A DEMOGRAPHIC AND ECOLOGICAL ANALYSIS OF *GEOCARPON MINIMUM* (CARYOPHYLLACEAE): A FEDERALLY THREATENED SPECIES IN SOUTHWEST MISSOURI

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ABSTRACT

A *Geocarpon minimum* population growing on a sandstone glade in Dade County, Missouri was monitored for ten years (1994–2003). Plants were counted annually in eight permanent plots at two scales (0.01 and 1.0 m^2) to determine population fluctuations through time. Soil depths as well as cover of bryophytes, lichens, vascular plants, and bare rock/soil were recorded in subplots between 1994 and 2000 to determine any possible association with *G. minimum* numbers. The number of *G. minimum* plants in the eight plots varied from 1 to 4230, with a mean of 1332. Mean soil depth of subplots containing *G. minimum* was 19 mm. There was a weak association ($r_s = 0.16$, $P < 0.001$) between soil depth and *Geocarpon* density. Regression analyses show that *G. minimum* numbers tend to increase with increasing soil depth to about 20 mm and decline thereafter. In addition, there were significant differences among vegetation types ($P < 0.05$) with the exception of lichens ($P \geq 0.05$). There was a significant difference between *G. minimum* population numbers and year ($P < 0.05$). There was discontinuity with scale and the Spearman rank correlations, however, when ecological groups were combined into larger categories (i.e., lichens and bryophytes were lumped into cryptogams), patterns were clearer across scales. Documentation of bare rock areas indicates a dynamic process of soil movement into and out of plots, but cover data did not indicate a consistent increase in coverage of moss, vascular plants, or lichens during the ten years of the study. It is concluded that *G. minimum* utilizes habitats with periodic soil disturbance and with minimal competition from bryophytes or perennial vascular plants. Although seed bank was not a subject of this study, its importance was evident from annual census data that showed the population is capable of rebounding dramatically following years with virtually no seed production.

RESUMEN

Una población de *Geocarpon minimum* fue monitoreada durante diez años (1994–2003) en un afloramiento de arenisca y suelo poco profundo en el condado de Dade en el estado de Missouri. Para determinar la fluctuación del número de plantas en la población durante el período de estudio, las plantas se contaron anualmente en ocho parcelas permanentes usando dos escalas (0.01 y 1.0 m^2). Durante los años 1994 hasta el 2000 fueron evaluados datos sobre profundidad de suelo, cobertura de briofitas, líquenes, plantas vasculares y área de tierra o rocas sin plantas en subparcelas con el propósito de determinar la posible asociación de estas variables con el numero de plantas de *G. minimum*. El número de plantas de *G. minimum* en las ocho parcelas varió de 1 a 4230 con un promedio de 1332. La profundidad promedio del suelo de las subparcelas con *G. minimum* fue de 19 mm. La asociación entre la profundidad de suelo y densidad de plantas de *Geocarpon* fue mínima ($r_s = 0.16$, $P < 0.001$). El análisis de regresión demostró que el número de *G. minimum* parece aumentar a medida que la profundidad de suelo alcanza los 20 mm y disminuye a mayor profundidad. Además, la diferencia entre tipos de vegetación ($P < 0.05$), con excepción de los líquenes ($P \geq 0.05$), fue significativa. La diferencia fue significativa también entre el número de plantas de *G. minimum* y el año del muestreo ($P < 0.05$). Se observó una discontinuidad entre escala y las correlaciones de rango de Spearman, sin embargo, al combinar los grupos ecológicos en categorías mayores (por ejemplo, los líquenes y las briofitas se unieron en la categoría de las criptógamas), los patrones fueron más claros a través de las escalas. La documentación sobre áreas de afloramiento de rocas indica la existencia de un proceso dinámico de movimiento del suelo dentro y fuera de las parcelas, pero los datos sobre cobertura no indican un crecimiento constante de cobertura de musgos, plantas vasculares o líquenes durante los diez años del estudio. La conclusión es que *G. minimum* utiliza hábitats de suelos que están cambiando constantemente y tienen poca competencia de briofitas y plantas perennes vasculares. Aunque el banco de semillas en el suelo no se investigó

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en este estudio, su importancia fue evidente. En base a los datos anuales, esta población de *G. minimum* tiene la capacidad para reproducirse considerablemente en años siguientes aunque no exista producción de semilla en años anteriores.

INTRODUCTION

Geocarpon minimum Mack. (Caryophyllaceae) is a tiny, succulent winter annual that grows on sandstone glades in Missouri, on saline soil prairies in Arkansas and Louisiana (U.S. Fish and Wildlife Service 1993; McInnis et al. 1993; Orzell & Bridges 1987), and on saline barrens in Texas (Keith et al. 2004) (Fig. 1). The diminutive height of the plant (up to 4 cm), its inconspicuous flowers, and its limited distribution are probably responsible for it not having been described until 1914 (Mackenzie 1914). Taller plants are usually multi-stemmed and many-flowered. The smallest plants are only a few mm in height and produce just one flower. Both morphologies are often present in a single population, requiring surveyors to acquire a broader search image to locate the full range of plant forms. Plants turn from a whitish-green to wine-colored to light brown as they mature and senesce.

Geocarpon minimum was designated by the U.S. Fish and Wildlife Service as a federally threatened species in 1987 because of low population numbers (U.S. Fish and Wildlife Service 1987). It is known today from fewer than 35 sites (Nienaber 2005). Twenty-four extant Missouri populations are known from Pennsylvanian-age sandstone glades in seven southwestern counties, giving it a state rank of S2 (Missouri Dept. of Conservation 2006). The sandstone glades occur in the Springfield Plain subsection of the Ozark Highlands ecological section and are considered imperiled (a rank of S2) because of their rarity within the state (Nelson 2005). *G. minimum* is considered extirpated from its type locality, Jasper County, Missouri, where suitable habitat may have been lost due to land-use changes.

Prior to this study, little was known about the management requirements for maintaining populations of *G. minimum* or the range of year-to-year population fluctuations. Several sites for the species occur on public lands where lack of information has led to a lack of management action. There was concern that some periodic disturbance might be necessary to maintain suitable microhabitat for *G. minimum*. On many of the glades where the species occurs, the thin soil near the rock/soil interface is dominated by dense mats of moss, except where trampling, off-road vehicle use, or water flow have maintained areas of loose sand. The purpose of this study was to gather long-term monitoring data that could provide needed insights for effective management of *G. minimum* populations. Specific objectives of this study were to:

1) provide a long-term census of *G. minimum* at the Flint Hills Glade site,

2) determine the correlation of bryophytes, lichens, vascular plants, and soil depth on the *G. minimum* population,

3) provide management recommendations for the conservation of this species.

MATERIALS AND METHODS

Study Site

The study site, Flint Hill Glades, is located in Dade County, Missouri, near Stockton Lake, on land owned and managed by the U.S. Army Corps of Engineers (Fig. 2). *Geocarpon minimum* was discovered at Flint Hill Glades during a 1989 survey for the species (Thurman & Hickey 1989). The site is atypical in one respect; the impoundment of Stockton Lake inundated the creek valley below the glade and floods the lower portions of the glade during extremely high lake levels, which occurred during the summer of 1993.

FIG. 1. *Geocarpon minimum* plant. Photo by Rick Thom

It is estimated that less than five-percent of the six-acre glade area is suitable habitat for *G. minimum*, which grows in greatest abundance in shallow sand- and pebble-filled depressions in the sandstone bedrock that are often devoid of other plants (Fig. 3). Based on research at another Dade County site, Morgan (1986) reported that optimum habitat was found in zones of shallow soils (1–5 cm) over sandstone bedrock. These microhabitats are maintained by flow of water over the bedrock that deposits sand and pebbles into the depressions. Water flow can also carry away previous deposition and prevent lichen or vascular plant succession. An intermittent drainage flows through the study site carrying runoff from adjacent grazed pasture on private property into Stockton Lake at the lower edge of the glade.

Much of the surface bedrock is covered by a thick mat of mosses (principally *Polytrichum ohiense* Ren. & Card.) intermixed with lichens, liverworts, and a few vascular plant species. Areas of deeper soil within the glade support grasses, shrubs (e.g. *Vaccinium arboreum* Marshall) and dwarfed trees (e.g. *Quercus marilandica* Muenchh. and *Amelanchier arborea* (F. Michx.) Fernald). *Geocarpon minimum* plants were observed in the grazed portion of the glade on adjacent private land during the course of this study. They are found only near a bedrock exposure where pasture grasses are not established. The dense beds of moss found on the study site are not present in the pasture. The trampling from cattle may help to maintain the loose sand particles that accumulate to form *G. minimum* microhabitats. The pasture area may be a source of *G. minimum* seed for the monitoring area. No monitoring plots were established in the pasture, primarily because cattle grazing is not viewed as a realistic management tool for most publicly-owned sites.

Data Collection
Ten plots were established at the site in April 1994. The 1.0 m × 1.0 m quadrats were sub-
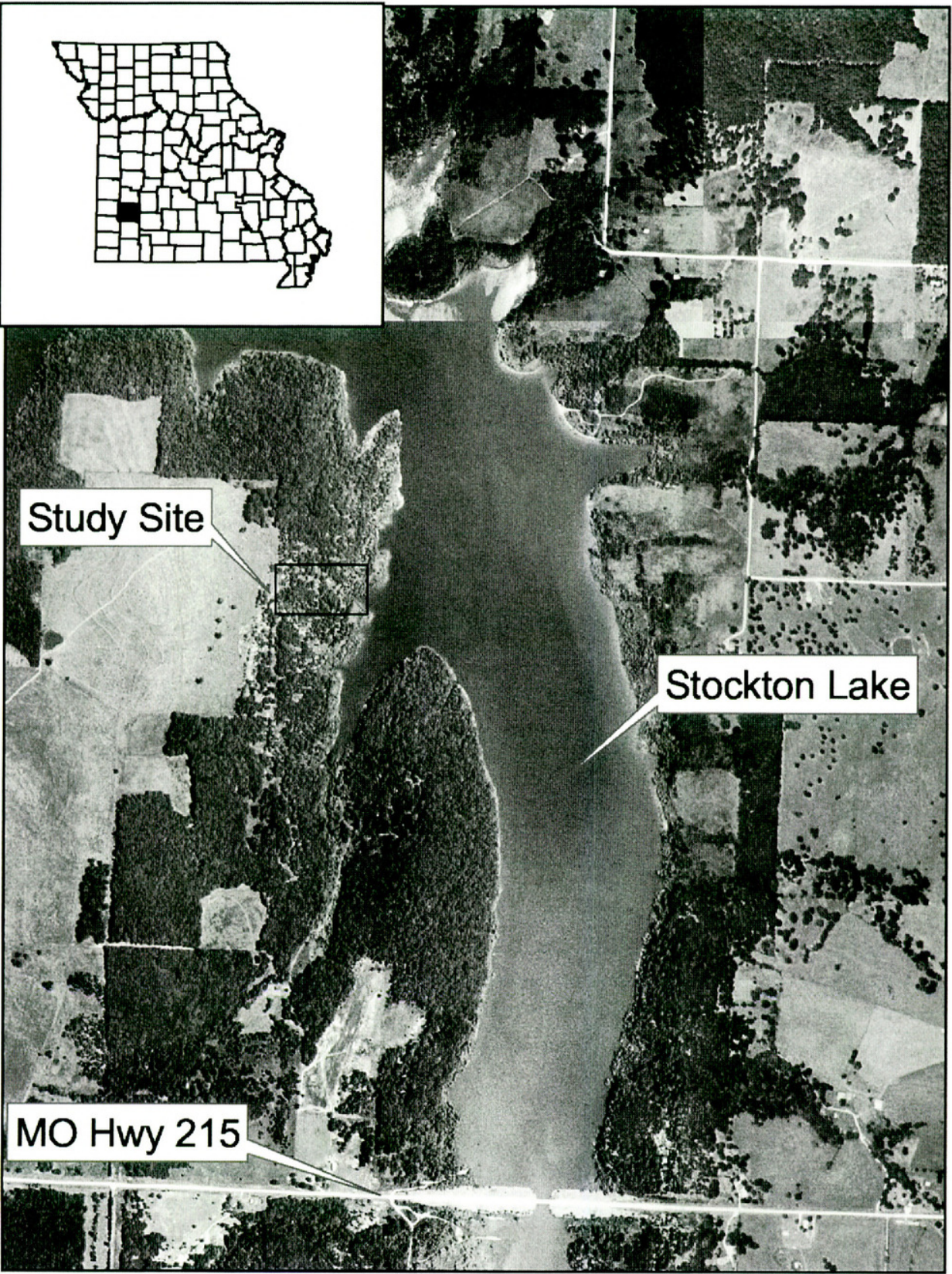
FIG. 2. Aerial photograph of Flint Hill Glade system, Stockton Lake, Dade County, Missouri.

jectively located in areas containing *G. minimum* in close proximity to areas dominated by mosses, lichens, or perennial vascular plants. Two opposite corners of each plot were marked by masonry nails driven into holes that were drilled into the bedrock.

Two of the original ten plots eventually were dropped from the study because they

Fɪɢ. 3. Habitat at Flint Hill Glades. Photo by Tim Smith.

did not support any *G. minimum* after 1994. Inundation of part of the glade in 1993 created temporary habitat in these plots due to silt and sand deposition with little vegetative competition. At one plot, sand and silt was deposited into a patch of bryophytes on bedrock, temporarily providing habitat that supported *G. minimum*. The bryophytes had been killed by the prolonged inundation and were soon gone, leaving only bare rock at subsequent surveys. The other plot was located near the lake shore and included essentially bare sand after the inundation, although it had deep enough soils to support perennial vascular plants. Although *G. minimum* was found in the plot when it was established in 1994, this plot thereafter became covered with debris from subsequent rises in the lake level and no longer contained exposed sand or *G. minimum*.

A 1 m × 1 m (1.0 m²) wooden frame was used to monitor the permanent plots. Fly-fishing line was strung on the inside of the quadrat to further subdivide the 1.0 m² plots into 100 subplots of 10 cm × 10 cm (0.01 m²). The number of *G. minimum* plants was recorded in each subplot. Soil depth was measured at the center of each subplot by using a nail to probe to bedrock and then measuring the length of the nail that had entered the soil. Bare rock was recorded as zero soil depth. Vegetative cover was estimated using seven cover classes (a modified Daubenmire cover class) and dominant cover was characterized as mosses, lichens, vascular plants or bare rock/soil (Daubenmire 1959) The seven cover classes were: 1 (0–1%), 2 (1–5%), 3 (5–25%), 4 (25–50%), 5 (50–75%), 6 (75–95%) and 7 (95–100%).

In the spring of 1995, three additional plots were established within the study area, in moss-dominated areas that did not contain *G. minimum*. These plots were created by removing a 1 m × 1 m section of dense moss to expose underlying mineral soil or bed-
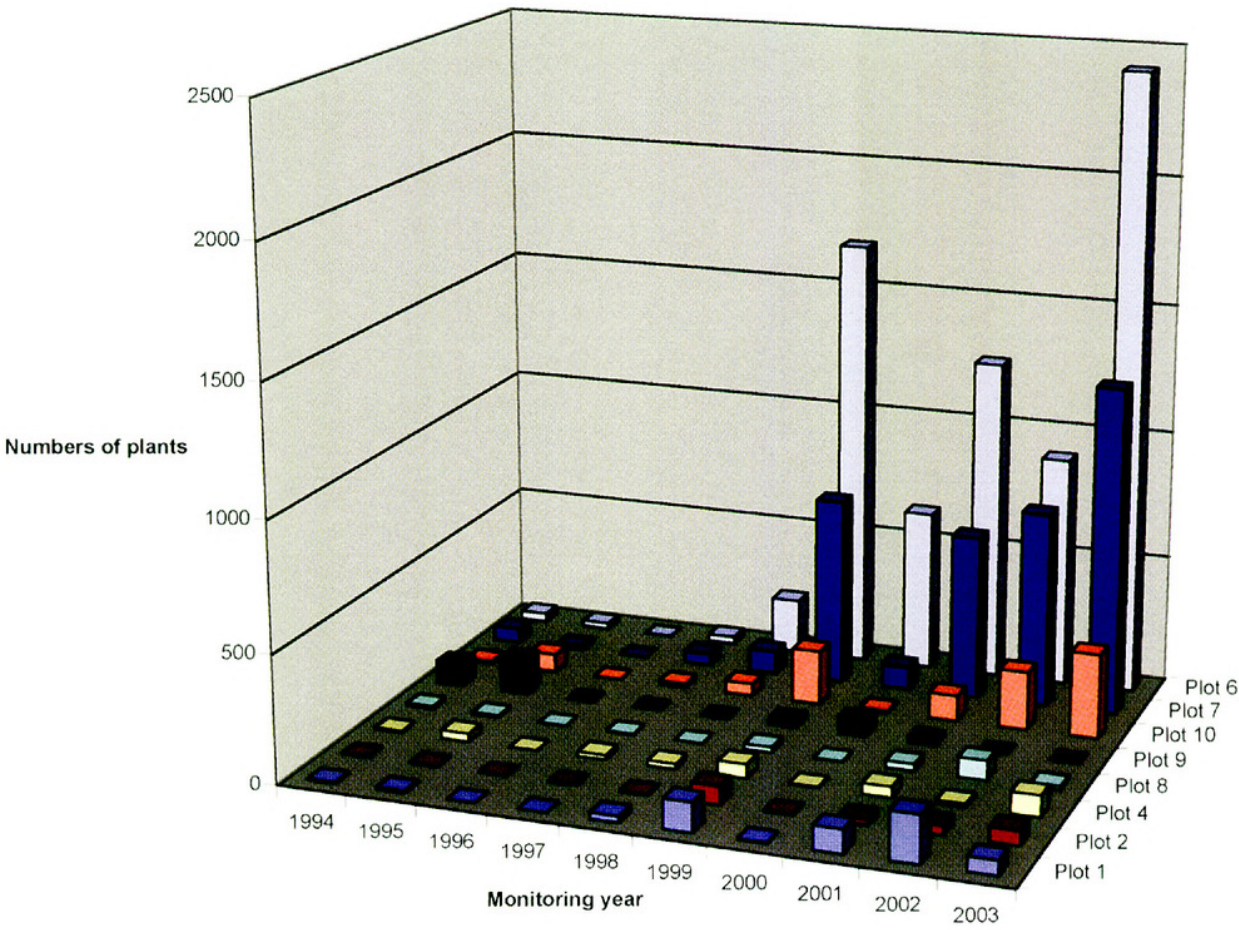
FIG. 4. Numbers of *Geocarpon minimum* plants in permanent plots from 1994 to 2003.

rock. These three plots were subsequently monitored for *G. minimum*, but soil and cover measurements were not taken.

Data Analysis

The subplot (0.01 m²) values of *G. minimum* numbers, soil depth, and cover classes for each vegetation type (see above) were summed within each large plot (i.e., 1.0 m²) and were subsequently used for all analyses (Spearman rank correlation, analysis of variance, and regression analyses). The independent variables were year, soil depth (mm), and cover values of bryophytes, lichens, and vascular plants. Lichens and bryophytes were combined into a single category (cryptogams) and vascular plants and cryptograms were also combined into a single category of total vegetation.

Spearman rank correlation coefficients, r_s, (Zar 1999; Sokal & Rohlf 1995) were calculated on both subplots and large plots in order to determine strength of association among *G. minimum*, year, soil depth, bryophytes, lichens, cryptogams, vascular plants, and total vegetation at two spatial scales (0.01 m² and 1.0 m²). In addition, partial correlations were also determined on ranked data controlling for the effect of year to determine potential associations among the vegetation types and soil.

Model II regression analyses were performed with the number of subplots that contain *G. minimum* as the dependent variable and soil depth as the independent variable. The regression analyses were performed on subplots only. Note that both soil depth and the number of subplots that contain *G. minimum* follow a normal distribution, as indi-

cated by a Kolmogorov-Smirnov normality test ($P > 0.05$). Specific regression analyses were performed independently on soil depth range of 1 to 20 mm and 21 to 110 mm. The justification for the latter was to show that the subplots containing *G. minimum* increase with increasing soil depth to 20 mm and declines thereafter.

A Friedman repeated measures (FRM) analysis of variance (ANOVA) (a non-parametric equivalent to the parametric repeated measures ANOVA) was used to determine differences among population numbers annually. Natural log transformed *G. minimum* numbers was the dependent variable, year was the repeated measures factor, and plot was the subject factor (Zar 1999; Sokal & Rohlf 1995). Because some of the plots had zeros and ones, it was necessary to add a count of 2 (a constant) to each observation for natural log (ln) transformation (Zar 1999; Sokal & Rohlf 1995). The transformation was done in order to improve statistical models (Quinn & Keough 2002) and to maximally normalize the data. Independent variables, with the exception of year and plot, were treated as random in all models because they were not specifically controlled (Zar 1999; Sokal & Rohlf 1995). The year 1996 was excluded from all analyses because only one *G. minimum* plant was observed for that year and thus it was considered as an outlier.

Additional FRM ANOVAs were performed on cover classes of bryophytes, lichens, vascular plants, cryptogams, total vegetation, and soil depth. There were three cover classes for bryophytes, lichens, vascular plants, cryptogams, and total vegetation while soil depth was placed into six. FRM ANOVA was performed on the large plots only. Independent variables were natural log transformed as needed. Additional repeated measure ANOVAs (Kruskal-Wallis) were performed without 1999 data in order to ascertain the relationship between soil depth and vegetation groups without the possibility of an interacting effect or confounding influence for the year 1999. The year 1999 was considered an outlier similarly to 1996 but with large numbers of *Geocarpon* observed for that year. The alpha level for all analyses was 0.05.

RESULTS AND DISCUSSION

Population Fluctuations
Winter annual glade plants commonly exhibit annual fluctuations in population size. Available moisture for fall germination and spring growth can vary greatly, with low moisture making shallow-soiled areas hostile for plant growth. Long-term monitoring is important in order to document the range of fluctuations in population size. Knowledge of this range improves our ability to interpret population data from sites where long-term data are not available. The ability of a species' seed bank to repopulate a site after a poor seed production year has obvious implications for long-term conservation.

Results of annual *G. minimum* counts in eight plots are depicted in Figure 4. The cumulative annual totals from all eight plots ranged from one plant (1996) to 4230 plants (2003). Although all of the plots are the same size, the amount and quality of the *G. minimum* habitat within each plot varies, with some plots containing more bare rock or denser vegetative cover. Plots 6 and 7, which often contained the most *Geocarpon*, provide a greater percentage of thin soil with little competition from bryophytes, lichens, or vascular plants. The small number of *G. minimum* plants at the site in 1996 was probably due to a prolonged dry period during early spring, prior to monitoring conducted in April. Only one additional *G. minimum* plant was observed outside of the plots during that year's monitoring. More substantial numbers of *G. minimum* were found at other sites in the region that spring, indicating the critical effect of very local drought on the popula-

tion at the study site. No insect herbivory of *G. minimum* was observed at the study site or at any other Missouri sites. There was a moderate positive correlation (r_s = 0.44, $P <$ 0.001) of *G. minimum* with year at the 1.0 m^2 scale (Table 1). Plot to plot variation was significant between 1997 and 1999 (RM: X^2 = 11.7, P = 0.045; Tukey: q = 4.16, $P <$ 0.05). Although the population fluctuated from year to year depending on local conditions, there was an overall increase in the population over the years.

Soil Depth Considerations

The stream and sheet flow of water over the glade due to precipitation creates a dynamic environment for *G. minimum*, with the depth and location of the loose, sandy soil with small pebbles changing dramatically through time. It was not uncommon to find *G. minimum* plants that had been uprooted and probably displaced by water and soil movement. It seems likely that the succulent stems are at least somewhat tolerant of displacement and can become established at new locations, especially when partially buried in sand.

The mean soil depth for subplots containing *G. minimum* was 19 mm (Fig. 5a, b). In comparison, Somers et al. (1986) found the shallowest soil depths on xeric communities of the limestone glades of Middle Tennessee to be (35 ± 17 mm), with such areas dominated by annuals and mosses, including several endemic species. In this study, soil depth was measured at the center of each subplot rather than at the actual location of any *G. minimum* plant. Therefore the high number of subplots with zero soil depth does not imply that plants were growing on bare rock but rather that they grew within about 7 cm (the distance from the center to a corner of a subplot) of the bare rock/soil interface. Nevertheless, there was a significant association between soil depth and *G. minimum* numbers (r_s = 0.16, $P <$ 0.001 at 0.10 m^2 scale; r_s = 0.41, $P <$ 0.001 at 1.0 m^2 scale)(Fig. 5b and Table 1). Note that the Spearman rank correlation between soil depth and the frequency of subplots containing *G. minimum* was -0.46 (Fig. 5a). It was observed that in areas of deeper soil, perennial vascular plants were more often present. Where vascular plants become numerous, fallen leaves from trees can lodge between stems and accumulate, whereas *G. minimum*-rich areas of the glade are windblown and/or washed by moving water and remain largely free of leaves.

Shallow soil, per se, is not a requirement for *G. minimum* growth. Rather, it is the mechanism by which plant competition is minimized on the sandstone glades. This was borne out by the growth of *G. minimum* on deeper soils following removal of other vegetation and litter by prolonged inundation and wave action on the lower portions of the study site in 1993. This is also apparent with the observation that *G. minimum* grows on deeper soils in the saline prairies of Arkansas, Louisiana and Texas, where high sodium levels prevent the growth of competing vegetation. In addition, there were significant differences with soil depth and the distribution of bryophytes, lichens, and vascular plants at the 0.01 m^2 scale as indicated by the Kruskal-Wallis analysis of variance and/or the Spearman rank correlation coefficients (bryophytes: H_4 = 19.96, $P <$ 0.001, r_s = -0.12, $P <$ 0.001; lichens: H_4 = 19.10, P = 0.002, r_s = -0.110, $P >$ 0.05; and vascular plants: H_4 = 17.18, P = 0.002, r_s = 0.445, $P <$ 0.001)(Fig. 5c, d, and Table 1).

Both soil depth and the number of subplots that contain *G. minimum* passed the normality test (Kolmogorov-Smirnov $P >$ 0.05). The results of the model II regression analysis show that *G. minimum* increases with increasing soil depth until about 20 mm ($F_{2, 18}$ = 4.45; $P <$ 0.05) albeit with a low adjusted r^2 (15.4%). The regression model accounted for fifteen percent of the variation and is consistent with the results of the Spearman rank correlations (Fig. 5a, b and Table 1). An additional regression analysis

TABLE 1. Spearman rank correlation coefficient for Year, *Geocarpon minimum*, bryophytes, lichens, vascular plants, cryptogams, total vegetation, and soil at the subplot (0.01 m²), n = 862, (above the diagonal) and large plot (1.0 m²), n = 50 (below the diagonal) scales. Correlations between large plot and subplot data (along the diagonal) were not calculated because the data are not paired. * = significance at the 0.05 level.

	Year	G. minimum	Bryophytes	Lichens	Vascular Plants	Cryptogam	Total Vegetation	Soil
Year	–	0.440*	-0.123*	-0.317*	0.022	-0.331*	-0.537*	0.038
G. minimum	0.190	–	-0.230*	-0.168*	0.186*	-0.305*	-0.236*	0.162*
Bryophytes	-0.161	-0.098	–	-0.160*	-0.577*	0.729*	0.362*	-0.118*
Lichens	-0.184	-0.045	0.367*	–	-0.442*	0.550*	0.298*	-0.027
Vascular Plants	-0.024	0.204	-0.154	-0.273	–	-0.781*	0.070*	0.165*
Cryptogam	-0.283*	-0.099	0.727*	0.829*	-0.346*	–	0.542*	-0.111*
Total Vegetation	-0.312*	-0.041	0.663*	0.755*	0.120	0.871*	–	0.043
Soil	0.042	0.408*	-0.199	-0.256	0.471*	-0.222	0.448*	–

shows that *G. minimum* numbers decrease with increasing soil depth beyond 20 mm ($F_{2, 88}$ = 68.45; $P < 0.0001$) with an adjusted r^2 of 43.1% (Fig. 5a, b). These results suggest that *G. minimum* numbers increase with increasing soil depth where competition is at a minimum but decreases thereafter. The latter observation is probably due to the competition from perennial vascular plants, which are more prevalent on deeper soils.

Vegetation Correlations

Large areas of the glade's sandstone bedrock are covered with dense bryophytes and it was expected that cover measurements would demonstrate that bryophytes were spreading into *G. minimum* populations. Although bryophytes were negatively correlated with *G. minimum* numbers at the subplot scale (r_s = -0.23, $P < 0.001$), they were not at the large plot scale. Similar results were observed with lichens and *G. minimum* numbers in that there was a negative relationship at the subplot scale but not at the large plot scale (Table 1). Although there is some discontinuity among scale with the latter two groups, there is a strong negative association (r_s = -0.78, $P < 0.001$) between cryptogams (combined category of bryophytes and lichens) and *G. minimum* numbers (Fig. 5f and Table 1). The latter may suggest that cryptogam competition is a factor in depressing *G. minimum* populations.

A positive association occurred with coverage by vascular plants and *G. minimum* (r_s = 0.19, $P < 0.001$) at the small plot scale but not at the next scale (Fig. 5e and Table 1). It may be that through time *G. minimum* has persisted only on those areas of the glade that are subjected to the same periodic disturbances that make it difficult for mosses and vascular plants to become established. Lichen cover declined steadily from 35.1% in 1994 to 10.9% in 1998. Perhaps this aspect of the monitoring would show better statistical trends if conducted over a longer period and with more detailed data collection with respect to the species of vascular plants and cryptogams across population sites. Certainly the movement of soil over the bedrock would explain the erratic variation in numbers of subplots dominated by bare soil or bedrock. There are similarities between *G. minimum* population dynamics and winter desert annuals in that there are large population number changes from year to year. Guo et al. (2002) discussed dramatic fluctuations in abundance, productivity, and diversity among desert winter annuals. Furthermore, the population dynamics of *Vulpia ciliata* Link. has been well studied (Watkinson et al. 2000; Watkinson 1990; Watkinson & Davy 1985; Watkinson & Harper 1978). This annual grass,
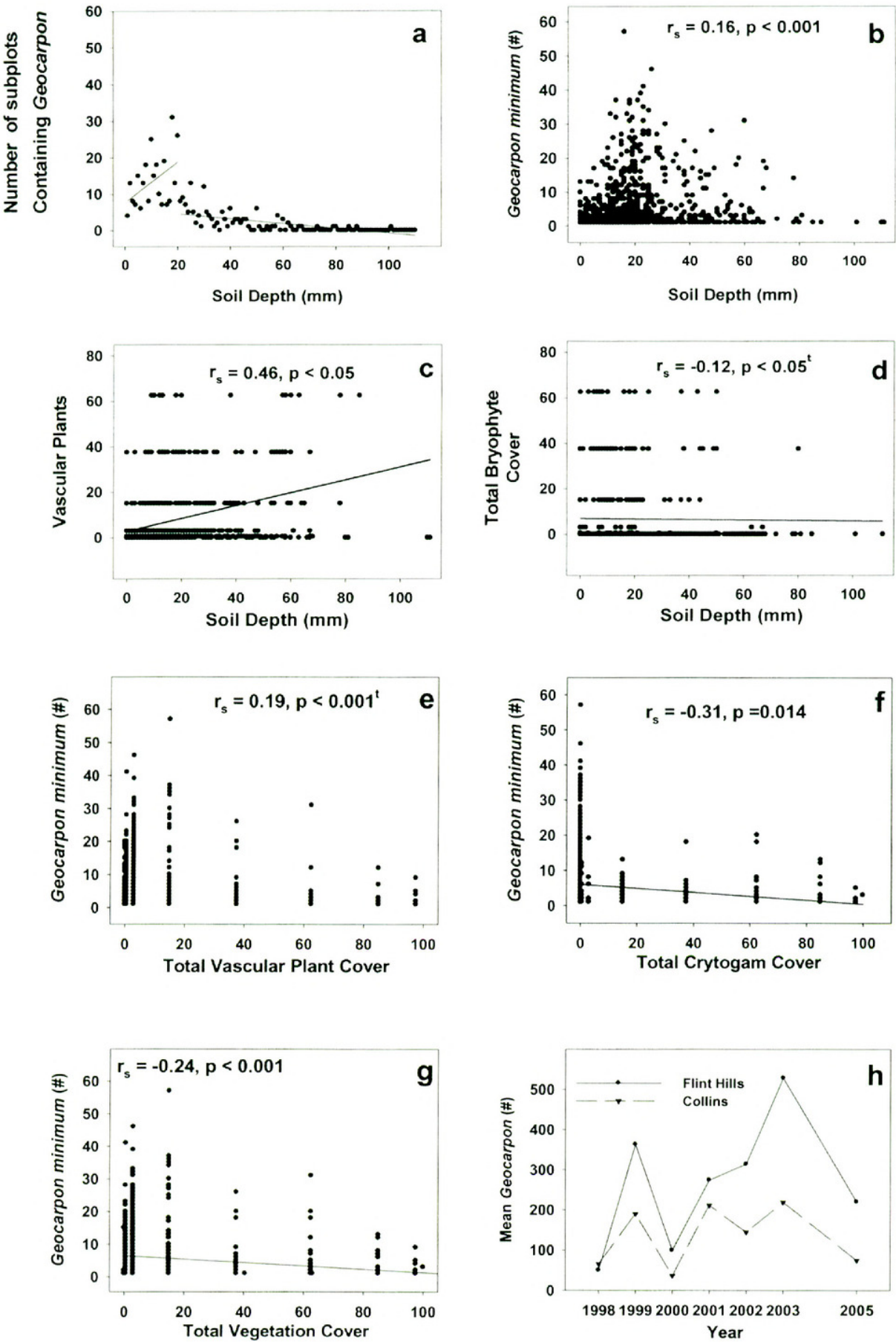
FIG. 5. Scatter plots of *G. minimum*, soil depth (millimeters), other vegetation types, with corresponding Spearman rank correlation coefficients and best fit lines, and population numbers of *G. minimum* from two populations (Flint Hills Glade and Collins relocation Site, Dade and St. Clair counties, Missouri). t indicates significance only at the large (1.0 m²) plot scale.

occurring on sandy heaths and warrens along coastal England, has similarities to *G. minimum* populations in that population dynamics probably occur at very small scales. It has been shown that other vegetation types depress *V. ciliata* populations significantly.

The coupled effect of all vegetation upon *G. minimum* populations further exemplifies that the persistence of this taxon may be dependent upon periodic disturbances. There was a significant negative correlation with *G. minimum* numbers at the subplot level (r_s = -0.24, $P < 0.001$) with the combined vegetation cover (cryptogams and vascular plants) (Fig. 5g and Table 1).

Colonization Plots

The three plots that were created in 1995 by removal of dense moss were not colonized by *G. minimum* during the study. Instead they were eventually recolonized by the moss, although there were several years following establishment when the habitat appeared suitable for *G. minimum*. The fact that these plots were nearly surrounded by undisturbed areas of dense moss may have precluded the water-transport of *G. minimum* seeds to the plots. Krieger et al. (2003) studied the temporal dynamics of ephemeral plant communities in seasonal rock pools on Ivorian inselbergs, monolithic outcrops of granites and gneisses along the Ivory Coast of Africa. These rock pools or depressions are typically several hundred years old and are seasonally wet with local edaphic conditions that may be typically xeric with a thin soil layer. They observed that plant communities in seasonal pools tend to follow the 'turnover hypothesis' which states that species that occur in discrete subpopulations tend to be at dynamic equilibrium with extinction and colonization. The turnover hypothesis is a significant part of island biogeography theory (MacArthur & Wilson 1967). The authors also noted that the turnover rate of an annual, *Cyanotis lanata* Benth. (Commelinaceae), was higher than other species. Although turnover was not studied here, the fluctuation in *G. minimum* population numbers from year to year may suggest that turnover does occur. The extent to which it may occur needs further study. Furthermore, Krieger et al. (2003) also examined physical characteristics of depressional pools including area, mean depth, volume, water depth, and precipitation for these rock pools. It seems that distance between pools limits the 'rescue effect', or the migration of propagules between pools. *G. minimum* gene flow among and between populations and subpopulations should be ascertained to determine if these populations are indeed isolated or have metapopulation characteristics.

To effectively establish *G. minimum* in additional plots, it is possible to move seeds into plots following soil disturbance. This has been done successfully at a highway mitigation site in St. Clair County, Missouri (Smith & Gardner 1999) by moving soil in the summer from areas where *G. minimum* had grown during the spring. It would seem prudent, however, to select establishment sites that are not subject to rapid recolonization by competitive plant species or offset recolonization by competitors with sufficient disturbance. The current study casts doubt on the efficacy of relying on an existing *G. minimum* seed bank in the created plots or on the rapid, natural dispersal of seeds into the newly-available habitat.

Climatic Effects

An aspect of this study that needs further work is the relationship between local and regional weather conditions and *G. minimum* populations. A graphical comparison of *G. minimum* populations between Flint Hill Glades and a relocated population, St. Clair County, Missouri, (Smith & Gardner 1999) shows a high degree of symmetry among popu-

lation numbers among years, indicating that precipitation and or temperature may play a key role (Fig. 5h). The differences between populations in particular years (2001 to 2002) may indicate that local precipitation and or temperature events may also influence geographically distinct populations. Weather data should be collected on each site for most accurate correlations because very local drought conditions at presumed critical life stages (fall germination of seed and early spring growth) would not be captured by available regional weather station measurements.

Management Implications

The long-term monitoring of *G. minimum* at Flint Hill Glades ecosystem provided insight on effective management of this threatened species. There is a negative association of cryptogams and the population of *G. minimum* as evidenced by the Spearman rank correlations (Fig. 5f and Table 1). Furthermore, *G. minimum* seems to utilize habitats where there is periodic soil disturbance and minimal competition from mat-forming mosses or perennial vascular plants. The level of soil disturbance necessary to keep water-carried sand moving into bedrock depressions will be difficult to quantify.

Geocarpon minimum population numbers appear at least partially dependent upon the amount of soil present (Fig. 5a, b; Table 1) as indicated by the results of the analysis of variance and type II regression, but there are other unknown factors that affect *G. minimum* numbers. Some level of grazing by cattle may benefit the plant by maintaining areas of loose sand with minimal plant competition, but excessive trampling or nutrient deposition would be a concern. Although it seems that many of the moss-dominated areas of the glade are currently unsuitable for *G. minimum*, we have little information on how abundant or widespread *G. minimum* was historically on Missouri's sandstone glades. Fire suppression following settlement of the region has nearly eliminated a critical process that may have previously altered the ratio of bare soil to heavily-colonized soil.

Management recommendations include providing periodic soil disturbances to the glade to assure that loose, sandy soil is available for movement by surface water. The periodic movement and accumulation of sand into shallow bedrock depressions should facilitate the development of suitable *G. minimum* habitat. Further studies are needed to address the frequency and type of disturbance required to achieve this result. More work is needed on the autecology and synecology of this taxon and associated species at other *G. minimum* suitable habitats. In addition, the physical environment needs to be characterized, as well as local and regional climate. It is encouraging that *G. minimum* was more abundant in the plots at this study site in 2003 than during any of the previous nine years and that the population is capable of rebounding following a year with little seed production.

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