

The Endangered Tennessee Purple Coneflower, *Echinacea tennesseensis* (Asteraceae): Its Ecology and Conservation

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Photo by Thomas E Hemmerly

ABSTRACT

The federally endangered Tennessee purple coneflower (*Echinacea tennesseensis* (Beadle) Small [Asteraceae]) is endemic to cedar glades of middle Tennessee, and limited to 5 population sites in an approximately 170 km² (66 mi²) area. Rarity is thought to be due to prehistoric factors and to ecological characteristics that limit the ability of the plant to colonize nearby glades. Protection of natural populations combined with the establishment of new populations and seed storage will greatly reduce the possibility of extinction. Several populations are now incorporated into natural areas. Moreover, since the plant is easily propagated, new populations have been established in middle Tennessee. Progress toward full recovery of the species has been successful.

KEY WORDS: rarity, narrow endemic, rare plant propagation, rare plant recovery

NOMENCLATURE: (plants) USDA NRCS (1999); (animals) ITIS (2001)

Tennessee purple coneflower (*Echinacea tennesseensis* (Beadle) Small [Asteraceae]) is known only from an approximate 170 km² (66 mi²) area in the Central (Nashville) Basin of Tennessee (Figure 1). The species was listed as federally endangered in 1979, and it was one of the first plants to be so designated (USFWS 1979; Somers 1983). In Tennessee, it is listed as endangered and is protected under the Rare Plant Protection and Conservation Act of 1985 (Nordman 1999). Rarity of the species is thought to be due more to natural causes than anthropogenic ones, and thus the species has probably always been limited to its present restricted geographical range (Somers 1983). As such, the plant would fit into the “small geographic range/narrow habitat specificity/locally abundant in a specific habitat” category of Rabinowitz’s (1981) 7 categories of rarity.

The purpose of our present paper is to review various aspects of the ecology and conservation of *E. tennesseensis*. Specifically, we examine the geographical distribution, habitats, systematic biology, phytotherapy, ecological life history, reproductive biology, ecophysiology, population structure and dynamics, and community ecology. Conservation-related items including possible causes of rarity, propagation, and recovery efforts also are discussed.

GEOGRAPHICAL DISTRIBUTION AND HABITATS

Echinacea tennesseensis was collected first by A. Gattinger in 1878 near LaVergne, Rutherford County, Tennessee, by H. Eggert in 1897 near LaVergne, and by R. McVaugh in 1936 (no location given, except Rutherford County) (McGregor 1968). McGregor (1968) was unable to locate any plants of *E. tennesseensis* between 1959 and 1961, and therefore, in his monograph of the genus he considered it possibly extinct. However, the species was known from a site in the LaVergne vicinity in 1967 (Hemmerly 1986). This site was developed into a trailer park in the early 1970s, and no *E. tennesseensis* plants have since been found. The precise place of the type locality is unknown, but it was suggested that the trailer park might have been the type locality (Quarterman and Hemmerly 1971; USFWS 1989).

In 1968, a population was reported from Davidson County, Tennessee (Baskin and others 1968), and then in 1970, a population was discovered in Wilson County, Tennessee (Quarterman and Hemmerly 1971). Two other populations were discovered in 1972 in Davidson County, but by 1975 they had been destroyed by residential development (USFWS 1989). It is also possible that some populations of this species might have been flooded when damming of Stones River created the J. Percy Priest Reservoir in the late 1960s; this area is near the center of distribution of *E. tennesseensis* (Kral 1983; Baskin 1993).

Presently, 5 extant population sites are known in Davidson, Rutherford, and Wilson counties (Figure 2). These 5 sites consist of 15 subpopulations (colonies, USFWS 1989) with 1 to 7 subpopulations per site (Shea 2000). In addition, 4 subpopulations of the species occur at Stones River National Battlefield in central Rutherford County (Figure 2). Two of the subpopulations at Stones River National Battlefield were planted, but the origins of the others are unknown (Hemmerly 1976; Hogan and others 1995). Although Small (1903, 1913, 1933) reported the species from Tennessee and Arkansas, Smith (1973) excluded it from Arkansas, and to our knowledge it is confined to Tennessee.

Echinacea tennesseensis is considered to be 1 of the 19 species of plants endemic to cedar glades of the southeastern US (Baskin and Baskin 1999). Cedar glades are rocky treeless areas dominated by herbaceous angiosperms and/or cryptogams that are usually surrounded by forest ecosystems which include eastern redcedar (*Juniperus virginiana* L. [Cupressaceae]), redcedar-hardwood, and hardwood communities (Figure 3). Within the Central Basin of Tennessee, glades occur primarily on outcrops of Ordovician-age Lebanon Limestone (Baskin and Baskin 1999). In addition to cedar glades, *E. tennesseensis* also grows in gravel along roadsides, in a gravel lot, in a fallow field with shallow soil, in a grazed pasture, on creek banks (USFWS 1989), in barrens (Drew 1991), and in sparse stands of *J. virginiana* (Kral 1983). Plants of *E. tennesseensis* grow in areas with mean soil depths of 5 to 12 cm (2 to 5 in) (Hemmerly 1976; Drew 1991).

SYSTEMATIC BIOLOGY

The taxon “*tennesseensis*” originally was considered to be black-samson echinacea (*E. angustifolia* DC.) by Gattinger (1887). Between 1841 and 1898, *E. angustifolia* was often synonymized with another species, pale purple coneflower (*E. pallida* Nutt. (Nutt.)), and together these 2 taxa were referred to as either *E. angustifolia* or *E. pallida* (or as *Brauneria pallida* (Nutt.) Britton) (Baskin and others 1993). Thus, thinking that *E. pallida*, which has long ray flowers, was *E. angustifolia*, and unfamiliar with the true short-rayed *E. angustifolia*, Beadle (1898) described the middle Tennessee plants with short rays as a new species (*Brauneria tennesseensis*). Baskin and others (1993) wondered whether *E. tennesseensis* would have been described if previous researchers had not made nomenclatural “blunders” in the taxonomy of *E. pallida* versus *E. angustifolia*.

Although Beadle (1898) placed “*tennesseensis*” in the genus *Brauneria*, Small (1933) reassigned it to the genus *Echinacea*. Since 1898, taxonomists have recognized the taxon at the (1) specific level in the genus *Brauneria* (Small 1903, 1913) or in the genus



Photo by Thomas E Hemmerly

Figure 1 • *Echinacea tenesseeensis* growing on a cedar glade in Davidson County, Tennessee.

Echinacea (Small 1933; McGregor 1968), or (2) varietal level (*E. angustifolia* var. *tenesseeensis* (Beadle) Blake; Blake 1929; Sharp 1935). However, others have recognized it as *E. angustifolia* (Fernald 1900; Dress 1961), as *B. angustifolia* (DC.) Heller (Robinson and Fernald 1908), as *B. pallida* (with *E. angustifolia* as a synonym, Gattinger 1901), or as “an eastern outlier” of *E. pallida* Nutt. var. *angustifolia* (DC.) Cronq. (Cronquist 1980; Gleason and Cronquist 1991).

Echinacea tenesseeensis is morphologically similar to *E. angustifolia* var. *angustifolia*, a species of dry prairies occurring from southeastern Saskatchewan and southern Manitoba to eastern Colorado and south central Texas (McGregor 1968; Baskin and others 1997). *Echinacea tenesseeensis* has a smaller stature, softer pubescence, smaller pollen grains, and more leafy stem than *E. angustifolia*. Moreover, the pinkish or purplish (rarely white) ray flowers of *E. tenesseeensis* are ascending rather than drooping (McGregor 1968; Foster 1991; Baskin and others 1993). The 2 species remained distinct in a common garden experiment (USFWS 1989) and both are genetically distinct based on allozyme electrophoresis (Baskauf 1993; Baskauf and others 1994). However, chemical constituents of *E. tenesseeensis* roots are similar to those of *E. angustifolia* (Bauer and others 1990). Both species are diploids ($n = 11$) (McGregor 1968; Robinson and others 1981; Baskin and others 1997) and can hybridize (Baskauf 1993; Baskin and others 1997).

Some data suggest that a closer relationship of *E. tenesseeensis* might exist with wavyleaf purple cone-

flower (*E. simulata* McGregor) than with *E. angustifolia*. *Echinacea simulata* ranges from Missouri to Indiana, south to Tennessee and Arkansas (USDA NRCS 1999). It is very similar to *E. pallida* differing primarily by yellow (versus white) pollen (McGregor 1968). Mean allozyme genetic identity was higher between *E. tenesseeensis* and *E. simulata* (0.918) than between *E. tenesseeensis* and *E. angustifolia* (0.826) (Baskauf 1993). Moreover, phylogenetic reconstructions (although largely unresolved) based on allozymes (Baskauf 1993), chloroplast DNA restriction site variation (Urbatsch and Jansen 1995), and combined internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA and chloroplast DNA restriction site variation (Urbatsch and others 2000) indicate *E. tenesseeensis* and *E. simulata* to be sister taxa. Clearly, additional phylogenetic studies are needed to better understand evolutionary relationships in the genus.

PHYTOTHERAPY

American Indians of the Plains group considered principally the eastern purple coneflower (*E. purpurea* (L.) Moench) and *E. angustifolia* to be a universal panacea (Foster 1991). They used them for such ailments as arthritis, snake bites, insect stings, sore throats, headaches, and toothaches; also for infectious diseases including colds, measles, mumps, and smallpox. As with other American medicinal plants, white settlers adopted the use of echinacea from the American Indians (Foster 1991). In the 19th century,

HCF Meyer, a self-taught physician, marketed "Meyer's Blood Purifier," later recognized to contain, among other ingredients, roots of echinacea. Though Meyer's claims for the nostrum were extravagant, Lloyd Brothers of Cincinnati made an echinacea preparation available that was widely prescribed. Dried rhizomes and roots of *E. angustifolia* and *E. pallida* were listed in the National Formulary between 1916 and 1950 (Vogel 1970). Early in the 20th century, the medicinal use of echinacea was introduced into Europe, where it soon became popular, especially in Germany. In that country, there are currently over 800 preparations containing the plant. Most of the products contain either above-ground parts of *E. purpurea* or root tinctures of *E. pallida* or *E. purpurea*. In the US, echinacea products are the best selling herbals in health food stores (Brevoort 1996).

The efficacy of echinacea products against bacterial and viral infections is a result of the stimulation of the nonspecific immune system (Bauer 1998; Robbers and Tyler 1999). A large number of active principles have been identified that have immunomodulatory activity; included is cichoric acid, alkamides, glycoproteins, and polysaccharides. Many recent placebo-controlled double-blind studies have confirmed the effectiveness of echinacea products, especially those of *E. purpurea* (Bauer 1998). As a result of such studies, German Commission E

approves the use of pressed juice from aerial parts of *E. purpurea* for the treatment of infections of the upper respiratory tract and lower urinary tract; also root tinctures from *E. pallida* for cold and flu-like infections. However, the value of echinacea products for the treatment of many other conditions, including yeast infections, arthritis, cancer, and others, remain unproven (Robbers and Tyler 1999).

Due to its scarcity and limited distribution, *E. tennesseensis* has been used in medicine much less frequently than the more abundant *Echinacea* species. At the time of European contact, few, if any, American Indians resided in central Tennessee (Pittard 1984). However, Gattinger (1894) listed it (as "*E. angustifolia*, occurring in cedar glades, infrequent" therefore, apparently *E. tennesseensis*) in his Medicinal Plants of Tennessee. It seems unlikely that the highly endemic plant was used for medicinal purposes to any appreciable extent. More recently, *E. tennesseensis* has been evaluated for its potential use in phytotherapy. It has been shown to lack phenol glycoside echinoside (Bauer and others 1990); also it did not exhibit antibacterial action against staphylococci (Hemmerly 1976). However, other compounds responsible for immunostimulation, including alkamides and caffeic acid, were found in *E. tennesseensis* (Bauer and others 1990). Pharmacological studies continue to ascertain any positive benefits of products from *E. tennesseensis*.

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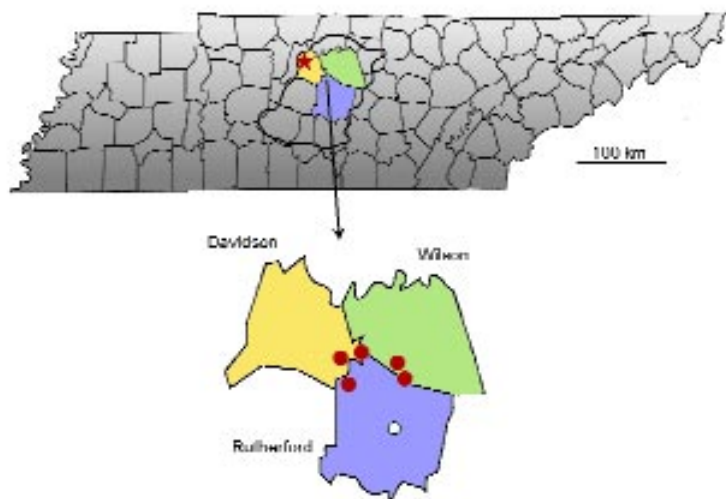


Figure 2 • Geographical distribution of *Echinacea tennesseensis*. The Central (Nashville) Basin of Tennessee is outlined in the upper part of the figure; star indicates the location of Nashville. The locations of the 5 known natural population sites (red circles) and the established site at Stones River National Battlefield (white circle) are shown in the bottom part of the figure. (Map modified from Chester and others 1997.)

ECOLOGICAL LIFE HISTORY AND REPRODUCTIVE BIOLOGY

Echinacea tennesseensis is a polycarpic perennial without vegetative reproduction (Snyder and others 1994). Growth of seedlings occurs primarily in April and May, with vegetative rosettes formed during the first growing season. Shoots senesce in autumn, and new leaves emerge in early spring with some plants flowering and setting achenes during the second growing season (Hemmerly 1986; Baskin and Baskin 1982; Drew and Clebsch 1995). Plants form an extensive root system during their first few years of growth. Mature plants have several main roots, each 25 to 50 cm (10 to 20 in) in length, which extend into the rocky cedar glade soil to depths of 10 to 30 cm (4 to 12 in), and spread laterally on solid bedrock (Hemmerly 1976). Individuals can live for at least 6 y; maximum lifespan is unknown (Baskauf 1993).

Flower buds are present on plants in late April. Anthesis begins in mid-May, reaches a peak during June and July, and is completed in October (Hemmerly 1976, 1986; Baskin and Baskin 1982). The species is a long-day plant, and vernalization is not required for flowering. The critical photoperiod for flowering is relatively short (<13 h and 11 min), and the onset of flowering in spring is delayed more by low temperatures than by daily photoperiod per se (Baskin and Baskin 1982). At anthesis, plants have 1 to 10 (up to 20) stems, usually about 40 cm (16 in) tall, with basally disposed leaves and general-

ly 1 flowering head per stem (McGregor 1968; Drew and Clebsch 1995).

Like other members of the genus (McGregor 1968), *E. tennesseensis* is self-sterile. Hemmerly (1976) determined experimentally that achenes were not produced when insects were excluded from flowers. The primary insect visitors are bumblebees (*Bombus* spp. [Hymenoptera: Apidae]), honeybees (*Apis mellifera* L. [Hymenoptera: Apidae]), and butterflies, such as the buckeye (*Junonia coenia* Huebner [Lepidoptera: Nymphalidae]), the sulfurs (*Colias* spp. [Lepidoptera: Pieridae]), and the whites (*Pieris* spp. [Lepidoptera: Pieridae]) (Hemmerly 1976; Drew 1991). Allozyme electrophoresis results indicate that *E. tennesseensis* is typical of other outcrossing plant species, with the inbreeding coefficient close to zero and the largest proportion of genetic variation within rather than among populations (Baskauf and others 1994).

Some achenes of this species mature by late July, and dispersal occurs primarily from mid-September to December with a few achenes remaining on the plants until the following spring. Plants produce many viable seeds each year, but those maturing in August produce a greater number of achenes than those maturing in July or September/October. A high percentage of the achenes fall within 50 cm (20 in) of the mother plant (Hemmerly 1976, 1986). Although Hemmerly (1976, 1986) reported very low seed predation, goldfinches (*Carduelis tristis* L. [Passeriformes: Fringillidae]) have been observed feeding on achenes (Drew 1991) and white-tailed deer (*Odocoileus virginianus* (Zimmermann) [Artiodactyla: Cervidae]) are known to graze on the mature flower heads of plants in a garden (USFWS 1989).

Achenes sown in autumn in the field or in an ambient-temperature greenhouse germinated in March and April of the following year. Numerous seedlings often emerge in mats of the square pleurochaete moss (*Pleurochaete squarrosa* (Brid.) Lindb. [Pottiaceae]) or under litter of poverty dropseed (*Sporobolus vaginiflorus* (Torr. ex Gray) Wood [Poaceae]). No germination occurred after the first (spring) germination period (Hemmerly 1986; Baskin and Baskin 1989; Snyder 1991). This indicates that the species likely does not form a persistent soil seed bank.

ECOPHYSIOLOGY

At maturity, a high percentage of *E. tennesseensis* achenes have nondeep physiological dormancy (Hemmerly 1976, 1986; Baskin and others 1993, 1997). Dormancy is broken during autumn and winter in the field or during several weeks of cold stratification at 5 °C (41 °F) in the laboratory. Achenes germinate first at intermediate temperatures (alternating 25 and 15 °C [77 and 59 °F]), and the maximum and minimum temperature increases and decreases, respectively, as they come out of dormancy. Nondormant

achenes germinate over a wide range of constant (15 to 35 °C [59 to 95 °F]) and alternating (15 and 6 °C to 35 and 20 °C [59 and 43 °F to 95 and 68 °F]) temperatures, with a higher percentage of them germinating in light than in darkness (Hemmerly 1976, 1986; Baskin and others 1993, 1997). A very low percentage of fresh achenes germinate without stratification, but seedlings from autumn-germinating achenes did not survive winter in an ambient-temperature greenhouse in Lexington, Kentucky. Dry storage up to 5 y under laboratory conditions and treatments with chemicals (for example, nitrogen-containing compounds or gibberellic acid) did not effectively break dormancy (Hemmerly 1976).

Echinacea tennesseensis utilizes the C₃ (non-Kranz) photosynthetic pathway (Hemmerly 1976; Baskin and Baskin 1985). Maximum photosynthetic rate was about 10 μmol CO₂/(m²•s), and light saturation of photosynthesis occurred at high light levels (full sun) (Baskauf and Eickmeier 1994). Net assimilation rate over the growing season was 0.52 mg/(cm²•d) (Snyder and others 1994). The values for maximum photosynthetic rate and net assimilation rate are low compared to typical rates for herbaceous heliophytes (Larcher 1995). However, the photosynthetic rate of *E. tennesseensis* did not differ from that of other glade species or of *E. angustifolia* (Baskauf 1993). Dark respiration [about 0.5 μmol CO₂/(m²•s)] and maximum transpiration [about 3.3 mmol H₂O/(m²•s)] of *E. tennesseensis* were below those recorded in other herbaceous heliophytes, but water-use efficiency [about 1.2 mmol CO₂/mol H₂O] was similar to that in other C₃ plants (Nobel 1991; Baskauf 1993; Baskauf and Eickmeier 1994; Larcher 1995).

Relative growth rate for the entire growing season under greenhouse conditions was 0.038 g/(g•d), which is somewhat low compared to other herbaceous heliophytes. Near the end of the growing season, mature plants of *E. tennesseensis* allocated approximately 35% dry biomass to shoots and 65% to roots. The root to shoot ratio was about 2.0 (Snyder 1991; Snyder and others 1994).

Light and soil moisture conditions are important environmental factors influencing growth and flowering of *E. tennesseensis*. Since plants of this species are shade intolerant, they do not grow in the woods beyond the edges of glades (Hemmerly 1976; Baskauf 1993). Plants grown under high-light conditions [800 to 1500 μmol/(m²•s) at noon] in a greenhouse produced more (root, shoot, and total) biomass, greater number of leaves, and shorter leaves, and had higher survivorship and flowering than those grown under low-light conditions [100 to 200 μmol/(m²•s)]. The light level in the low-light treatment was similar to that under the woodland canopy near a glade edge, 50 to 190 μmol/(m²•s) (Baskauf 1993). *Echinacea ten-*

nesseensis tolerates a wide range of soil moisture conditions in the field, but high moisture levels are best for growth and flowering. Low moisture levels under greenhouse conditions decreased biomass and photosynthesis of plants. In the field, photosynthesis was lowest on the driest sampling date and shoots may partially or completely die during droughts (Baskauf 1993; Baskauf and Eickmeier 1994).

POPULATION STRUCTURE AND DYNAMICS

The estimated number of *E. tennesseensis* plants in 1987 per population site ($n = 5$) ranged between 3700 and 89,300 covering an area from 470 to 13,860 m² (562 to 16,576 yd²). Density varied between 6.2 and 20.7 plants/m² (5.2 to 17.3 plants/yd²) (Drew 1991; Drew and Clebsch 1995). Plant density tends to be highest along the glade and woodland edge (Drew 1991; Baskauf 1993), and a gradient from the western (high density) to the eastern (low density) edge was found in 1 glade (Baskauf 1993). Although plants in the center of this glade received the most hours of light, and soil was deeper along the glade edges than in the middle, soil depth was similar for both edges. Moreover, there was no correlation of soil moisture with the density of *E. tennesseensis*, except on 1 sampling date when soil on the western edge of the glade was more moist than that in the center or on the eastern edge (Baskauf 1993). Likewise, Hemmerly (1976) found that soil depths did not differ appreciably between quadrats with *E. tennesseensis* plants as compared to those without this species.

Stage class distributions (determined by total leaf length and number of flowering heads) were similar among 4 sites, that is, the number of small (nonflowering) plants exceeded that of large (flowering) ones. However, the stage class distribution of the fifth site had more moderate-sized plants than either small or large plants suggesting high mortality among seedlings and/or juveniles. The ratio of nonflowering to flowering plants varied from 1.6 to 4.8 among the 5 population sites. Mortality decreased with increased leaf length (plant size) among nonflowering plants, and also decreased with increased number of flowering heads among flowering plants (Drew 1991; Drew and Clebsch 1995).

Seedlings and juveniles can experience high mortality, especially during droughts. Drew and Clebsch (1995) found that nonflowering plants with a total leaf length of ≤ 30 cm (12 in) had only a 50% chance of surviving the extreme summer drought of 1988, whereas those with a total leaf length of ≥ 31 cm (12 in) and all flowering plants had an approximate 70% to 85% chance. Baskauf (1993) noted only 2% of 417 seedlings and juveniles observed in permanent quadrats in spring 1990 were still alive in autumn 1990, and none of 19 observed in spring

1991 were alive in autumn 1991. On the other hand, during a time of normal rainfall 68% of plants marked as seedlings in spring 1971 were still alive in August 1972 (Hemmerly 1976). Hemmerly also observed that seedling survivorship tends to increase with increased soil depth.

Flowering is also dependent on the amount of rainfall during a particular growing season. Forty-one percent of the plants that flowered during the 1987 growing season with normal rainfall failed to do so during the exceedingly dry summer of 1988. However, 68% of the plants that did not produce flowers in 1988 did so when rainfall conditions returned to normal during the 1989 growing season (Drew and Clebsch 1995).

COMMUNITY ECOLOGY

Hemmerly (1976) listed 47 vascular plant associates of *E. tennesseensis* at 2 population sites; 16 of the taxa were present at both sites. Species occurring most frequently with *E. tennesseensis* were broomsedge bluestem (*Andropogon virginicus* L. [Poaceae]), hogwort (*Croton capitatus* Michx. [Euphorbiaceae]), purple tassels (*Dalea gattereri* (Heller) Barneby [Fabaceae]), roundseed St Johnswort (*Hypericum sphaerocarpum* Michx. [Clusiaceae]), cleft phlox (*Phlox bifida* Beck ssp. *stellaria* (Gray) Wherry [Polemoniaceae]), browneyed susan (*Rudbeckia triloba* L. [Asteraceae]), and *Sporobolus vaginiflorus*. Species composition was about the same in quadrats with and without *E. tennesseensis*.

Fifty-nine vascular plant taxa were recorded with *E. tennesseensis* at all 5 population sites (Drew 1991; Drew and Clebsch 1995; also see Baskin and Baskin 1999). Vegetation of 4 sites was similar, but species composition at the fifth site differed apparently reflecting human disturbance. Narrowleaf gumplant (*Grindelia lanceolata* Nutt. [Asteraceae]) had the highest importance value (based on cover and frequency) at 1 site, and diamondflowers (*Hedyotis nigricans* (Lam.) Fosberg [Rubiaceae]) and *Sporobolus vaginiflorus* at 2 sites each. *Sporobolus vaginiflorus* had the highest importance value averaged over all 5 sites, followed by *E. tennesseensis*. *Echinacea tennesseensis* was an important component of the vegetation at 3 sites. Other important species included *Dalea gattereri*, *Hypericum sphaerocarpum*, fluxweed (*Isanthus brachiatus* (L.) B.S.P. [Lamiaceae]), fringeleaf wild petunia (*Ruellia humilis* Nutt. [Acanthaceae]), little bluestem (*Schizachyrium scoparium* (Michx.) Nash [Poaceae]), whorled rosinweed (*Silphium trifoliatum* L. [Asteraceae]), and lavender oldfield aster (*Symphotrichum priceae* (Britt.) Nesom [Asteraceae]). Six communities were described and named according to the dominant plant taxon/taxa. The communities were: *E. tennesseensis*, *E. tennesseensis*–*R. humilis*, *E. tennesseensis*–*S. scoparium*, *H. nigricans*–*S. vagini-*

florus, *S. vaginiflorus*–*D. gattereri*, and *S. scoparium*–*H. nigricans*. Total vegetation cover associated with *E. tennesseensis* was low (39% to 58%) at all population sites. Frequency and cover of *E. tennesseensis* among the 5 sites were 48% to 77% and 2% to 12%, respectively. Ranges in mean percentage cover of various substrates were: bare soil, 14 to 42; gravel, 37 to 72; flagstone, 0 to 7; bedrock, 0; witch's butter (*Nostoc commune* Vaucher [Nostocales:Nostocaceae]), 0 to 1; bryophyte, 0 to 12; lichen, 0; and litter, 14 to 23.

The vegetation of 10 cedar glades, 3 of which contained *E. tennesseensis*, was sampled by Somers and others (1986). They identified 7 glade communities that differed in soil depth and named them according to the dominant taxon/taxa. *Echinacea tennesseensis* was recorded in 4 of them: *Dalea gattereri*, *Nostoc commune*–*Sporobolus vaginiflorus*, *Pleurochaete squarrosa*, and *S. vaginiflorus*. *Echinacea tennesseensis* had a frequency of 2.5% and cover of 0.5%. The plots in which *E. tennesseensis* occurred were farther from the glade/woodland edge, higher in cover of gravel, and had less moss, plant litter, and bare soil than plots in which the species was absent.

A correlation analysis was used to evaluate plant associations with *E. tennesseensis* at 1 population site (Baskauf 1993). None of 19 vascular plant species showed a significant positive correlation with *E. tennesseensis*, but *D. gattereri* had the strongest positive one. There were more species with negative rather than positive correlations. However, only *Hypericum sphaerocarpum* and glade violet (*Viola egglesonii* Brainerd [Violaceae]) had a significant negative association.

Competitive interactions have been investigated between *E. tennesseensis* and two of its associates: *Sporobolus vaginiflorus* (Hemmerly 1976, 1986) and *Schizachyrium scoparium* (Snyder 1991). In a growth chamber experiment, seedlings and juveniles of *E. tennesseensis* were grown with and without clipped or unclipped *S. vaginiflorus* seedlings/juveniles on a 2-, 4-, and 8-d watering schedule. Dry biomass of roots and shoots of *E. tennesseensis* plants grown with unclipped *S. vaginiflorus* was reduced at the 3 watering regimes, but that of plants grown with clipped *S. vaginiflorus* was reduced only at the 2-d watering regime (Hemmerly 1976). In the field, however, more seeds of *E. tennesseensis* germinated and more plants survived in plots containing *S. vaginiflorus* and *D. gattereri* or containing *S. vaginiflorus* only than in plots dominated by *D. gattereri* alone or in those lacking vegetation (Hemmerly 1986). Snyder (1991), using a de Wit (1960) replacement series experiment, grew *S. scoparium* with *E. tennesseensis* under greenhouse conditions at a density of 6 plants per pot for 154 d. Both the relative yield and aggressivity index indicated that *S. scoparium* was far more aggressive than *E. tennesseensis*.



Figure 3 • A cedar glade at Stones River National Battlefield, Rutherford County, Tennessee with an established population of *Echinacea tenesseeensis*. This population was planted by T Hemmerly in the early 1970s.

Photo by Thomas E Hemmerly

Allelochemical interactions have been studied under laboratory conditions (Hemmerly 1976, 1986). The following conclusions were reached: (1) litter from *Dalea gattingeri* and extracts of *Juniperus virginiana* inhibited germination of *E. tenesseeensis* seeds, and (2) extracts of *E. tenesseeensis* inhibited germination of *D. gattingeri*, *Ruellia humilis*, slimspike threeawn (*Aristida longespica* Poir. [Poaceae]), and purple lovegrass (*Eragrostis spectabilis* (Pursh) Steud. [Poaceae]) seeds but stimulated germination of its own seeds. Whether these various effects observed in Petri dishes are of importance in the field is unknown.

POSSIBLE CAUSES OF ENDEMISM

Rarity of *E. tenesseeensis* is not thought to be due exclusively to anthropogenic causes, as only a few populations are known to have been destroyed by humans (Somers 1983). Thus, several studies have sought to understand the potential natural causes of rarity in *E. tenesseeensis* by comparing its biology with the closely-related, geographically widespread congeners *E. angustifolia* var. *angustifolia* and/or *E. pallida*.

The hypothesis that plants of *E. tenesseeensis* have a more narrow physiological tolerance than those of *E. angustifolia* was tested by Baskauf and Eickmeier (1994; also see Baskauf 2001). They examined the photosynthetic response of each species, following various light and soil moisture preconditioning regimes, over a range of photosynthetic photon irradi-

diances and temperatures in a growth chamber. However, no differences were found between the 2 species in the instantaneous rates of photosynthesis or dark respiration based on leaf area.

The competitive ability of *E. tenesseeensis* was compared to *E. angustifolia* and *E. pallida* using a multiple de Wit (1960) replacement series experiment (Snyder and others 1994). All pairwise combinations of the 3 taxa were grown under greenhouse conditions at several densities (8, 12, 16 plants per pot) for 175 d. The hierarchy of competitive ability (based on relative yield and aggressivity) was *E. pallida* > *E. tenesseeensis* > *E. angustifolia*. Differences in competitive abilities were not related to relative growth rate, net assimilation rate, leaf area ratio, specific leaf weight, root to shoot ratio (Snyder and others 1994), seed size, or germination phenology (Baskin and others 1997). Plant size was the best predictor of competitive ability. The habitat of *E. pallida* includes mesic tallgrass prairie communities, whereas the other 2 species occur in the dry prairie (*E. angustifolia*) or cedar glade (*E. tenesseeensis*) community. Thus, competition would be expected to be more intense in tallgrass prairies than the stressful dry prairies or cedar glades (Snyder and others 1994).

Baskauf and others (1994; also see Baskauf 2001) found that *E. tenesseeensis*, based on allozyme electrophoresis, had substantially less genetic variability than *E. angustifolia* at both the species and population levels. Expected heterozygosity and per-

centage of polymorphic loci were about twice as great for *E. angustifolia* than for *E. tennesseensis*, and *E. angustifolia* had a higher number of alleles per locus than *E. tennesseensis*. However, *E. tennesseensis* is not entirely devoid of variability. Fluctuations in population size or extinction and colonization events might have occurred historically and decreased genetic variability in *E. tennesseensis* (Baskauf and others 1994) or the species might never have had much genetic variability originally.

A comparison via an in-depth literature review of various morphological, physiological, ecological, and life history characteristics of *E. tennesseensis*, *E. angustifolia*, and *E. pallida* did not reveal any outstanding differences in their general biologies that might account for the narrow endemism of *E. tennesseensis* (Baskin and others 1997). Baskin and others (1997) relied on historical and ecological factors to reach an explanation for the development and maintenance of narrow endemism in *E. tennesseensis*. They suggested that the origin of *E. tennesseensis* was connected with the climatic warming and drying trend of the Hypsithermal Interval. In middle Tennessee during the Hypsithermal (about 8000 to 5000 y before present), the number and areal extent of cedar glades increased, mesic deciduous forests became open and dominated by more xeric species, and an influx of prairie species, and presumably *E. angustifolia*, took place (Klippel and Parmalee 1982; Delcourt and others 1986). Temperatures became cooler, rainfall increased, and closed mesic deciduous forests returned to the area as the Hypsithermal ended, and only plants of *E. angustifolia* growing in the cedar glades survived. This presumed ancestral species apparently gave rise to *E. tennesseensis*. However, *E. tennesseensis* occurs on only a few of the many glades in middle Tennessee probably due to its poor colonization ability. For example, plants of this species produce large achorous seeds, are self sterile, are shade intolerant, have no vegetative reproduction, do not form a persistent soil seed bank, and have relatively high seedling and juvenile mortality (Hemmerly 1986; Drew and Clebsch 1995; Baskin and others 1997).

PROPAGATION

Growing *E. tennesseensis* from seeds to the flowering stage is relatively easy. The optimum conditions necessary for maximum seed germination is a 12 or 16-wk (moist) stratification treatment at 5 °C (41 °F) followed by incubation in light at 15 °C (59 °F) or at 25 °C (77 °F) (Hemmerly 1986; Snyder 1991). Once germinated, seedlings grow on a variety of soil (or gardening) substrates in the greenhouse or garden but best in full sun (Baskauf 1993). Plants form a rosette the first year of growth and flower the second year in both the field and greenhouse (Baskin and Baskin

1982; Drew and Clebsch 1995). Banrot® has been used to control damping-off fungi, Dipel® for cabbage loopers (*Trichoplusia ni* (Hübner) [Lepidoptera: Noctuidae]), and an (unspecified) insecticide for thrips (Thysanotera) in the greenhouse (Baskauf 1993; Snyder and others 1994).

Seeds of *E. tennesseensis* are available through several commercial nurseries that are licensed to sell the plant (USFWS 1989; Snyder 1991; Foster 1991). Caution should be taken when growing *E. tennesseensis* in gardens with other species of *Echinacea* as hybridization can occur, for example, with *E. purpurea* (USFWS 1989). When ordering *E. tennesseensis* it should be kept in mind that the stock may not be “pure” if it was simultaneously grown with other species of *Echinacea* at the nursery. Plants have been grown at such places as a botanical garden and a nature center in Nashville, Tennessee, and at the Missouri Botanical Garden. Publicity on the species has had a positive educational value. It has led to the discovery of new subpopulations, and there are no known adverse effects of the publicity (USFWS 1989).

RECOVERY EFFORTS

The largest threat to *E. tennesseensis* is the destruction of habitat by development for residential housing, industrial facilities, or roads (Quarterman and Hemmerly 1971; USFWS 1989). The species grows on glades in which heavy equipment operation, off-road-vehicle use, and trash dumping have occurred. Once, a large number of plants was removed from a site. High mortality of small (juvenile) plants at 1 site was suggested to be caused by competition with weedy species (USFWS 1979; Drew and Clebsch 1995).

Protection of natural populations, seed storage, and establishment of new populations will reduce the threat of extinction for *E. tennesseensis* (Somers 1983; Baskauf and others 1994). Five of the 15 (natural) subpopulations are located in state natural areas managed by the Tennessee Department of Environment and Conservation and/or Tennessee Division of Forestry, one is in a preserve owned by The Nature Conservancy, and one is in a state park. The other subpopulations are on private land, and agreements have been made (or negotiations are currently underway) with the owners to preserve the plants on several of these private properties. For instance, the owner of an industrial facility fenced the area around the population of plants on the property and cleared away debris (USFWS 1989; Shea 2000).

In most cases, the glade habitat will need little (if any) management to maintain it (Baskin and others 1994), that is, succession is extremely slow or nonexistent. However, some plants grow in areas that are in a seral stage of secondary succession, and thus, some form of disturbance might be needed to maintain the openness of the habitat. Experiments to remove

woody vegetation by prescribed burning and mowing are currently being conducted (Shea 2000). Plants can tolerate a limited level of disturbance, since some of them occur at sites in which mowing and grazing by cows and horses have taken place. The coneflowers were not browsed in preference to other plants (Hemmerly 1976; USFWS 1989). Population increases due to soil disturbance have been noted (Drew 1991).

Representative material from all known subpopulations have been placed into cultivation, and seeds are maintained at the National Seed Storage Laboratory in Ft Collins, Colorado (USFWS 1989). Fifteen subpopulations have been established in glades primarily on state forest, state park, and US Army Corps of Engineers property close to preexisting (natural) subpopulations, and additional plants have been added to a few natural subpopulations (USFWS 1989). As mentioned earlier, 4 subpopulations now occur at Stones River National Battlefield (Figure 3). The source of seeds used to establish new populations does not need to be a critical concern since populations have a low level of genetic differentiation (Baskauf and others 1994). Moreover, no detectable population site differences were found in seedling and juvenile survivorship in a reciprocal transplant experiment, indicating little (or no) local adaptation (Hemmerly 1976).

The species will be considered recovered when there are "... at least five secure wild populations, each with three self-sustaining colonies [subpopulations] of at least minimal size" (USFWS 1989). A subpopulation is self-sustaining when the ratio of juvenile to flowering plants is two. Minimal size is defined as 15% cover of plants over a 669 m² (800 yd²) area of suitable habitat. Percentage cover, area of population, and ratio between juvenile and adult plants are based on estimates taken from the 2 largest existing subpopulations in the least disturbed habitats. Reclassification to the status of threatened will be considered when each population has at least 2 self-sustaining subpopulations (Somers 1983; USFWS 1989). Recovery of the species has progressed well since it was federally listed in 1979, and it will probably be recommended for reclassification in the near future (Shea 2000).

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