the Gamelands are also accounted for by these landscape differences.

7) When seeds and seedlings of select legume species were introduced along the slopes of bean dips and pea swales on the Refuge, several interesting trends were revealed that will be useful to restoration practitioners. First, it was shown that mortality was generally low among the transplanted seedlings. Less than 4% mortality was observed for both mesic species (*Galactia volubilis* and *Amorpha herbacea* var. *herbacea*), and *Galactia regularis*, a xeric species, was similarly successful. 68% of *Baptisia cinerea* seedlings, the other xeric species, survived the experimental period. Two species, one xeric and one mesic, showed survivorship trends that mimicked adult distribution patterns observed the previous season. Twice as many *Baptisia cinerea* seedlings survived on the upper slopes, and *Galactia volubilis* survivorship decreased systematically with increasing sand class.

8) Biomass trends among transplanted seedlings revealed that productivity was significantly higher in the bottoms (slope class 1 + 2) than on the slopes (slope classes 3 + 4) for one of the mesic species (*Amorpha herbacea* var. *herbacea),* and both xeric species *(Galactia regularis,* and *Baptisia cinerea).* This result indicates that edaphic conditions in the bottoms are not inherently unfavorable for growth of species that occur most frequently on the upper slopes and rims in unaltered bean dips and pea swales. Interspecific competition was cited as the probable mechanism limiting some

species to the xeric extreme of the gradient, although a number of other potentially important environmental variables, such as light conditions, were not measured in this study.

9) Germination and survivorship trends for seeds indicate that some legumes can be successfully established by this means. Average germination and survivorship of both *Galactia* spp. exceeded 40%. *Tephrosia virginiana* and *Baptisia cinerea* were less successful, with 20% and 4% of their seeds germinating and surviving one growing season. Only three germinules of *Amorpha herbacea* var. *herbacea* remained at the end of the experimental period, and no germination of *Stylosanthes biflora* was observed, although both of these species germinated well under greenhouse conditions. No interactions between seed performance and sand/slope class were detected, but both %SAND/slope position and species had a significant effect on germination and survivorship when variation in the other was held constant. It is expected that interactions would become evident if this experiment were continued over multiple growing seasons. A "Mixed Bag" seed treatment, containing seeds of twenty legume species, was also introduced to plots established along the topographic gradient. The results of this treatment generally mimicked adult legume distribution patterns that were observed in unaltered bean dips and pea swales: increasing legume species richness and density with decreasing slope class.

10) Many abandoned agricultural fields and wildlife food plots occur in former loamy soil communities, and, based on limited observations, once abandoned, they fail to

recover to their natural conditions. Because unaltered loamy soil communities are expected to contribute more to regional biodiversity, restoration of degraded examples is likely to become a goal for land managers. The combined results of the legume seedling transplant and seed sowing experiment should help guide these activities. It was recommended that initial attempts to restore these communities should begin with seeds, since this method was successful for many species, but less costly in terms of time and labor. Supplemental transplants of rare species or species that germinated poorly under field conditions may be necessary. In addition, it was recommended that seed introduction efforts should be concentrated in the bottoms and on lower slopes for all species, since germination and survivorship were generally higher here. Although xeric species may eventually be out-competed in these locations, these species are commonly encountered throughout the Sandhills, and are, therefore, more likely to recover through natural regeneration.

Although this study has provided much in the way of understanding a previously poorly-understood plant community, several avenues of inquiry were not explored and should be considered for future research. Of particular interest are patterns among species other than legumes. A community level approach to vegetation changes along the slopes of loamy soil communities would provide a more complete description of the gradient. Grasses and composites also appear to change with some predictability along these gradients. It is expected that similar patterns of decreasing species richness and density with increasing slope class would be found for these taxonomic groups. In addition, research on nitrogen cycling in loamy soil communities may be important for restoration goals. Specifically, it would be useful to know what role legumes play in maintaining nitrogen levels, and how that role varies under different fire regimes. Finally, the question of how to restore these communities in areas with altered soil chemistry and aggressive exotic species is one that deserves special attention and is likely to present significant challenges.

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