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THE ROLE OF TENNESSEE CONEFLOWER, *ECHINACEA TENNESSEENSIS*, IN ITS NATIVE HABITAT: THE VEGETATION AND A DEMOGRAPHIC ANALYSIS

A Thesis

Presented for the

Master of Science

Degree

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Mark Brian Drew

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DEDICATION

This work is dedicated to my parents, George and Barbara Drew.

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ABSTRACT

Tennessee coneflower, *Echinacea tennesseensis* (Beadle) Small, is a rare endemic of the limestone cedar glades and barrens of Middle Tennessee. At the time this study was initiated there were only five native populations known. Due to its limited numbers, the federal government lists the species as endangered.

There are two primary objectives, and therefore two main parts to this study. The first objective is to analyze the vegetation of the five coneflower sites; the second objective is to study the demography of the species.

Vegetation data were collected using half meter square quadrats placed at defined points on a grid extending over the coneflower population at each of the five sites. The percent cover of each plant species was estimated within each quadrat. Approximately five percent of the total area occupied by the coneflower was sampled.

Approximately 100 individuals were selected at random from each population, and these individuals were monitored for two growing seasons. Mortality and life history characteristics were recorded, and an initial stage class distribution was constructed.

Percent cover of each species was estimated for each population, and the species composition was found to vary among sites. Plant communities were identified in order to classify the vegetation and to compare environmental factors, such as soil depth, among communities.

Mortality and growth varied greatly between growing seasons, and mortality were highest among juvenile (non-flowering) plants both years. The stage class distribution is such that there are many more

juvenile (non-flowering) plants than adult (flowering) plants.

Six communities were identified from the plot data. Two of the communities are considered barrens habitat and are characterized by greater than 50 percent cover of perennial grasses and relatively deep soils. Four of the communities are considered glade habitat and are characterized by more than 50 percent cover of annual grasses and excedingly thin soils. Tennessee coneflower occupies all the communities and both types of habitat, however cedar glade is considered the primary habitat of Tennessee coneflower because the majority of the habitats sampled are glades.

The obvious reason for high mortality the first season is the severe drought of the summer of 1988. High mortality among juvenile plants both years and the stage class distribution suggest that established (larger) plants have a better chance of surviving the summer drought.

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CHAPTER I

INTRODUCTION

A large part of Middle Tennessee is occupied by an oval topographical depression known as the Central Basin. It extends north almost to Kentucky and south approximately 190 kilometers (120 miles) so that a small portion extends into Alabama. The Central Basin averages 80 kilometers (50 miles) across, and is almost entirely surrounded by the Highland Rim. It occupies approximately 130,000 square kilometers (5,000 square miles). The elevation ranges from 150 to 220 meters (500 to 700 feet) which is 90 to 150 meters (300 to 500 feet) lower than the surrounding Highland Rim (Luther 1977).

The geologic history of the Central Basin is an interesting one. During the last part of the Cambrian period (500 to 600 million years ago), most of what is now the interior portion of the United States was the bed of a shallow sea. During the next 225 million years lime precipitated from these sea waters and hardened into the limestone that came to cover most of this area. These rock layers are now deeply buried in much of the region, but they appear at the surface in Middle Tennessee.

Approximately 470 million years ago forces within the earth, still not well understood, pushed the limestone and dolomite layers up into two broad, low domes; the Ozark Dome to the west and the Nashville Dome, which occupied what is now the Central Basin, to the east. The uplift eventually raised the dome above sea level, and there is no evidence that any Middle Tennessee bedrock has been submerged since

300 million years ago (Luther 1977).

At the time of upheaval the soft limestone was capped with harder rock such as that found today capping the Highland Rim. Due to the uplift of the dome this overlying rock was stretched. These forces resulted in deep cracks in the upper layer, often extending down to the softer limestone.

As rain fell on the exposed dome, erosion began; erosion was more rapid on the softer limestone exposed by the cracks. Since there were more cracks near the top of the dome, erosion was most rapid there. The hard cap was quickly eroded from the top of the dome, but was, for the most part, left on the sides of the dome. The exposed soft limestone was then eroded rapidly from the top of the dome, and the rainwater causing this erosion flowed through the few deep cracks on the sides of the dome creating deep river gorges from the middle of the dome through what would become the Highland Rim. Over many millions of years, rapid erosion of the exposed limestone in the middle of the dome resulted in the oval depression surrounded by the Highland Rim through which there are a few deep river gorges that drain the basin.

The limestone of the Central Basin is rich in fossils of ancient marine organisms that inhabited the shallow seas. Many of these organisms are thought to have had the ability to extract phosphate from the sea water with which to make their shells. As a result, most soils formed from this limestone are very rich in phosphorous.

Prior to European settlement of the Central Basin, the deep and

extremely fertile soil supported a magnificent mixed mesophytic forest composed of yellow poplar, black walnut, maple, hickory, elm, and oak, all of immense size (Quarterman 1950a). Subsequent to settlement, the region has been almost entirely cleared, and presently the Central Basin is typified by rolling upland pastures and rich alluvial farmland.

In contrast, an approximated five to six percent of the Central Basin is occupied by natural rocky flats with thin soils (Bowman 1911). These areas, now known as "cedar glades" and "cedar barrens", are generally small (1-10 acres) openings in the forest, and are usually enclosed by cedar/hardwood forest thereby isolating most glades/barrens from one another. The thin soils of the glades and barrens are unable to support large woody plants, and the climax community is dominated by herbaceous plants. The exceedingly thin soil of the cedar glades makes the land useless for crop farming, so these areas have remained relatively intact. The only continuous use has been light grazing and, more recently, urban development.

One of the first to describe the unique cedar glades that occupy the Central Basin (Safford 1869) defined cedar glades as "...rocky places, generally flat, covered more or less, with red cedar, (*Juniperus virginiana*)." More recently, Quarterman defined cedar glades as "... open spaces occasioned by the presence of rock at or near the surface. They may be simply exposed rock surfaces or gravelly or grassy expanses surrounded by cedar woods" (Quarterman 1950b). This definition works equally well for the cedar barrens located in the same geographic area, so it is necessary to distinguish

between the two terms. A "glade" is defined here as open spaces as described above in which more than 50 percent of the grass cover is composed of annual grass species. A "barren", on the other hand, is defined here as open spaces as defined above in which more than 50 percent of the grass cover is composed of perennial grass species (Deselm, personal communication 1988).

The cedar glades of the Central Basin occur almost exclusively on Lebanon limestone. It was noted as early as 1874 that Glade Limestone (renamed Lebanon Limestone) was the rock on which the Red Cedar forests of the Central Basin grow. In fact, the boundaries of the Lebanon Limestone outcrop could be mapped by these forests (Killebrew and Safford 1874).

The cedar glades of the Central Basin are formed where horizontal layers of Lebanon Limestone are exposed (Quarterman 1950b). Lebanon Limestone is Ordovician rock of the Stone's River series (Wilson 1949), which is the oldest geologic formation in Middle Tennessee that is now exposed. Therefore, cedar glades generally lie near the lowest part of the basin, and are separated from each other laterally by hills and uplands that were not eroded as quickly (Quarterman 1950b) and across the basin by older Ordovician layers of limestone.

Lebanon Limestone is made up of layers of thin, dense limestone, separated by thin films of shale. This limestone weathers rapidly by freezing and thawing and by solution of rainwater and groundwater. Weathering is mainly at or near the surface, and the soluble portion of the rock is dissolved and eroded away. The small fraction of

insoluble clay is so finely divided that it is removed by each rain, as fast as it is produced. So, the only soil to accumulate is in the numerous cracks and joints in the limestone. The surface is of massive exposed limestone in broken slabs or gravels (Galloway 1919).

The only situation in which the cedar glades will accumulate soil is if they become nearly level, or if soil from surrounding uplands washes onto a glade. If the soil depth reaches five or six inches, freezing and thawing become inoperative and weathering is slowed considerably (Galloway 1919). Thus, the soil over Lebanon Limestone is seldom deep, and probably averages less than one foot.

The soil on the cedar glade is therefore too shallow to support tree species of any appreciable growth, so the climax plant communities are herbaceous. The openness of the glades, the shallow soil, and the characteristics of the underlying bedrock (horizontal layers of Lebanon limestone) combine to produce a harsh environment subject to seasonal extremes in light, temperature, and moisture (Freeman 1933). For example, the shallow soil, high temperature, full sunlight, and low rainfall combine to form a xeric environment in the late summer. But, in early spring lower temperatures, higher rainfall, and impermeable bedrock close to the surface combine to form pools of water on the glades which usually keep them wet during this time of year.

The unique flora inhabiting the cedar glades of The Central Basin was noted by some of the first botanists in the region. Gattinger commented on several plant species that he believed were unique to the cedar glades, and noted that some plants on the cedar glades were

previously thought to be exclusively western U.S. species (Gattinger 1901). Since Gattinger's era the flora of the cedar glades has been studied extensively. Presently, 29 plant taxa are considered endemic (i.e. restricted to a specific and frequently limited geographic area) or nearly-endemic to cedar glades (Baskin 1986). Some scientists believe the cedar glades of Middle Tennessee represent one of the few habitats in North America where recently evolved plant species still occupy their place of origin (Quarterman 1973). In addition to endemic plant species, the cedar glades are at or near the eastern limit of many prairie species, and some of these populations are thought to be prairie disjuncts (Bridges and Orzell 1986).

One of the most rare of the endemic plant species of the cedar glades is the Tennessee Coneflower, *Echinacea tennesseensis* (Beadle) Small. There were five known populations of *E. tennesseensis* at the time this study was initiated, all in cedar glade communities and located within 14 miles of one another in Davidson, Wilson, and Rutherford counties (Somers *et al* 1982). Population is defined here as a group of individuals of a single species in which the probability of gene exchange is high. The five known populations are all a minimum of 3.5 miles apart and are considered distinct. All of the known populations of *E. tennesseensis* occur on cedar glades and barrens, but it is not known exactly why the species is so highly endemic and so sparsely distributed.

E. tennesseensis exhibits many characters seemingly adapted to life on the cedar glades and barrens, but does not appear suited for, or

does not generally disperse to, any other habitat. For example, *E. tennesseensis* has thick, fibrous taproots necessary for survival on the often xeric cedar glades. The narrow, pubescent leaves conceivably help to conserve water during drought. In addition, *E. tennesseensis* grows slowly and produces a short, woody stem. This is sufficient in the openness of the cedar glade. But, in other habitats, such as the surrounding cedar/hardwoods forest, it is likely, although not demonstrated, that the tall and rapidly growing plant taxa easily outcompete the coneflower (Somers *et al* 1982).

One would expect a glade endemic to possess the ability to disperse from one glade to another. On the contrary, *E. tennesseensis* does not possess observed means for easy dispersal. The seeds (achenes) are too large to be wind-borne (except in extremely high winds), and lack any evidence of adaptation for animal dispersal.

According to one study, 83 percent of the achenes sampled during one growing season were dispersed within 0.5 meters from the parent plant, and nearly all were dispersed less than one meter. This study concluded that it is highly unlikely that any appreciable number of achenes are dispersed more than one meter from the parent plant (Hemmerly 1976).

E. tennesseensis has never been observed growing in the cedar/hardwood forest which usually surrounds the glade/barren habitat. It is not certain what factors contribute to the exclusion of coneflower from this habitat, but the seeming inability of the species to tolerate more than 50 percent shade limits its ability to disperse into or through cedar/hardwood forest.

Due to its limited numbers and limited habitat, the U.S. Fish and Wildlife Service officially listed *E. tennesseensis* an endangered species on June 6, 1979 (USDI/FWS, 1979). In June of 1982 the Tennessee Coneflower Recovery Plan was drafted by a team of four scientists under the leadership of Dr. Paul Somers of the Tennessee Natural Heritage Program, Department of Conservation. The ultimate goal of the Recovery Program is to secure a minimum of five natural populations, each with three self-sustaining colonies of a minimal size.

CHAPTER II

METHODS

Five native populations were sampled in July, August, and September of 1987 using standard sampling methods as described by Barbour *et al* (1987). Half meter by half meter plots were positioned every 4.72 meters (four meters between each quadrat) along a given compass heading beginning at one end of the population boundary and ending at the opposite boundary; the number of plots and compass heading of each transect depended on the population boundaries. This ensured that the area sampled is that in which *E. tennesseensis* occurs, which is important in estimating total number of individuals per population and the percent cover of species in association with the *E. tennesseensis*. Each sample plot of each site was permanently marked on a designated corner with an aluminum tag attached to a nail and embedded in the soil. The marked corner was chosen arbitrarily, but each plot in a given site was marked on the same corner. For example, all plots at the Mt. View site were marked on their northeast corner. When the corner happened to lie on bedrock or the trunk of a small tree, the corner was marked by spray-painting a small dot.

The boundaries of each population were measured with a meter tape and sketched to scale. For the Allvan, Mt. View, Vesta, and Vine sites the scale of 1 cm = 1 meter was used. For the Couchville site the scale of 1 inch = 100 feet was used.

Each sketch indicated the boundaries of the *E. tennesseensis* population. In addition, each sketch contained the location of the

permanent sample plots and various landmarks and compass bearings in order to establish a permanent record of the boundaries of the *E. tennesseensis* and to aid in relocating the sampled plots. These maps were also used to determine the total area occupied by the coneflower in order to determine average density of coneflower by site.

The percent cover of each vascular plant species and the total cover of all vascular plant species between ground level and one meter in height were estimated for each sample plot. In cases of overlapping vegetation, cover for only the uppermost taxon was estimated. Nomenclature follows mainly that of Baskin, Quarterman, and Caudle (1968) and Baskin and Baskin (1975). Nomenclature of taxa not included in the above treatments, mainly woody species, follows that of Gleason (1952).

The percent cover of the various substrates was estimated for each plot. Since nonvascular photosynthetic organisms cover considerable areas of some glades, they were treated as substrate types in addition to the various physical substrates. Biological substrates were treated categorically as "bryophyte", "foliose lichen", and *Nostoc*. Substrate types include bare soil, bedrock, bryophyte, flagstone, gravel, foliose lichen, and *Nostoc*. Flagstone is defined here as any loose piece of stone occupying an area of 10 x 10 cm or greater.

Nine soil depths were recorded at predetermined points within each sampling plot. The soil depths were determined using a long, thin screwdriver and a metric ruler.

In each of the half meter quadrats described above a maximum of five

individuals of *E. tennesseensis* were permanently marked. Two strings were tied to the diagonal corners of the quadrat and were crossed in order to locate the center of the quadrat. The five individuals nearest the center were marked and measured in order to obtain a random sample of individuals.

Each individual was marked by placing color-coded roofing nails of various sizes in the soil beside the plant. A crude sketch of the relative locations of the marked individuals within each plot was made to aid in relocating the individuals. For juvenile (non-flowering) plants the total number of leaves for each individual was recorded as well as the length of the longest leaf (to the nearest cm). For the mature (flowering) plants the total number of flowering heads and the height of the plant were recorded. All measurements were made using a flexible plastic ruler.

A total of 455 plants were marked in July, August, and September of 1987, and the above measurements were recorded. The above measurements were repeated in August of 1988 and again in August of 1989. In addition, mortality of any marked individuals was recorded.

The total number of coneflowers was recorded in each plot in order to estimate average density and total number of plants of each population. The number of mature (flowering) and juvenile (non-flowering) coneflowers was also recorded in order to determine the ratio of adults to juveniles.

Pollinators that were observed on the flowering heads of *E. tennesseensis* were collected when possible. The collected specimens were stored and identified at a later date. Any possible predation of

E. tennesseensis was documented.

CHAPTER III

HYPOTHESES

1. H_0: The total percent plant cover is identical at each site.

   H_a: The total percent plant cover is not identical at each site.

2. H_0: The species composition of each sample plot is identical.

   H_a: The species composition of each sample plot is not identical, and similar plots can be grouped to identify communities.

3. H_0: The vegetation clusters generated using CLUSTER analysis have identical average soil depth.

   H_a: The vegetation clusters generated using CLUSTER analysis do not have identical soil depth characteristics.

4. H_0: The soil depth characteristics are identical at each of the five sites.

   H_a: The soil depth characteristics are not identical at each of the five sites.

5. H_0: The substrate characteristics are the same at all sites.

   H_a: The substrate characteristics are not the same at all sites.

6. H_0: The percent cover of *E. tennesseensis* is identical at each of five sites.

   H_a: The percent cover of *E. tennesseensis* is not identical at each of the five sites.

7. H_0: Each of the population sizes are equal at all sites.

   H_a: Each of the population sizes are not equal at all sites.

8. H_0: The ratio of juvenile (non - flowering) to mature (flowering) is 2:1 at each site and overall.

   H_a: The ratio of juvenile (non - flowering) vs. adult (flowering) deviates from 2:1, and varies among sites.

9. H_0: The density of *E. tennesseensis* is identical at each of the five sites.

   H_a: The density of *E. tennesseensis* is not identical at each of the five sites.

10. H_0: The species as a whole is stable with regard to population growth.

    H_a: The population growth rate of the species is decreasing at a given rate.

    H_a: The population growth rate of the species is increasing at a given rate.

11. H_0: There are no pollinators nor predators on *E. tennesseensis*.

    H_a: There are various pollinators and/or predators on *E. tennesseensis*.

CHAPTER IV

THE VEGETATION AND ENVIRONMENTAL CHARACTERISTICS

RESULTS

Plant Taxa by Site

A total of 59 vascular plant taxa were observed in the sampling plots. A total of 44 vascular plant taxa were observed in at least one of the 30 plots at the Allvan site (Table 1), 11 of which had a frequency of 20 percent or more. A total of 27 vascular plant taxa were observed in at least one of the 96 plots at the Couchville site (Table 2), 12 of which had a frequency of 20 percent or more. A total of 30 vascular plant taxa were observed in at least one of the 33 plots at the Mt. View site (Table 3), of which seven had a frequency of 20 percent or more. A total of 37 vascular plant taxa were observed in at least one of the 96 plots at the Vesta site (Table 4), of which nine had a frequency of 20 percent or more. A total of 26 vascular plant taxa were observed in at least one of the 33 plots at the Vine site (Table 5), of which nine had a frequency of 20 percent or more.

In order to classify the overall vegetation, and the vegetation of each site, into communities, the procedure CLUSTER of the Statistical Analysis System (SAS institute Inc. 1982) was used to identify communities by grouping similar plots. These communities were then used to compare the vegetation among sites. The average linkage method of CLUSTER was used. Average linkage CLUSTER analysis is an iterative, agglomerative, hierarchical technique.

Table 1. Frequency and percent cover of species at the Allvan site.

Taxon	Frequency (n=30)	Cover (%)
Grindelia lanceolata	.90	9
Aster sp.	.60	8
Echinacea tennesseensis	.57	1
Ruellia humilis	.53	1
Petalostemon gattingeri	.50	2
Sporobolis spp.	.47	2
Silphium trifoliatum	.43	3
Isanthus brachiatus	.43	1
Schizachyrium scoparium	.27	1
Hypericum sphaerocarpum	.27	<1
Croton monanthogynous	.20	<1
Tridens flava	.17	<1
Croton capitatus	.13	<1
Euphorbia corollata	.13	<1
Euphorbia dentata	.13	<1
Erigeron strigosus	.13	<1
Juniperus virginiana	.10	<1
Rosa carolina	.10	<1
Allium sp.	.10	<1
Heliotropium tenellum	.10	<1
Panicum philadelphicum	.10	<1
Pycnanthemum tenuifolium	.10	<1
Sorghum halepense	.10	<1
Ambrosia artemisiifolia	.07	<1
Cassia fasciculata	.07	<1
Desmanthus illinoensis	.07	<1
Forestiera ligustrina	.07	<1
Ipomoea pandurata	.07	<1
Lespedeza virginica	.07	<1
Rhus aromatica	.07	<1
Agalinis tenuifolia	.03	<1
Celtis laevigata	.03	<1
Danthonia spicata	.03	<1
Digitaria sp.	.03	<1
Euphorbia serpens	.03	<1
Festuca arundinacea	.03	<1
Fraxinus americana	.03	<1
Houstonia sp.	.03	<1
Liatris aspera	.03	<1
Panicum flexile	.03	<1
Setaria sp.	.03	<1
Solidago sp.	.03	<1
Trifolium sp.	.03	<1
Verbena canadensis	.03	<1

Table 2. Frequency and percent cover of species at the Couchville site.

Taxon	Frequency (n=48)	Cover (%)
Houstonia sp.	.88	10
Echinacea tennesseensis	.77	1
Sporobolis spp.	.75	2
Grindelia lanceolata	.73	1
Schizachyrium scoparium	.60	7
Hypericum sphaerocarpum	.44	<1
Ruellia humilis	.38	<1
Heliotropium tenellum	.33	<1
Croton monanthogynus	.27	<1
Isanthus brachiatus	.25	<1
Petalostemon gattingeri	.25	<1
Euphorbia corollata	.17	<1
Viola sp.	.10	<1
Helianthus divaricatus	.08	<1
Rhus aromatica	.08	<1
Agave virginica	.04	<1
Euphorbia sp.	.04	<1
Panicum flexile	.04	<1
Phlox bifida	.04	<1
Asclepias viridiflora	.02	<1
Croton capitatus	.02	<1
Erigeron strigosus	.02	<1
Euphorbia dentata	.02	<1
Forestiera ligustrum	.02	<1
Hypericum frondosum	.02	<1
Rosa carolina	.02	<1
Rudbeckia hirta	.02	<1

Table 3. Frequency and percent cover of species at the Mt. View site.

Taxon	Frequency (n=33)	Cover (%)
Sporobolis spp.	.87	12
Ruellia humilis	.67	2
Echinacea tennesseensis	.63	5
Hypericum sphaerocarpum	.53	1
Petalostemon gattingeri	.47	4
Isanthus brachiatus	.40	<1
Croton monanthogynus	.25	<1
Ambrosia artemisiifolia	.13	<1
Grindelia lanceolata	.11	<1
Croton capitatus	.09	<1
Panicum flexile	.09	<1
Allium sp.	.07	<1
Heliotropium tenellum	.07	<1
Houstonia sp.	.07	<1
Juniperus virginiana	.07	<1
Euphorbia dentata	.05	<1
Forestiera ligustrum	.05	<1
Phlox bifida	.05	<1
Rosa carolina	.04	<1
Rudbeckia hirta	.04	<1
Viola sp.	.04	<1
Agave virginica	.02	<1
Desmanthus illinoensis	.02	<1
Diodia teres	.02	<1
Erigeron strigosus	.02	<1
Fraxinus quadrangulata	.02	<1
Panicum philadelphicum	.02	<1
Rhus aromatica	.02	<1
Verbena canadensis	.02	<1

Table 4. Frequency and percent cover of species at the Vesta site.

Taxon	Frequency (n=96)	Cover (%)
Sporobolis spp.	.68	6
Petalostemon gattingeri	.55	2
Echinacea tennesseensis	.48	4
Schizachyrium scoparium	.42	3
Ruellia humilis	.44	1
Croton capitatus	.29	<1
Grindelia lanceolata	.24	<1
Heliotropium tenellum	.19	<1
Houstonia sp.	.19	<1
Helianthus divaricatus	.14	<1
Euphorbia dentata	.11	<1
Isanthus brachiatus	.10	<1
Croton monanthogynus	.06	<1
Hypericum sphaerocarpum	.06	<1
Agave virginica	.05	<1
Bouteloua curtipendula	.04	<1
Forestiera ligustrina	.04	<1
Panicum flexile	.04	<1
Festuca sp.	.03	<1
Verbena canadensis	.03	<1
Cassia fasciculata	.02	<1
Juniperus virginiana	.02	<1
Panicum philadelphicum	.02	<1
Rhus aromatica	.02	<1
Senecio smallii	.02	<1
Solidago sp.	.02	<1
Tridens flava	.02	<1
Ambrosia artemisiifolia	.01	<1
Asclepiodora viridis	.01	<1
Danthonia spicata	.01	<1
Diodia teres	.01	<1
Erigeron strigosus	.01	<1
Eragrostis frankii	.01	<1
Euphorbia sp.	.01	<1
Fraxinus quadrangulata	.01	<1
Hypericum frondosum	.01	<1
Rosa carolina	.01	<1

Table 5. Frequency and percent cover of species at the Vine site.

Taxon	Frequency (n-33)	Cover (%)
Echinacea tennesseensis	.73	8
Houstonia sp.	.82	8
Sporobolis spp.	.73	4
Schizachyrium scoparium	.33	1
Petalostemon gattingeri	.27	<1
Ruellia humilis	.45	<1
Forestiera ligustrina	.12	<1
Rhus aromatica	.09	<1
Diospyros virginiana	.03	<1
Croton monanthogynus	.33	<1
Croton capitatus	.18	<1
Panicum flexile	.18	<1
Gutierrezia drancunculoides	.09	<1
Heliotropium tenellum	.09	<1
Hypericum sphaerocarpum	.09	<1
Juniperus virginiana	.09	<1
Verbesina virginica	.09	<1
Agave virginica	.06	<1
Isanthus brachiatus	.06	<1
Panicum philadelphicum	.06	<1
Solidago sp.	.06	<1
Diodia teres	.03	<1
Erigeron strigosus	.03	<1
Grindelia lanceolata	.03	<1
Phlox bifida	.03	<1
Rudbeckia triloba	.03	<1

The analysis was performed for 11 of the most common species selected from the total 59 species on the basis of total cover. Any species with a minimum of one percent total cover at any one of the five sites was included in the analysis (Table 6).

The Combined Vegetation of the five Sites

The analysis resulted in six clusters of closely related species composition, hereinafter refered to as communities one through six. The total number of plots in the six clusters is 197, which leaves 65 plots that are not similar enough to be grouped into a particular community and are judged to be "outliers". These "outliers" were not included in most of the following analyses.

Summaries of percent cover of the 11 vascular plant taxa, percent cover of substrates (Table 7), and soil depth characteristics (Table 8) were then prepared for each of the six clusters and the group of unrelated outliers. The following are descriptions of the six clusters (communities); each community is named for the dominant or codominant vascular plant species in that community.

Description of the Communities:

1. *Echinacea / Ruellia* community (C-1 of Table 7): This community is characterized by a low percent vegetative cover. The most common species include *Echinacea tennesseensis, Ruellia humilis*, and *Grindelia lanceolata*, all of which are in relatively low percent cover. Bare soil and gravel are the dominant substrates and percent cover of litter is moderate. The mean soil depth of this community is

Table 6. The 11 most common species and their percent cover by site.

Taxon	A[a]	C[b]	M[c]	Ve[d]	V[e]
Aster sp.	4	0	0	0	0
Echinacea tennesseensis	1	1	5	4	8
Grindelia lanceolata	9	1	<1	<1	0
Houstonia sp.	0	10	<1	<1	8
Hypericum sphaerocarpum	<1	<1	1	<1	<1
Isanthus brachiatus	1	<1	<1	<1	0
Petalostemon gattingeri	2	<1	4	2	<1
Ruellia humilis	1	<1	2	1	<1
Schizachyrium scoparium	1	7	<1	3	1
Silphium trifoliatum	3	0	0	0	0
Sporobolus spp.	2	2	12	6	4

[a]Allvan
[b]Couchville
[c]Mt. View
[d]Vesta
[e]Vine

Table 7. Percent cover of species, substrates, and litter by community (plot data combined from all sites).

Taxon	C-1	C-2	C-3	C-4	C-5	C-6	OUT
Aster sp.	0	0	<1	0	0	0	1
Echinacea tennesseensis	2	2	3	38	1	16	1
Grindelia lanceolata	1	<1	<1	<1	<1	<1	4
Houstonia sp.	<1	14	<1	<1	5	<1	<1
Hypericum sphaerocarpum	<1	<1	1	<1	<1	<1	1
Isanthus brachiatus	<1	<1	<1	0	0	0	<1
Petalostemon gattingeri	<1	1	6	1	<1	1	2
Ruellia humilis	1	<1	1	1	<1	1	1
Schizachyrium scoparium	<1	<1	<1	<1	19	15	3
Silphium trifoliatum	<1	0	<1	0	0	0	<1
Sporobolus spp.	1	4	18	3	1	1	9
Total Percent cover	28	29	43	55	43	52	58
Substrates							
Bare Soil	26	16	23	28	32	42	
Bedrock	<1	<1	0	0	0	1	
Bryophyte	10	1	1	9	<1	1	
Flagstone	4	2	5	4	3	4	
Gravel	34	71	59	42	56	32	
Lichen	<1	0	<1	<1	0	<1	
Nostoc	<1	1	<1	<1	<1	<1	
Litter	16	11	16	15	25	27	

Table 8. Mean soil depth by community.

Community	Soil depth (cm)	Duncan grouping
#3	5.2 +/- 1.9	A
#2	6.1 +/- 2.4	A B
#1	6.5 +/- .9	A B
#4	6.3 +/- 2.7	A B
#6	7.1 +/- 3.3	A B
#5	7.5 +/- 5.0	B

6.5 cm. Nearly half of the plots that comprise this community are from the Vesta site and a substantial number are from Mt. View and Vine (Table 9). Table 10 indicates the site source of the plots comprising each community.

2. Houstonia / Sporobolus community (C-2 of Table 7) : This community is also characterized by a relatively low percent vegetative cover. Houstonia sp. is the dominant species in this community; Sporobolus spp. and Echinacea tennesseensis are also important contributing species to this community. Gravel is by far the most abundant substrate, and bare soil is also a substantial contributor. Percent cover of litter is lower in this community than in any other. Almost half of the plots that comprise this community are from the Couchville site; the Vine and Vesta sites also contribute substantially to the total number of plots that represent this community.

3. Sporobolus / Petalostemon community (C-3 of Table 7) : This community is characterized by average percent vegetative cover. Sporobolus spp. constitutes almost half of the total plant cover; Petalostemon gattingeri and Echinacea tennesseensis are also important species in this community. Gravel is the dominant substrate in this community, and bare soil is also a substantial contributor. Average soil depth is the lowest of any community. Percent cover of litter is about average. The majority of the plots that comprise this community are located at Mt. View, and a considerable number are at Vesta.

4. Echinacea community (C-4 of Table 7) : This community has the highest percent vegetative cover of any community. E. tennesseensis

Table 9. Percent of plots from each site for each community.

Site	C-1	C-2	C-3	C-4	C-5	C-6	OUT
Allvan	8	0	6	0	0	0	39
Couchville	4	47	0	0	45	5	12
Mt. View	24	2	59	37	0	5	15
Vesta	48	17	35	42	38	85	32
Vine	16	34	0	21	17	5	2
Total	100	100	100	100	100	100	100

Table 10. Percent of plots of each site in given community.

Site	C-1	C-2	C-3	C-4	C-5	C-6	OUT	Total
Allvan	7	0	10	0	0	0	83	100
Couchville	2	52	0	0	27	2	17	100
Mt. View	11	2	55	13	0	2	17	100
Vesta	13	9	19	8	11	18	22	100
Vine	12	55	0	12	15	3	3	100

accounts for most of the vegetative cover, and *Sporobolus* spp. also contribute substantially. Gravel and bare soil are the most common substrates, and percent cover of bryophyte and flagstone are relatively high. Soil depth is about average, and percent cover of litter is about average. Plots located at Vesta and Mt. View account for almost 80 percent of the total plots that represent this community.

5. *Schizachyrium* / *Houstonia* community (C-5 of Table 5) : This community is characterized by an average percent vegetative cover relative to other communities. *Schizachyrium scoparium* is the most important plant species, in terms of total cover, in this community; and *Houstonia* sp. makes a substantial contribution to the total vegetative cover. Gravel and bare soil are the most common substrates. This community has the highest average soil depth of all the communities. And this community has a relatively high percent cover of litter. More than 80 percent of the total plots of this community are from Couchville or Vesta, and Vine contributes the balance.

6. *Echinacea* / *Schizachyrium* community (C-6 of Table 7) : *E. tennesseensis* and *Schizachyrium scoparium* are the codominant species in this community with almost identical percent cover. The percent vegetative cover for this community is slightly above average. Bare soil is the most important substrate and is highest here than in any other community. Gravel is secondary in importance. Although flagstone is only four percent of the cover, it is higher in this community than in any of the others. Percent cover of litter is higher than in any other community. Plots from Vesta account for 85 percent of the total

plots in this community.

7. Outliers ("OUT" of Table 7) : The plots that were not similar enough to be grouped with the six communities were grouped into this community. It should be emphasized that these plots were not grouped according to their similarity to each other, but rather by their dissimilarity to the six communities.

This group has a higher percent vegetative cover than any of the communities. *Sporobolus* spp. are the dominant plant species in this group; *Grindelia lanceolata, Schizachyrium scoparium, Petalostemon gattingeri, Echinacea tennesseensis,* and *Ruellia humulis* also contribute to the group substantially. Gravel and bare soil are the most important substrates. Soil depth and percent cover of litter are both above average. Plots located at Allvan had the highest frequency in this group, and Vesta and Mt. View also contribute substantially to the total number of plots that comprise this group.

The Vegetation by Site

An average linkage CLUSTER analyis was performed using plot data from each of the five sites seperately. Described below are the results of these analyses. All analyses were performed on arcsine transformed values of the original percentage data; all means are reported as backtransformed values.

Allvan Site

The analysis resulted in four clusters of plots closely related in terms of species composition, hereinafter referred to as communities

1, 2, 3, and 4. Communities 1, 3, and 4 are each comprised of 5 plots, and each accounts for 17 percent of the sample plots at this site; community 2 is comprised of 11 plots which accounts for 37 percent of the sample plots at this site. This leaves four plots (13 percent of the total) that were judged to be outliers and were not included in any of the communities.

Description of the Communities:

1. *Silphium* community : This community has 78 percent vegetative cover, the highest of any community at this site. The dominant plant species is *Silphium trifoliatum* with 37 percent cover. *Aster* sp. and *Grindelia lanceolata* also make a substantial contribution to the vegetative cover of this community (six percent each). Bare soil and gravel are the dominant substrates in this community, accounting for 51 and 48 percent cover, respectivey. Percent cover of litter is high in this community (61 percent); recall that litter is not treated as a substrate in this study. The average soil depth in this community is 11.5 cm, the deepest of all the communities at this site.

2. *Grindelia / Petalostemon* community : This community has the lowest total percent vegetative cover of all the communities at this site (52 percent). The dominant plant species is *Grindelia lanceolata* with 17 percent cover; *Petalostemon gattingeri* makes a substantial contribution to the total plant cover (8 percent), and *Echinacea tennesseensis* makes a minor contribution (3 percent). Gravel is the main substrate (90 percent cover), and bare soil accounts for most of the remainder (9 percent cover). Percent cover of litter is relatively low in this community (14 percent). The average soil depth of this

community is 6 cm, the lowest of any community at this site.

3. *Sporobolus* community : This community has a percent vegetative cover of 56 percent, slightly less than average for this site. The dominant plant species in this community are *Sporobolus* spp. with 29 percent cover; *Grindelia lanceolata, Hypericum sphaerocarpum,* and *Petalostemon gattingeri* also make minor contributions to the total vegetative cover, accounting for five, three, and two percent cover, respectively. Gravel and bare soil are the codominant substrates with 51 and 47 percent cover, respectively. Percent cover of litter is 21 in this community. The average soil depth is 8 cm, about average for the site.

4. *Aster / Grindelia* community : This community has a total vegetative cover of 55 percent, slightly less than average for this site. The dominant plant species of this community is *Aster* sp. with 31 percent cover; *Grindelia lanceolata* contributes 9 percent to the total vegetative cover; *Sporobolus* spp. make a minor contribution to the total plant cover (2 percent). Gravel is the main substrate in this community (85 percent cover), and bare soil accounts for the remaining 15 percent of the substrate cover. The percent cover of litter is 24 percent. The average soil depth for this community is 8 cm which is above average for this site.

Couchville Site

The analysis resulted in two clusters of plots closely related in terms of species composition, hereinafter refered to as communities 1 and 2. Community 1 is comprised of 16 plots which accounts for 33

percent of the sample plots at this site. Community 2 is comprised of 26 plots or 54 percent of the total plots. This leaves six plots (12 percent of total) that were judged to be outliers and were not included in either community.

Description of the Communities:

1. *Schizachyrium / Houstonia* community : This community has a total vegetative cover of 52, double that of community 2. The dominant plant species is *Schizachyrium scoparium* with 28 percent cover; *Houstonia* sp. also makes a substantial contribution (8 percent). Gravel and bare soil are the major substrates in this community accounting for 57 and 37 percent cover, respectively. Percent cover of litter is relatively high in this community (26 percent). The average soil depth in this community is 10.5 cm.

2. *Houstonia* sp. / *Sporobolus* community : The percent vegetative cover in this community is 26. The dominant plant species in this community is *Houstonia* sp. with 15 percent cover; secondary in importance is *Echinacea tennesseensis* with four percent cover. The majority of the substrate is gravel (87 percent cover), and bare soil is a minor contributor (10 percent cover). Percent cover of litter is relatively low (8 percent cover). The mean soil depth for this community is 7.5 cm, substantially less than community 1.

Mt. View Site

The analysis resulted in three clusters of plots closely related in terms of species composition, hereinafter refered to as communities 1, 2, and 3. Community 1 is comprised of 21 plots (38 percent of the

total number of plots at this site); community 2 is comprised of seven plots (13 percent of the total number of plots at this site); community 3 is comprised of 19 plots (35 percent of the total plots). The remaining eight plots were judged to be outliers and were not included in any of the communities.

Description of the Communities:

1. *Sporobolus* community : The average vegetative cover of this community is 45 percent - about average for this site. The dominant vascular plant species in this community are *Sporobolus* spp. with 29 percent cover; *Hypericum sphaerocarpum* and *Petalostemon gattingeri* make less significant contributions to the plant cover with five and three percent cover, respectively. Gravel is the most common substrate in this community (62 percent cover on the average); bare soil, flagstone, and moss account for the remaining cover with 16, eight, and two percent cover, respectively. Cover of litter in this community (12 percent) is slightly less than average for this site. The average soil depth in this community is six cm.

2. *Echinacea* community : The vegetative cover of this community (49 percent) is about average for this site. *Echinacea tennesseensis* is the dominant vascular plant species in this community (eight percent cover). Moss is the most common substrate in this community with 37 percent cover; gravel and bare soil account for 21 and 18 percent cover, respectively. The percent cover of litter is 25 in this community - higher than any other community at this site. The average soil depth of this community is six cm.

3. *Echinacea / Sporobolus / Petalostemon* community : The average vegetative cover of this community (45 percent) is about average for this site. The codominant vascular plant species in this community are *Echinacea tennesseensis* (12 percent cover), *Sporobolus* spp. (ten percent cover), and *Petalostemon gattingeri* (seven percent cover). Gravel is the major substrate in this community representing 61 percent of the total cover; bare soil, flagstone, and moss are the minor substrates each of which contribute eight percent cover. Percent cover of litter in this community (12 percent) is slightly below average for this site. The average soil depth is five cm for this community.

Vesta Site

The analysis resulted in three clusters of plots closely related in terms of species composition refered to as communities 1, 2, and 3 from here to the end of the discussion. Community 1 is comprised of 39 plots, or 41 percent of the total plots at this site; community 2 is comprised of 32 plots, or 33 percent of the total plots; community 3 is comprised of 18 plots, or 19 percent of the total plots. The remaining 7 percent of the total plots (7 plots) were judged to be outliers.

Description of the communities:

1. *Petalostemon / Sporobolus* community : This community has the least vegetative cover (27 percent) of all communities at this site. The codominant plant species are *Petalostemon gattingeri* and *Sporobolus* spp. with five and three percent cover, respectively.

Gravel and bare soil are the major substrates with 51 and 41 percent cover, respectively. Cover of litter in this community (12 percent) is low relative to the other two communities. The average soil depth of the plots in this community is five cm, about average for this community.

2. *Echinacea* community : The vegetative cover of this community is 49 percent, somewhat above average for this site. The dominant plant species of this community is *Echinacea tennesseensis* with 16 percent cover; *Schizachyrium scoparium* and *Sporobolus* spp. contribute less significantly, five and two percent, respectively. Bare soil and gravel account for the majority of the substrates in this community with 46 and 34 percent cover, respectively; flagstone occupies six percent, a relatively high proportion of the substrate cover. The percent cover of litter is 24 percent which is about average for this site. The average soil depth, about average for this site, is seven cm in this community.

3. *Sporobolus / Schizachyrium* community : The average vegetative cover of this community is 58 percent, the highest of all communities at this site. The dominant plant species in this community are *Sporobolus* spp. with 30 percent cover; second in importance is *Schizachyrium scoparium* with ten percent cover; *Petalostemon gattingeri* and *Ruellia humilis* also make a minor contribution with three and two percent cover, respectively. Gravel and bare soil account for the majority of the substrate in this community with 45 and 40 percent cover, respectively. Flagstone and bryophyte make minor

contributions. Percent cover of litter is 25 in this community, about average for this site. The soil depth, also about average for this site, is five cm.

Vine Site

The analysis resulted in three clusters of plots closely related in terms of species composition that, hereinafter refered to as communities 1, 2, and 3. Community 1 is comprised of seven plots, or 21 percent of the total number of plots at this site; community 2 is comprised of 20 plots, or 61 percent of the total plots; community 3 is comprised of four plots, or 13 percent of the total. The two remaining plots were judged to be outliers and were not included in any of the communities.

Description of the Communities:

1. *Echinacea / Schizachyrium* : The plots that comprise this community have a relatively low average vegetative cover (40 percent). The codominant species in this community are *Echinacea tennesseensis* and *Schizachyrium scoparium* with five percent cover each. Moss is the most common substrate accounting for 53 percent of the cover of the sampled area; the second most common substrate is bare soil (19 percent); gravel is a minor contributor with four percent cover. The percent cover of litter in this community is 22 percent. The average soil depth of this community is 7.5 cm, and is higher than any other community.

2. *Houstonia* community : The percent vegetative cover of this community is relatively low (35 percent). The dominant taxon in this

community is a species of *Houstonia* which has 15 percent cover; secondary in importance are *Echinacea tennesseensis* and *Sporobolus* spp. with six and five percent cover, respectively. The major substrate in this community is gravel which occupies 58 percent of the area sampled; secondary in importance is bare soil with 23 percent cover. The percent cover of litter in this community (15 percent) is the lowest of all communities at this site. The average soil depth of this community is 5 cm, lowest of all the communities of this site.

3. *Echinacea* community : The percent vegetative cover averages 65 percent for this community which is higher than any other community at this site. *Echinacea tennesseensis* is, by far, the most abundant species in this community with 46 percent cover. *Houstonia* sp., *Ruellia humilis*, and *Sporobolus* spp. all make minor contributions to this community with three, two, and two percent cover, respectively. Moss, bare soil, and gravel are all common substrates in this community with 36, 26 and 21 percent cover, respectively; flagstone accounts for five percent of the substrate sampled. Litter cover in this community (20 percent) is about average for this site. Soil depth averages 7 cm in this community.

Percent Vegetative Cover by Site

The total vegetative cover (excluding litter) at each of the five sites was averaged from the plot data. All statistical analyses were performed on arcsin transformed values of the original percentage data. The Kruskal-Wallis test was used to analyze the variation among

sites, and the sites were determined to be significantly different at the $P \leq .05$ significance level. Therefore the null hypothesis is rejected and the alternate hypothesis that the percent cover varies from site to site is accepted. Duncan's Multiple Range Test was then employed to determine which of the means are significantly different (Table 11). Sites with the same letter are not significantly different, and sites with different letters are significantly different. Estimates of means are presented as backtransformed values provided with asymmetrical confidence limits rather than standard error.

Soil Depth

The mean soil depth was calculated for each site from the plot data. The Kruskal-Wallis test was employed to analyze the variance among sites. Soil depth was determined to be different among sites at the 05 significance level. Therefore the null hypothesis is rejected and the alternative hypothesis that soil depth varies among sites is accepted. Duncan's Multiple Range Test was then used to determine which sites have significantly different soil depths (Table 12); sites with the same letter are not significantly different, and sites with different letters are significantly different.

Substrates

Percent cover of substrates was calculated from the plot data. All statistical analyses were performed on arcsin transformed values of the original percentage data. The Kruskal-Wallis test was then used to

Table 11. Percent vegetative cover by site.

Site	Mean	Confidence limits: lower / upper		Duncan Grouping
Allvan	59	56.0	62.3	A
Mt. View	45	42.9	48.0	B
Vine	42	38.2	45.2	B
Couchville	39	35.6	41.6	B
Vesta	41	38.7	43.5	B

Table 12. Mean soil depth by site

Site	Mean (cm)	Standard deviation	Duncan grouping
Allvan	7.6	3.26	A
Couchville	8.6	3.57	A
Mt. View	5.3	1.79	B
Vesta	5.5	2.83	B
Vine	5.8	1.96	B

determine if the difference in percent cover was significantly different among sites. With the exception of bedrock, all of the substrates were determined to be different between sites at the .05 significance level. A Duncan's Multiple Range Test was then employed to determine which substrates vary significantly (Table 13); sites with the same letter are not significantly different, and sites with different letters vary significantly. The estimates of the means of substrates by site are presented as backtransformed values furnished by asymmetrical confidence limits rather than by their standard errors.

Litter

Since litter was not treated as a substrate in this study, plot data for percent cover of litter was analyzed separately from the substrate data. All statistical analyses were performed on arcsine transformed values of the original data. The Kruskal-Wallis test was used to determine if the percent cover of litter is significantly different among sites; percent cover of litter among sites was determined to be significantly different at the .05 significance level. Duncan's Multiple Range Test was used to determine which sites are significantly different (Table 14); sites with the same letter in the table are not significantly different, and sites with different letters are significantly different. Estimates of the mean percent cover of litter of each site are presented as backtransformed values furnished by asymmetrical confidence limits.

Table 13: Percent cover of substrates, confidence limits, and Duncan grouping of each substrate.

Site	Mean	Confidence Limits: Lower / Upper		Duncan Grouping
		Bare Soil		
Allvan	20	18.2	28.8	A
Couchville	23	18.5	27.0	A
Mt. View	14	11.2	16.7	A
Vesta	42	38.6	44.8	B
Vine	25	20.8	28.6	A
		Gravel		
Allvan	71	64.9	77.5	A
Couchville	72	67.6	76.3	A
Mt. View	54	48.9	59.7	B
Vesta	45	42.1	48.4	B & C
Vine	37	30.2	43.5	C
		Flagstone		
Allvan	0	0.0	0.0	A
Couchville	1	0.7	1.7	B
Mt. View	7	5.4	8.9	C
Vesta	3	2.3	3.7	B
Vine	2	1.2	3.4	B

Table 13 (continued)

Site	Mean	Confidence Limits: Lower / Upper		Duncan Grouping
		Bedrock		
Allvan	0	0.0	0.0	A
Couchville	0	0.0	0.0	A
Mt. View	0	0.0	0.0	A
Vesta	0	0.0	0.0	A
Vine	0	0.0	0.0	A
		Nostoc		
Allvan	0	0.0	0.0	A
Couchville	0	0.0	0.0	A
Mt. View	0	0.0	0.0	A
Vesta	0	0.0	0.0	A
Vine	1	0.7	1.5	B
		Bryophyte		
Allvan	0	0.0	0.0	A
Couchville	0	0.0	0.0	A
Mt. View	7	4.6	10.1	B
Vesta	0	0.0	0.0	A
Vine	12	7.9	17.9	B

Table 14: Percent cover of litter, confidence limits, and Duncan Grouping by site.

Site	Mean	Confidence limits: Lower / Upper	Duncan Grouping
Allvan	23	19.4 / 27.4	A
Couchville	14	12.1 / 15.9	B
Mt. View	14	12.3 / 16.1	B
Vesta	19	17.6 / 20.4	A & B
Vine	18	16.2 / 19.6	A & B

DISCUSSION

The Overall Communities

The CLUSTER analysis of the plot data of all sites combined resulted in six clusters of closely related plots (communities). Coneflower was found to contribute, at least minimally, to each of these six communities.

Coneflower makes its greatest contribution to community 4 where it accounts for most of the vegetative cover. Soil depth is about average in this community suggesting that coneflower does well in soil about five cm deep. Eighty percent of the plots that comprise this community are from either Mt. View or Vesta suggesting that the coneflower is locally very dense at these sites.

One would expect the Vine site to make a major contribution to community 4 because the overall density of the coneflower is highest at this site. But, there are very few plots in this community located at the Vine site. Apparently the coneflower has a high overall density at the Vine site, but the density at Vine is more uniform than the localized areas of extremely dense coneflower at the Mt. View and Vesta sites. These areas of extremely high density at Mt. View and Vesta tend to be along the periphery of the population - close to the edge of the glade opening. This area lies between the very shallow soils in the middle of the glade and the deeper soils at the edge of the glade along the border of woody vegetation.

The areas of extremely high coneflower density observed at Mt. View and Vesta usually have low numbers of other species so that only the

coneflower exists. The plots at Vine, on the other hand, generally have coneflower in lower density mixed with other species.

Echinacea tennesseensis is the most common species, in terms of percent cover, in community 1 as well as in community 4. The difference between community 1 and community 4 is that the coneflower, and the vegetation as a whole, is much less dense in community 1 than in community 4. In addition, community 1 has species other than coneflower that make substantial contributions to the vegetative cover, namely *Ruellia humilis* and *Grindelia lanceolata*. Community 4, on the other hand, is composed of coneflower to the virtual exclusion of any other species.

Since the average soil depth of communities 1 and 4 is practically identical, there is no explanation offered here as to why the community composition varies between the two. It should be noted, however, that the soil depth varies more in community 4 than in community 1; that is, the standard deviation is much higher in community 4 than in community 1. Generally, variation in soil depth on a glade is due to the presence of a relatively high number of cracks in the limestone where soil accumulates. When this is the case, vegetation develops densely above the cracks resulting in thick vegetation in localized areas. This fact may offer some explanation as to why the percent vegetative cover is higher in community 4 than in community 1.

The deepest average soil depths among the communities is encountered in communities 5 and 6. *Schizachyrium scoparium* accounts for the

majority of the cover of these two communities, and total vegetative cover is high in both of these communities. This suggests that the vegetation, in general, and *Schizachyrium scoparium*, in particular, grows more densely in deeper soils.

The community with the deepest average soil depth is community 6; the codominant species in this community are *Schizachyrium scoparium* and *Echinacea tennesseensis*. This suggests that 1. these two species cohabitate well, although it is not clear what degree of competition exists between the two species, and 2. these two species grow well in deep glade soils.

This is interesting in light the fact that *Echinacea angustifolia*, considered by some to be the closest extant relative of Tennessee coneflower, exists in large numbers in the prairie habitat of Kansas and other midwestern prairie states. Many of the prairie species observed on the glades and barrens of Middle Tennessee are believed to have migrated into the area during hotter and drier periods of the hypsothermal, and have found refuge on the relatively thin soils of the glades and barrens where there is little competition from woody plant species.

The communities with the shallowest soils are communities 3 and 2. Both these communities have a low percent of vegetative cover, and *Sporobolus* spp. make a major contribution to the vegetative cover in both these communities. This suggests that *Sporobolus* spp. compete well in the thin glade soils where they are often the dominant plant species. On practically all glades of any appreciable size in Middle Tennessee, *Sporobolus* spp. occur; they are most often encountered on

the thin soils near the center of the glade opening, and become less common in the deeper soils toward the periphery of the glade opening. Since the *Sporobolus* species are annual grasses, these areas are considered glades rather than barrens. Other species contributing to these thin-soil glade communities include *Houstonia* sp., *Petalostemon gattingeri,* and *Echinacea tennesseensis*.

A "barrens" is defined here as an area where more than half of the vegetative cover is attributed to a perennial grass species, namely *Schizachyrium scoparium*, and a glade is an area where more than half of the vegetative cover is attributed to an annual grass species (DeSelm, personal communication 1988). By this definition, communities one, two, three, and four are considered glades, and communities five and six are considered barrens. Due to the varying density of coneflower in both the barrens and the glades, it is impossible to determine to which habitat the coneflower is more suited.

It would be of scientific merit to compare the vegetation of the five glades sampled in this study with previous studies regarding the vegetation of glades not necessarily inhabited by Tennessee coneflower, such as the 1986 study by Somers *et al*. Unfortunately, a direct comparison of these two studies is not possible due to inconsistent methods of data collection. For example, in this study, only vascular plant species were considered to contribute to total vegetative cover, and only vascular plant species were used in the CLUSTER analysis to identify communities; all nonvascular plant species, lichens, and cyanobacteria are considered substrates in this

study. In contrast, Somers *et al* considered nonvascular plant species, lichens, and cyanobacteria to contribute to total vegetative cover, and all of these forms were used in their CLUSTER analysis to identify communities.

In addition, plots in the Somers *et al* study were sampled twice during the growing season in order to account for seasonal vegetation change; whereas this study was limited to one sampling period in the late summer. This may account for some of the differences in the communities identified. For example, community 1 (*Panicum capillare* community) of the Somers study does not compare well with any community identified in this study. The presence of some species in this community, such as *Arenaria patula* and *Sedum pulchellum*, would indicate that this is primarily an early summer community since these species tend to decrease in percent cover during the summer drought. These species, perhaps due to the late summer sampling date, were seldom encountered in this study. As for the comparatively low percent cover of *Panicum capillare* in this study, no explanation is offered here.

In spite of these methodological inconsistencies, an indirect comparison of the communities identified in the two studies is possible. For example, community 2 (Foliose lichen community) of the Somers study compares well with community 3 (*Sporobolus / Petalostemon* community) of this study. The two dominant vascular plant species are the same, and the soil depth is similar. However, there is a large discrepency in percent cover of lichen between these two communities.

Community 3 (*Sporobolus / Petalostemon* community) of this study is perhaps more similar to community 4 (*Dalea gattingeri* community) of Somers. The species composition is, for the most part, comparable, and the soil depth is relatively similar.

Community 1 (*Echinacea / Ruellia* community), community 4 (*Echinacea* community) and community 6 (*Echinacea / Schizachyrium* community) of this study are not represented in the Somers study. These communities are all dominated by Tennessee coneflower; since only three of ten glades sampled in the Somers study are inhabited by Tennessee coneflower, it is reasonable that these communities are not represented.

Community 5 (*Schizachyrium / Houstonia* community) of this study represents a barrens habitat, and is not represented in the Somers study. This is due to the purposeful selection of glade habitat for sampling in the Somers study, as compared to the purposeful selection of Tennessee coneflower habitat, which is often barrens, in this study.

The communities identified in this study have, in general, deeper soils than those identified in the Somers study. Only three of the seven communities identified in the Somers study (communities 5, 6, and 7) have soil depths comparable to the communities in this study.

Communities 5 and 6 are considered to be barrens, and can be compared with with a barren Located in the vicinity of the Couchville site and sampled by DeSelm (1991). The relative number of annual vs. perennial grass cover was comparable, but the species composition was different. *Schizachyrium scoparium* is the only perennial grass species

that accounts for appreciable percent cover in the barren habitat identified in this study. The barren studied by Deselm, on the other hand, is occupied by a relatively large proportion of *Sporobolus asper*, a perennial grass not identified in any of the plots in this study.

Communities by Site

One's initial reaction upon visiting the Allvan site is that it has experienced recent human disturbance; this site is the least pristine of all the sites in terms of human impact. This is evidenced by the fact that this site has the highest percent vegetative cover of all the sites, and there is a high species diversity; there are more species identified in the Allvan sample plots than in any other site. This is important, especially considering that the Allvan site occupies the least area, and therefore had the least number of sample plots, of all the sites. In addition, many of the plant species encountered at the Allvan site are considered weedy, such as *Tridens flavus, Ambrosia artemisiifolia, Ipomoea pandurata, Lespedeza virginica*, et cetera. There is also evidence that the area has been used as a dump site by the Allvan Corporation, which still owns the land.

There has been some speculation that the coneflower is not actually native to this site, but rather was transported from another glade site in a load of crushed limestone (gravel). Whatever the origin of the coneflower, it is evident that the population is currently in competition with the many weedy species present at the site, and these

species seem to thrive on the human disturbance in the area. It should be noted that coneflower seems to thrive on disturbance as well, so it is not clear what degree of competition the disturbance has caused.

The other four sites have approximately equal numbers of species present suggesting that they have been subjected to equal amounts of human disturbance. With the exception of Vesta, these sites have between 26 and 29 species. Vesta has 37 species identified in the sampling plots; the relatively high number is probably best explained by the large number of sample plots at Vesta due to the large area occupied by the coneflower. So the relatively high number of species at Vesta is due to sampling bias rather than high species diversity.

The CLUSTER analysis for the Allvan site generated four clusters of plots (communities). This is a high number of communities considering the relatively small geographic area that was sampled at this site. This indicates that the vegetation is relatively heterogenous, and species composition changes rapidly from one point to another at this site.

Of the two communities identified at the Couchville site, one is dominated by *Schizachyrium scoparium* and *Houstonia* sp., and the other by *Houstonia* sp. and *Sporobolus* spp. These two communities at Couchville illustrate the "barren" and "glade" habitat. The Couchville site is an extensive area with glade vegetation on the thinner soils and barrens vegetation around the periphery of the glades where the soils are deeper. As the soils get deeper on the periphery of the site, the vegetation gives way to cedar / hardwood forest.

Sporobolus spp. constitute a large percent of the vegetative cover of the Mt. View site, and account for the majority of community 1. The high percent cover of annual grass and the relatively shallow soil of the site make Mt. View the best overall example of the glade habitat. Except for historical reports of grazing (Somers, *et al* 1986), the site has experienced very little disturbance in recent years.

The Vesta site is somewhat similar to the Couchville site in that the area includes both the glade and the barren habitat. The coneflower occurs, for the most part, on the shallow soils of the glades. These glades are surrounded by deeper soils supporting more of a barrens vegetation. The entire area is surrounded by cedar / hardwood forest on deeper soils and in the many sinkholes in the area. Since the only area sampled was in the coneflower population, communities 1 and 2, 74 percent of the area sampled, are comprised mostly of cedar glade vegetation. Community 3 is intermediate between glade and barrens vegetation.

It should be noted that the coneflower in one portion of the Vesta site has expanded since the 1987 sampling; this expansion has been in the southernmost part of the population along the recently constructed road (and the recently disturbed soil associated with building the road). In 1987 the coneflower in this area was excedingly sparse, and the increased density of the coneflower in this area seems to be attributable to the disturbance associated with road construction.

The Vine site is unique both in its numbers of coneflower and the associated species. Although the area occupied by the coneflower is less than all other sites except Allvan, the coneflower is more dense

at Vine than any other site. In addition, there is a high density of the *Houstonia* species, and very little *Schizachyrium scoparium*. The Vine glade is almost entirely enclosed by cedar / hardwood forest, and there seems to be a steep gradient from shallow soil supporting a glade vegetation to a deep soil supporting cedar / hardwood forest. Therefore there is little available habitat with intermediate soil depth to support a barrens vegetation; the coneflower exists in high numbers on the thin glade soils with seemingly little competition from the barrens species or from weedy species.

Substrates

The substrates appear to be relatively homogenous throughout the six communities, the exception being the moss substrate which is significantly more abundant in communities 1 and 4. Coneflower is the dominant plant species in both of these communities. This suggests that moss does not impede the germination and subsequent growth of coneflower. But since coneflower becomes established in other communities in the absence of moss, there is no evidence in support of the theory that moss is necessary for its establishment.

Soils

Allvan and Couchville have significantly deeper soils than Mt. View, Vesta, and Vine. This may account for the predominance of barrens vegetation at the Couchville site, as discussed earlier. The fact that Allvan has relatively deep soils may partially account for the high

species diversity and the high degree of weedy species present. The shallower soils of the Mt. View, Vesta, and Vine sites probably account for the predominance of glade vegetation at these sites. Mt. View was described earlier as the best example the glade habitat, and this site has the thinnest soil of all the sites.

Litter

Percent cover of litter does not vary significantly among sites with the exception of the Allvan site where it is highest. This is probably a result of the high percentage of vegetative cover at the Allvan site.

CHAPTER V

POPULATION DYNAMICS AND THE STATUS OF THE SPECIES

RESULTS

Percent Cover of *E. tennesseensis* by Site

The percent cover of *E. tennesseensis* at each site was calculated from the plot data. All statistical analyses were performed on arcsine transformed values of the original percentage data. The Kruskal-Wallis test was used to analyze the variance among sites. Percent cover was determined to be different among sites at the .05 significance level. Therefore the null hypothesis was rejected and the alternative hypothesis that percent cover of *E. tennesseensis* varies among sites is accepted. Duncan's Multiple Range Test was then employed to determine which sites are significantly different (Table 15). In the table, sites with the same letter are not significantly different from each other, and sites with different letters are significantly different. Estimates of the means are presented as backtransformed values provided with asymmetrical confidence limits rather than by their standard error.

Ratio of Juvenile to Adult Plants

The ratio of juvenile (non-flowering) plants to adult (flowering) plants was calculated from the plot data (Table 16). Due to the nature of ratio data an analysis of variance was not possible. Since the ratio is not identical at each site, the null hypothesis is rejected and the alternate hypothesis that the ratio is not identical at all

Table 15. Percent cover of *E. tennesseensis* by site.

Site	Mean	Confidence limits: lower / upper		Duncan grouping
Allvan	1.2	0.0	1.9	A
Couchville	1.0	0.0	1.4	A
Mt. View	5.1	3.8	6.7	B
Vesta	4.0	3.2	4.9	B
Vine	7.9	5.8	10.4	B

Table 16. Ratio of juvenile to adult *E. tennesseensis* by site.

Site	Ratio
Allvan	2.21:1
Couchville	4.77:1
Mt. View	1.58:1
Vesta	3.45:1
Vine	2.49:1

sites is accepted.

Density of *E. tennesseensis* and the total number of Plants by Site

In order to estimate density and total number of plants of *E. tennesseensis* it was necessary to estimate the total area occupied by the species at each site. The total area occupied by the species was estimated using a planimeter and the scaled, overhead sketches of each population. The average density of *E. tennesseensis* was then determined using the plot data and the estimated total area. The Kruskal-Wallis Test was used, and the density of *E. tennesseensis* was determined to be significantly different at the .05 level of significance. Duncan's Multiple Range Test was used to determine which sites are significantly different. Sites with the same letter are not significantly different from each other, and sites with different letters are significantly different (Table 17).

The total number of plants at each site was estimated using the plot data and the estimated total area. Any patches of plants too small or too isolated to be indicated in the sketches were counted or estimated and added to the number calculated using the total area and density data in order to obtain an accurate estimate of total plants per site (Table 17). Since the estimated number of plants is different at each of the five sites, the null hypothesis is rejected and the alternate hypothesis is accepted.

Demographics of *E. tennesseensis*

Demography is the study of changes in population size and structure

Table 17. Total area in which *Echinacea tennesseensis* occurs, density of *E. tennesseensis*, and total number of *E. tennesseensis* plants by site.

Site	Total Area (m^2)	Average Density (plants/m^2)	Duncan grouping	Estimated Total # Plants
Allvan	470	6.2	A	3,700
Couchville	13,860	6.2	A	89,300
Mt.View	830	12.9	A	12,000
Vesta	1,420	13.1	A	20,900
Vine	800	20.7	B	20,200
Total	17,370	--	--	146,000

over time. A demographic study involves the collection of data on the births, deaths and fecundity of individuals of each age in a population. From these data it is possible to predict the overall change in population structure with time (Barbour *et al* 1987).

The Leslie matrix model (Leslie 1945) is a classic discrete time model based on uniform age classes, and is commonly used for animal species. The fecundities of each age class, and the probability of each individual of age t surviving to age t+1 are recorded and assumed to be constant through time. These data are used to predict the eventual stable age distribution of the population and to determine if the population is expanding, shrinking, or stable through time.

The Leslie model relies on conventional demographic theory that fecundity and survival depend on the age of an individual. This type of model is useful for many species, such as homeothermic vertebrates, in which life-history characteristics are correlated with age. But with many species, especially herbaceous plant species, the effect of size is more important than that of age in determining birth, death, and fecundity of an individual. The variability of growth rate within a population of herbaceous plants is sufficiently large that size of an individual is a better indicator of its fecundity and life expectancy (Kirkpatrick 1984).

A modified version of the Leslie model has been used to study many herbaceous, perennial plant populations (Werner and Caswell 1977, Caswell and Werner 1978, Bierzychudek 1982, Meagher and Antonovics 1982, Kirkpatrick 1984). This modified version of the Leslie model is known as the Lefkovich model (Lefkovich 1965), and utilizes life

history stage classes rather than age classes.

Although the Lefkovich model is more appropriate in this study than the Leslie model, there are a number of inherent problems in using this model for *Echinacea tennesseensis*. The only permanent parts of the plant are the below ground perennial root stock the sampling of which would be destructive to the plant. Many herbaceous perennials exhibit clonal growth (Bierzychudek 1982). Although *Echinacea tennesseensis* does not seem to reproduce asexually, there is, nevertheless, the problem of identifying individuals with accuracy. Again, the only foolproof method of determining actual individuals often requires destructive excavation of the perennial rootstock, so an "individual" is sometimes designated arbitrarily.

Despite these difficulties, two one-year transition matrices were calculated for each of the years 1 and 2; the two transition matrices were based on 1). total leaf length, and 2). the number of flowering/seed heads. In the first matrix, all plants in flower were grouped together as "adults". In the second matrix, all non-flowering plants were grouped together as "juveniles".

The reasons for using these characteristics for constructing transition matrices are substantiated by field observations. Total leaf length is a good characteristic for the "juvenile" (non-flowering) plants because total leaf length is a good indicator of photosynthetic capacity and of the future success of the plant. The leaves of juvenile plants are all generally very similar length, so the total leaf length can be approximated by multiplying the length of

the longest leaf by the total number of leaves. Total leaf length is not, however, a good characteristic to use with plants of reproductive age because reproductive age plants have comparatively few leaves, and it is assumed that energy used for flowering was stored during previous years in which the plant may have been juvenile.

The number of flowering heads that a plant has is a good characteristic to use for stage classifications in the "adult" plants because the number of seeds produced by a particular plant will in part determine its contribution to the growth rate of the population. Since seed heads are generally the same size, the contribution a particular plant makes to the reproduction of the population is directly correlated to the number of flowering/seed heads it has. This characteristic is, however, impossible to use with the "juvenile" stage classes, and all "juvenile" plants must be grouped when using this classification scheme.

One-year transition probabilities were calculated for all marked individuals in years 1 and 2. If a high degree of certainty as to the identity of the individual was not possible either by relocation of the tagged plant or relocation of the plant using the map, then the individual was excluded from the computations. Mortality was only recorded if the marker was located, and therefore only when mortality was reasonably certain.

Each of the transition matrices was then tested for temporal constancy (Anderson and Goodman 1957). Temporal constancy is in effect when the probability of moving from stage class i to stage class j is the same each year.

One year transition probabilities (Tables 18-21) are not constant through time (X^2 = 140.4, df = 20, $p < 0.001$ for the pair of matrices with stage classes based on total leaf length; X^2 = 258.0, df = 30, $p < 0.001$ for the pair of matrices with stage classes based on number of flowering heads). In the pair of matrices based on total leaf length, the greatest deviation from constancy (X^2=62.7, df = 4, $p < 0.001$) is observed in the "adult" catagory (those plants that were initially observed to have one or more flowering heads); the least deviation from constancy (X^2=8.8, df = 4, $p < 0.001$) is observed in the "1-30" catagory (those plants that had an initial total leaf length between one and 30 cm). In the pair of matrices based on number of flowering heads, the greatest deviation from constancy (X^2=132.8, df = 4, $p < 0.001$) is observed in the "1" catagory (those plants that were initially observed to have one flowering head); the least deviation from constancy (X^2=1.4, df = 4, $p < 0.001$) is observed in the "4-8" catagory (those plants that were initially observed to have between four and eight flowering heads).

Since the marked individuals were chosen randomly, it is possible to use these data to determine the initial stage class structure. As is expected in a perennial plant species, the sample population displays a type III survivorship curve (Barbour *et al* 1987). That is, the stage class distribution is such that there are far more individuals in the stage classes with less total leaf length or less flowering heads than those with greater total leaf length or greater number of flowering heads (Figures 1 and 2).

Table 18. Transition probabilities for first year stage classes based on number of flowering heads.

Stage	Juv.	1	2-3	4-8	>8
Juv.	.530 (175)	.554 (36)	.378 (14)	.095 (2)	--
1	.067 (22)	.092 (6)	--	.095 (2)	--
2-3	.033 (11)	.031 (2)	.243 (9)	.286 (6)	--
4-8	--	.015 (1)	.108 (4)	.286 (6)	1.0 (6)
>8	--	--	--	--	--
Dead	.370 (122)	.308 (20)	.270 (10)	.238 (5)	--
Total	330	65	37	21	6

Table 19. Transition probabilities for second year stage classes based on number of flowering heads.

Stage	Juv.	1	2-3	4-8	>8
Juv.	.563 (85)	.150 (3)	.250 (5)	--	--
1	.172 (26)	.300 (6)	--	--	--
2-3	.113 (17)	.350 (7)	.350 (7)	--	--
4-8	.093 (14)	.200 (4)	.400 (8)	.308 (4)	--
>8	.007 (1)	--	--	.615 (8)	--
Dead	.053 (8)	--	--	.077 (1)	--
Total	151	20	20	13	0

Table 20. Transition probabilities for first year stage classes based on total leaf length.

Stage	1-30	30-90	>90	Adult
1-30	.168 (28)	.088 (11)	.053 (2)	.015 (2)
30-90	.257 (43)	.232 (29)	.079 (3)	.102 (13)
>90	.078 (13)	.248 (31)	.395 (15)	.287 (37)
Adult	.012 (2)	.128 (16)	.395 (15)	.326 (42)
Dead	.485 (81)	.304 (38)	.079 (3)	.271 (35)
Total	167	125	38	129

Table 21. Transition probabilities for second year stage classes based on total leaf length.

Stage	1-30	30-90	>90	Adult
1-30	.160 (4)	.017 (1)	--	.019 (1)
30-90	.440 (11)	.333 (20)	.015 (1)	.038 (2)
>90	.160 (4)	.367 (22)	.333 (22)	.094 (5)
Adult	--	.250 (15)	.651 (43)	.830 (44)
Dead	.240 (6)	.033 (2)	--	.019 (1)
Total	25	60	66	53

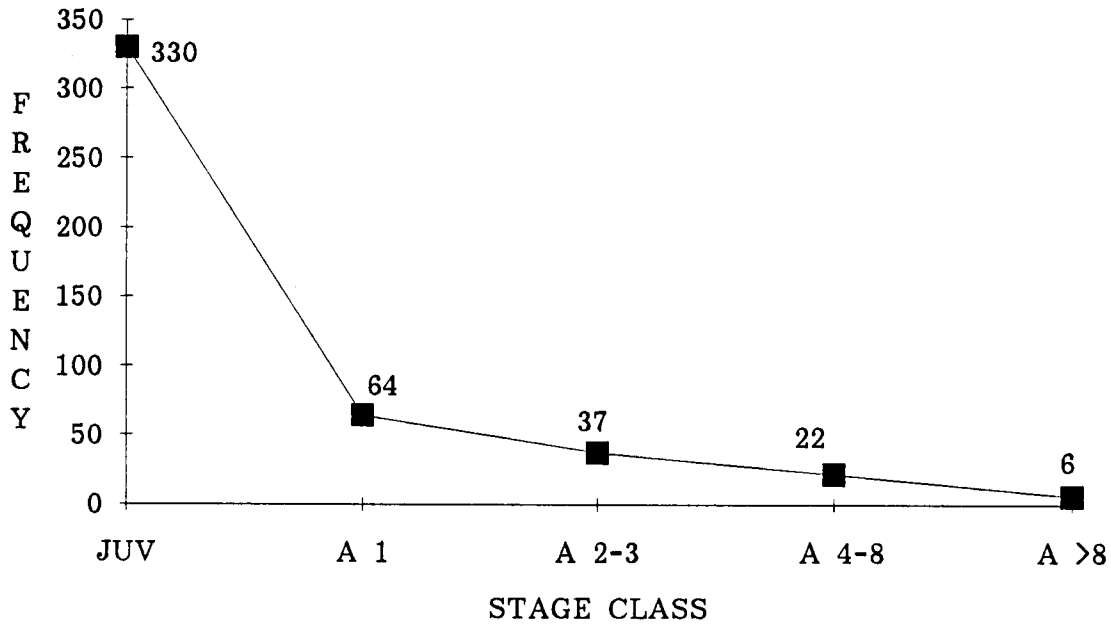


Figure 1. Initial stage class distribution based on number of flowering heads.

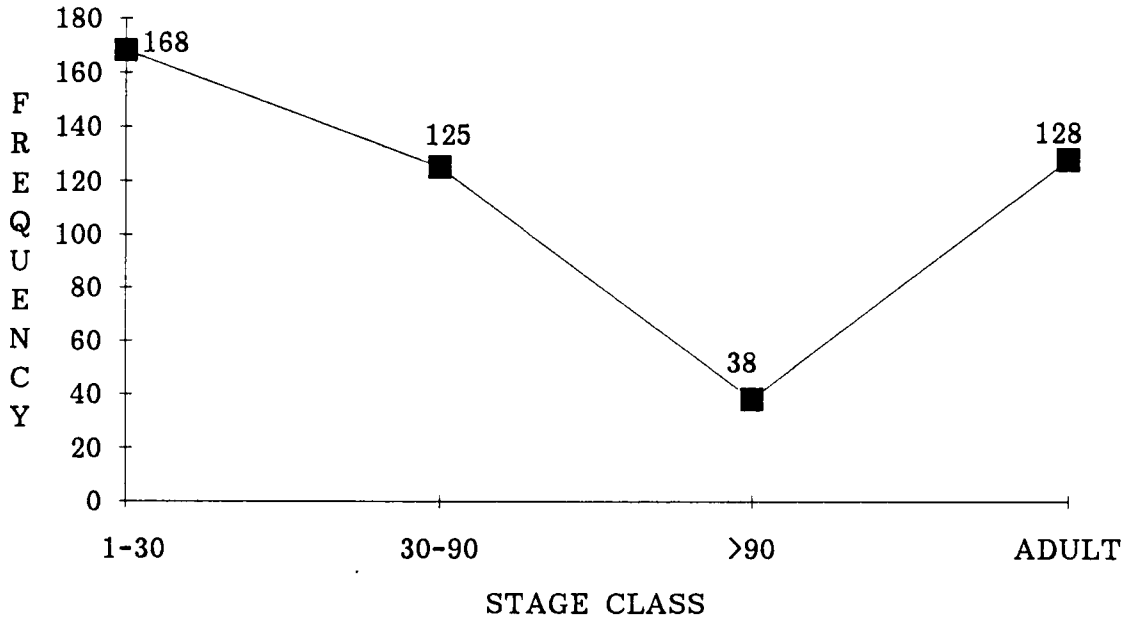


Figure 2. Initial stage class distribution based on total leaf length.

Discussion

The percent cover and density of *Echinacea tennesseensis* are lowest at the Couchville and Allvan sites. These sites also have significantly deeper soil depth than the other three sites (Table 12). This suggests that Tennessee coneflower does best in the shallower glade soils, but there is no reason to believe that shallow soil, in and of itself, enhances the growth of the coneflower. In fact the species is observed to grow well when planted in deep soils. Therefore it is more reasonable to postulate that in shallow soils Tennessee coneflower eludes competition from other species with rapid growth rates; these species are able to outcompete the coneflower in the deeper soils by growing more rapidly and subsequently shading the coneflower.

It seems that Tennessee coneflower is faced with an evolutionary double-edged sword. On the one hand, the plant grows well in deep soils, but competition is more intense in the deep soils. In the shallower soils, on the other hand, the coneflower risks drought stress which can be intense on the glades in the summer months. It seems that the coneflower is better suited for competition in the drought conditions than in the shade.

In some small areas at sites such as Mt. View and Couchville, the coneflower can be observed growing very densely around the periphery of the glade (along the boundary between forest and glade/barren). This microhabitat provides both deep soil and sufficient light intensity.

Despite its low density and percent cover at the Allvan and Couchville sites, these populations seem to be reproducing well. This is evidenced by the fact that both of these populations have high ratio of juvenile to adult plants.

The Type III survivorship curve observed as the initial stage class distribution is such that there are far more individuals in stage classes with less total leaf length and fewer flowering heads than those with greater total leaf length and more flowering heads. A high rate of juvenile mortality followed by reduced mortality rate in established plants accounts for this distribution.

There are a large number of seeds set at each site on any given year; due to the early spring rains, many of these seeds germinate. If the summer droughts are not too severe, the seedlings have a good chance of surviving the first winter. If the summer droughts are not too severe for several years, the young plants will have a chance to develop thick perennial roots characteristic of the mature plants. Once these thick perennial roots have developed the plant has more of a chance of surviving the summer droughts due to an increased capacity to acquire water and store carbohydrates.

When a population undergoes drought stress it is the juvenile plants that have not become established that succumb in the greatest numbers. So a population may lose a large proportion of its juvenile in a particularly dry year.

In theory, a transition probability matrix can be used to predict the eventual stage distribution of a population if the assumptions of the model are met. Since one year transition probabilities are not

constant through time, it is not possible to predict the eventual stage class distribution.

Although these data are not appropriate to be used in a temporally constant Lefkovich model, the transition probabilities can be used to observe trends in the population dynamics and to compare mortality rates between stage classes. The transition probabilities can also be used to compare these phenomena between the two years. The following qualitative assessments are possible from these data:

1. Overall mortality was observed to be much higher in year 1 than in year 2. This is probably due to extremely dry conditions in the spring and summer of 1988 as compared to that of the spring and summer of 1989.

2. Mortality is highest among juvenile plants. The highest percent mortality of any stage class in both years was observed in the 1-30 stage class in year 1 in which almost 50 % of the marked plants died. The lowest mortality rate was consistently observed in the flowering stages or in the "> 90" (leaf length > 90 cm) category.

3. Mortality decreases with increased leaf length or increased number of flowering heads. This is a consistent trend in all of the transition matrices suggesting that as a plant becomes established it is less likely to succumb to drought stress. This may be due to energy stored in its rootstock during more favorable growing seasons.

4. In the one-year transition matrices based on total leaf length, the greatest deviation from constancy is observed in the "adult" category. This is probably because many of the plants that flowered in

1987 did not flower in 1988 due to the extremely dry growing season that year. In the more humid growing season of 1989, a much greater number of the "adult" plants of 1988 continued to flower in 1989.

In addition, it should be noted that not only did many plants that flowered in 1987 fail to flower in 1988, but many of these plants returned to their flowering status in 1989. This suggests that established plants have the ability to flower sporadically depending on the conditions of the particular growing season.

5. In the one-year transition matrices based on total leaf length, the least deviation from constancy is observed in the "1-30" category (plants with an initial total leaf length of one to 30 cm). The reason for this relative constancy is due to high mortality in this stage class in both growing seasons. That is, plants in this stage class consistently die.

6. In the one-year transition matrices based on number of flowering heads, the most deviation from constancy is observed in the "1" category (those plants initially with one flower). This suggests that plants with one flower are in a precarious situation; they may flower with any number of flowers the next year if conditions are good for growth, or they may not flower at all if conditions for growth are poor.

7. In the one-year transition matrices based on number of flowering heads, the least deviation from constancy is observed in the "4-8" category (those plants initially having four to eight flowering heads). This suggests that the more flowering heads a plant has, the more predictable its flowering will be the next year. Also there is a

larger range of flowering heads within this category. So the number of flowers can fluctuate more and still remain in this category. It should be noted that the "> 8" category was excluded from this comparison because there were no plants tagged with more than eight flowering heads in the summer of 1988.

CHAPTER VI

PREDATION AND POLLINATION

A total of ten goldfinches (*Astragalinus tristis*) were observed on nine separate occasions in August and September feeding on the achenes of coneflower. The birds were observed perched on the uppermost portion of the stem of the coneflower close to the seed head containing mature seed. The goldfinches would occasionally "peck" their beaks into the aggregation of achenes. Subsequent to these observations the ground under which the goldfinches had been feeding was examined; the remnants of the seeds were located and collected; the embryos had been extracted and the achenes were destroyed.

From these observations, it is concluded that the goldfinch is a common seed predator of coneflower. Since there is no obvious morphological adaptation of the coneflower achenes to attach to the feathers of birds, it is not probable that the goldfinch functions as a disperser of the coneflower.

The most common pollinators observed were members of the bumblebee genus *Bombus*, of which there were several. The most common lepidopteran pollinators were the buckeye (*Precis coenia*) and the sulfur (*Colias* spp.) butterflies.

Orthopterans were observed on the stems and leaves of coneflower on many occasions, but it is not certain if they were predaceous on the coneflower. These orthopterans were identified as members of the subfamily Oedopodinae.

CHAPTER VII

SUMMARY AND CONCLUSIONS

Tennessee coneflower exists on cedar glade or cedar barren habitat at all of the five sites sampled in this study. The majority of the sites and communities identified were judged to be glades, so it is concluded that the predominant habitat for coneflower is glade. It is interesting that the community with the highest percent cover of coneflower (community 4 of Table 7) has an average soil depth and is somewhat of an intermediate between a glade habitat and a barren habitat. In consideration of all the data presented here, it is concluded that coneflower exists primarily on glades. Coneflower actually grows more densely in the barrens habitat, but does not compete well with many of the species found in the deeper soils most likely due to shading.

The Mt. View site is the best overall example of a cedar glade habitat. The Mt. View site is characterized by relatively shallow soil (the shallowest of the five sites); the dominant vascular plants are annual grass species of *Sporobolus*, and perennial grasses are nearly excluded from this site. In addition, there is a relatively high percentage of the glade moss *Pleurochaete squarrosa*. The entire glade is enclosed by cedar/hardwood forest except where a road has been cut on the corner of the glade.

At the Couchville and Vesta sites the glade habitat grades into barrens habitat. At the Vesta site the coneflower is located predominantly on the glades, but a small portion of the population

exists on the barrens that, in large part, surround the glades. Therefore, the coneflower at the Vine site is primarily associated with the annual grass species of *Sporobolus*, and, to a lesser degree, with perennial grass species (Table 5). The Vesta habitat is therefore considered to be glade.

In contrast to the Vesta site, the coneflower at the Couchville site is primarily associated with the perennial grass species *Schizachyrium scoparium*, and, to a lesser degree, with the annual grass species of *Sporobolus*. Although a *Houstonia* species (mostly *H. nigricans*) is the dominant vascular plant species at Couchville, the habitat is considered a barren because more than 50 percent of the cover of the grasses are perennial species (Table 3).

The vegetation of the Vine site is, in many respects, distinctive. The dominant vascular plant species are Tennessee coneflower and a *Houstonia* species; this is the only site where coneflower functions as dominant or codominant, and the density of coneflower is higher than at all of the sites. In contrast to all other sites, none of the grass species at the Vine site are dominant or codominant. Couchville is the only site to which Vine has an affinity; this is primarily due to the high percent cover of *Houstonia* at both these sites.

The most distinctive of the five sites (in terms of vegetation, species present, and total vegetative cover) is the Allvan site. This is presumed due to the high degree of recent human disturbance associated with this site. Many of the species present at Allvan are considered weedy, two of which, *Grindelia lanceolata* and an *Aster*

species are the codominant species. The origin of this population is dubious; it has been speculated that coneflower seed was brought to this site in a load of crushed limestone.

Although the vegetation is variable among all five sites, it is, with the exception of the Allvan site, adjudicated stable and natural. This judgement is supported by extensive field experience involving the visitation of nearly 300 glades in Middle Tennessee. There is no reason to believe the coneflower at these four sites is in danger of extinction due to competition from other species present.

In contrast to the other four sites, the vegetation of the Allvan site is adjudicated unstable and unnatural; due to the high percent cover of weedy species at this site, the continued existence of this population is uncertain.

Among the sites, percent vegetative cover and percent cover of perennial grasses increase with increasing soil depth; the barrens habitat has deeper soil, on the average, than the glade habitat. Coneflower exists in almost all degrees of soil depth, but does best on medium to relatively deep soils; coneflower grows best in deeper soils, but escapes competition in shallower soils. Coneflower is also observed to grow in areas of very thin soil with its roots growing submerged into cracks or holes in the limestone bedrock, so it is often hard to determine what the actual soil depth is.

The primary difficulty in constructing a Lefkovich matrix model of the population dynamics of this species is that the model assumes the one year transition probabilities are constant through time. This assumption was not met, or even approached, due to the extreme

discrepancy in rainfall between the two growing seasons. In any given year, the population dynamics of this species is strongly dependent on the amount of rainfall during that growing season, so one or two years of data are not adequate to assess the population dynamics of the species over time. This difficulty could possibly be circumvented by gathering demographic data over a period of many years, and then using average values of the one year transition probabilities to construct a Lefkovich model.

In both growing seasons, mortality was greatest in the juvenile (non-flowering) stage classes than in the adult (flowering) stage classes. In addition, among the juvenile (non-flowering) stage classes in the matrix based on total leaf length, mortality was highest in the stage class with the least total leaf length (i.e. the "1-30" stage class). This suggests that small (and generally young) plants have a high rate of mortality; as plants grow and develop a large perennial root system, they have a better chance of surviving the summer drought. The high juvenile mortality contributes to the inability of the species to disperse to other glades by chance introductions of achenes by high winds, etc. That is, very few achenes disperse to neighboring glades, and due to high juvenile mortality far fewer germinate and survive to maturity.

A higher rate of mortality among juveniles would be expected in a species that displays this type of stage class distribution. The extremely high rate of mortality during the first growing season is actually no reason to be alarmed about the fate of the species. The

stage class distribution, the decreased mortality rate the following year, and common sense suggest that populations of this species growing in this environment will experience periodic population crashes in extremely dry years. As suggested earlier, a good understanding of the demographics of this species would require many years of demographic data.

A high ratio of juvenile (non-flowering) to adult (flowering) plants was observed at four of the five sites (Table 15). This is an indication that these four sites are reproducing well. Mt. View was the only site to fall below a 2:1 ratio (1.6:1). The fact that the Mt. View site has the shallowest average soil depth indicates that this may increase juvenile mortality.

The initial stage class distributions (Figures 1 and 2) are as would be expected in an herbaceous plant species growing in a harsh environment. A type III survivorship curve (Barbour *et al*, 1987) is observed in which there are far more individuals in stage classes with less total leaf length and less number of flowering heads than in stage classes with greater total leaf length and greater number of flowering heads. It is suspected that this type of stage class distribution would be observed most anytime a population is sampled; the failure to observe this type of stage class distribution would indicate that the population is not reproducing well.

The goldfinch was identified as a seed predator, but predation is not so intense as to cause an observable problem. Predation was observed on only nine occasions during two months of sampling. In addition, overall seedset seems sufficient, and many germinals (with

cotyledons) were observed in the spring at both sites where predation was observed. The goldfinch may possibly, although they are unlikely to function as dispersers of coneflower seed thereby benefiting the species.

Pollination is judged adequate in the species. Several species of pollinators were collected and identified, and many others were observed but not identified. This indicates that the frequency of outcrossing is high.

As an overall conclusion, the role of *Echinacea tennesseensis* in its native habitat has been assessed; the vegetation at four of the five sites is judged to be natural and stable, and there is no reason to believe these populations are in danger of extinction due to competition from other vascular plant species or from predation. In addition, factors relating to the population structure and dynamics have been described. Although more demographic data are needed for an accurate assessment, all populations are adjudicated stable and in no danger of extinction.

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