RESEARCH ARTICLE

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Extinction, Colonization, and Persistence of Rare Vascular Flora in the Longleaf Pine–Wiregrass Ecosystem: Responses to Fire Frequency and Population Size

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ABSTRACT: We examined factors likely to be important in management of rare flora of the longleaf pine–wiregrass ecosystem on Fort Bragg and Camp Mackall Military Reservations in North Carolina, USA. We documented 1,268 occurrences of thirty-six rare plant species during two inventories conducted from 1991 to 1993 and 1998 to 1999. Of these occurrences, 891 (70.3%) persisted, 258 (20.3%) went extinct, and 119 (9.4%) colonized between the first and second inventories; extinctions exceeded colonizations by 139 occurrences. We used analyses of contingency table frequencies and logistic regressions to test hypotheses about temporal responses of local occurrences of rare flora. We found statistically significant effects of fire frequency on the colonization and extinction of rare flora; extinctions declined and colonizations increased with increasing fire frequency. There were statistically significant effects of both area occupied and stem number on the persistence and extinction of rare flora; extinctions declined and persistences increased with increasing area occupied and stem number. Our analyses emphasize the importance of fire and population size for the conservation of rare flora in this landscape.

Extinción, Colonización, y Persistencia de Flora Vascular Rara en los Ecosistemas de Longleaf Pine–Wiregrass: Respuestas a la Frecuencia del Fuego y el Tamaño Poblacional

RESUMEN: Examinamos factores que podrían ser importantes en el manejo de flora rara en el ecosistema de longleaf pine–wiregrass en las reservas militares de Fort Bragg y en Camp Mackall en Carolina del Norte. Documentamos 1268 ocurrencias de 36 especies de plantas raras durante dos inventarios realizados desde 1991 a 1993 y entre 1998 y 1999. De esas ocurrencias, 891 (70,3%) persistieron, 258 (20,3%) se extinguieron, y 119 (9,4%) fueron colonizadas entre el primer y el segundo inventario; las extinciones superaron a las colonizaciones por 139 ocurrencias. Usamos análisis de contingencia, tablas de frecuencias, y regresiones logísticas para testear la hipótesis sobre la respuesta temporal de ocurrencias locales de flora rara. Encontramos efectos significativos de los efectos de la frecuencia del fuego en la colonización y extinción de flora rara; las extinciones disminuyeron y las colonizaciones aumentaron con un aumento de frecuencia de fuego. Hubo efectos significativos del área ocupada y del número de troncos en la persistencia y la extinción de la flora rara; la extinción declinó y la persistencia aumentó con el aumento del área ocupada y el numero de troncos. Nuestro análisis enfatiza la importancia del fuego y del tamaño poblacional para la conservación de flora rara en el paisaje.

Index terms: rare species, fire frequency, longleaf pine, extinction, colonization

INTRODUCTION

Fire is the primary tool used in the management of rare flora associated with the longleaf pine-wiregrass ecosystem. The role of fire in increasing species richness (Sparks et al. 1998, Kush et al. 2000), causing seasonal effects (Sparks et al. 1998, Engle et al. 2000), altering phenology (Platt et al. 1988, Brewer and Platt 1994), influencing demographics (Menges and Kohfeldt 1995, Brockway and Lewis 1997), influencing open space (Hawkes and Menges 1996), and perpetuating longleaf pine itself (Heyward 1939, Glitzenstein et al. 1995) is well documented at the community level for the longleaf pine–wiregrass ecosystem. In addition, studies of individual taxon responses to fire are becoming more prevalent in the literature (Hawkes and Menges 1995, Menges and Kimmich 1996, Kirkman et al. 1998, Quintana-Ascencio et al. 1998, Lamont et al. 2000, Garnier and Dajoz 2001). Yet, there is an acute lack of knowledge of the temporal responses of rare vascular flora to fire, and, in particular, to fire frequency. Further, we know of no community-level analysis of the responses of rare flora to fire, where temporal responses are examined across suites of rare vascular species. Over time a rare plant occurrence will either persist or go extinct and new occurrences may become established, by way of colonization. Knowing how fire frequency drives and influences colonization, extinction, and persistence is crucial to the effective management of rare flora associated with the longleaf pine wiregrass ecosystem.

Fire suppression and habitat loss have directly contributed to the high incidence of rare flora associated with the longleaf pine–wiregrass ecosystem. Hardin and White (1989) identified 191 rare vascular species associated with longleaf pine-wiregrass, while Walker (1993) identified 389 rare vascular species associated with longleaf pine over the species' entire range (including areas where wiregrass does not grow). Many of the rare vascular species associated with this system are either federally protected or state listed and are highly restricted geographically. Department of Defense installations harbor a disproportionate number of rare species, as compared to lands managed by other federal agencies, due to the range of habitats sought for diversified military training (Leslie et al. 1996), and the protection and management afforded these habitats.

Increasing the population size of rare plants is central to their conservation because risk of extinction falls steeply with increasing population size. Because of the confluence of negative genetic and demographic factors, small occurrences may be doomed by an extinction vortex (Gilpin and Soulè 1986, Westemeier et al. 1998). Few studies in the plant literature have tested this largely theoretical hypothesis. The evaluation of abundance classes (Fischer and Stöcklin 1997), outcrossing rates (Van treuren et al. 1993), reproductive success (Widen 1993), and percentage of seed germination (Menges 1991) support the expectation that extinctions decline with increasing population size. Ouborg (1993) demonstrated that occurrences that went locally extinct were smaller on average and that larger occurrences were more likely to persist through time.

This study examined the interaction between fire frequency, and the extinction, colonization, and persistence of rare plant occurrences, responses likely to be important in the management of 36 rare species on Fort Bragg and Camp Mackall Military Reservations, North Carolina, USA. It is clear that with so many rare plant species imperiled, a single species approach to research and management is prohibitive and, in such a diverse system with one dominant disturbance regime, will not work. As it would not be feasible to develop separate management plans for each of these species, the Department of Defense has developed and implemented an ecosystem management policy for its land management activities. Budget constraints and lack of personnel require managing suites of species that inhabit an ecosystem (Leslie et al. 1996). A multiple-species approach may be particularly useful in the absence of individual life history information, a problem common to rare vascular flora (Walker 1993). Thus, the focus of our analyses are directed across species and functional groups. Such broad-based analyses represent a conservative approach. Given the diversity of species involved, detecting responses to fire frequency and population size will be more difficult when compared to detecting responses of individual species.

We specifically sought to quantify temporal responses of rare plant occurrences to fire frequency and population size by testing the following hypotheses: (1) frequent fire increases colonization rates and decreases extinction rates of rare plant occurrences; (2) there are differences between functional groups in response to fire frequency; (3) frequent fire increases both density and area occupied for persistent rare plant occurrences over time; (4) local extinctions decline and persistence of rare plant occurrences increases with increasing stem number and area occupied.

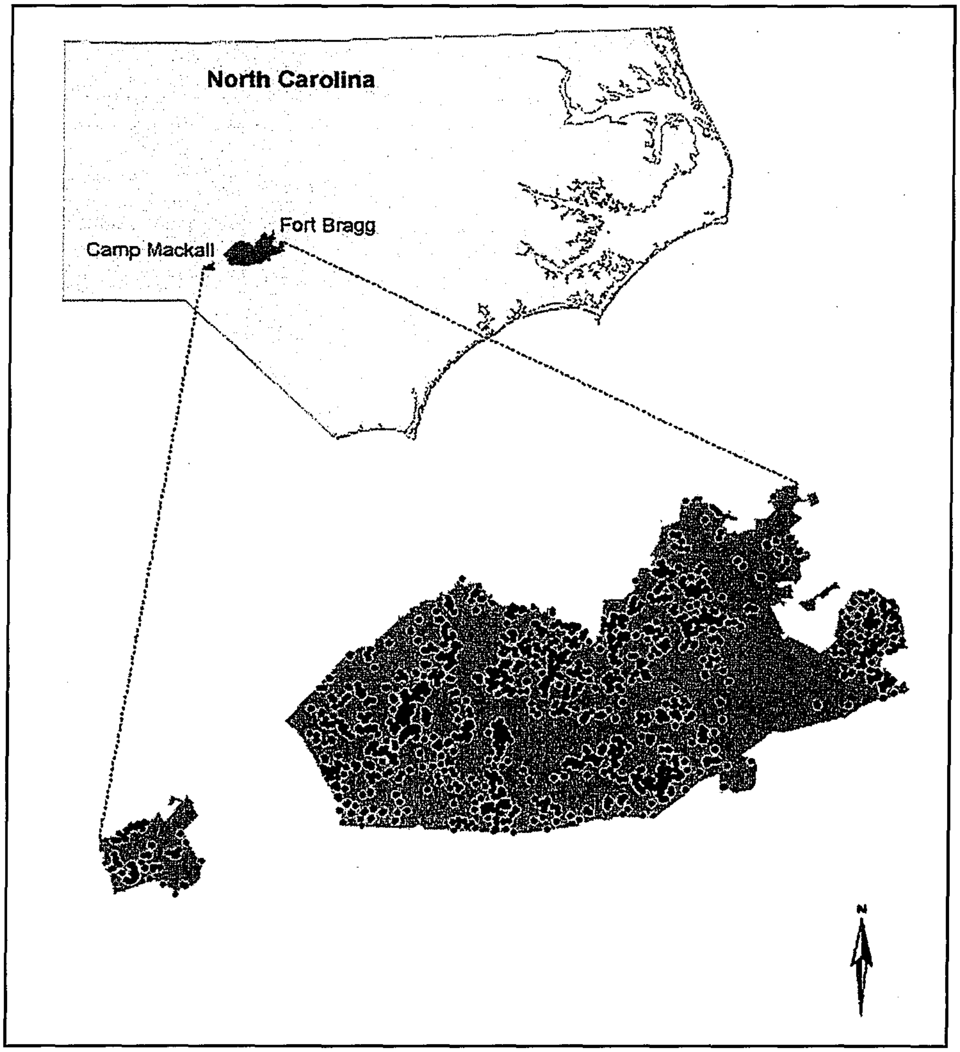

Figure 1. The rare plant occurrences found on Fort Bragg and Camp Mackall Military Reservations. Each dot represents a rare plant occurrence.

METHODS

Study Area

Our study areas, Fort Bragg and Camp Mackall Military Reservations, occupy approximately 65,000 ha of the longleaf pine–wiregrass ecosystem. The reservations are located within the sandhills region of the inner coastal plain physiographic province, North Carolina, USA (Figure 1).

The communities of the region are arrayed along a moisture gradient from xeric entisols to mesic/wet ultisols. Soils are derived from Cretaceous and/or Tertiary deposits of fluvial and marine sediments, ranging from arkosic, feldspar-rich sands to micaceous, arenaceous, compact clays. The underlying sediments have a basal conglomerate of pebbles and cobbles (Daniels et al. 1984). Mean annual temperature is 22.2°C and mean annual precipitation for 30 y prior to and including 1999 was 1,186.2 mm y^{-1}.

To date, 58 rare plant species have been identified on Fort Bragg and Camp Mackall Military Reservations. These rare species inhabit a number of communities contained in the longleaf pine-wiregrass ecosystem that are burned on a 3- to 5-y rotation. These communities include xeric sandhill scrub, pine scrub/oak sandhill, mesic pine flatwoods, streamhead pocosins, and sandhill seeps (nomenclature after Schafale and Weakley 1990). For our study, we considered 36 of the 58 rare species that inhabit those longleaf pine communities most influenced by fire. Of these, 27 (75.0%) are herbaceous perennials, a proportion consistent with previous findings that the vast majority of herbaceous rare flora associated with longleaf pine throughout its range are perennials (Walker and Peet 1983, Hardin and White 1989, Walker 1993). Twenty-three (64.0%) of the 36 species inhabit mesic to wetland communities. This is also consistent with the finding that rare vascular flora associated with longleaf pine are more likely to be found in wet habitats (Walker 1993) and thus are now limited to pocosin/savanna ecotones (Frost 1995).

Surveys for Rare Flora

A comprehensive survey for rare flora was conducted on Fort Bragg and Camp Mackall during 1991–93 by The Nature Conservancy (Table 1). A two-step process was used to identify rare plant occurrences. The first consisted of habitat assessment surveys conducted from October 1991 to November 1992 using a parallel, zigzag transect surveying technique. Habitat was assessed by each transect team as low, medium, or high quality based on observations of degree of fire suppression, amount of soil disturbance, level of species diversity, and the presence of rare species.

Step two of the inventory for rare flora consisted of return visits to high and medium priority areas. Rare plant occurrences encountered throughout the two assessment periods were mapped on 1990 black and white aerial photographs (scale 1:12,000) (Russo et al. 1993) and later transposed into a geographic information layer (GIS). Biological data recorded, pertinent to this study, included the scientific name of each occurrence, stem count, and area occupied (Russo et al. 1993). Rare plant occurrences were defined as discrete entities separated by a minimum of 0.8 km.

The reservations were surveyed a second time in 1998–99. Local occurrences documented during the initial survey were revisited to determine presence or absence. The area occupied by each persistent occurrence was globally positioned to the nearest meter and the number of stems was recorded. Suitable habitat was systematically surveyed for newly colonized occurrences with an emphasis on areas surrounding existing occurrences. Suitable habitats for potential colonizations were not identified, thus the proportion of colonizations to potential colonizable sites is not known. The fire history, comprising both dormant and growing season burns, was obtained for each occurrence for the period 1991 through 1999.

RESULTS

Survey Results for Rare Flora

Among 1,268 occurrences of rare species, there were 891 (70.3%) persistences, 258 (20.3%) extinctions, and 119 (9.4%) colonizations. Twenty-two (61.1%) of the 36 species considered declined in the number of occurrences between the two surveys. Of the 36 rare species, some were more common than others. At one extreme, two rare species, *Solidago pulchra* Small and *Xyris elliotti* Chapman, represented by one occurrence each in 1991, were locally extinct by 1999. At the other extreme, the state endangered sandhills pyxie moss (*Pyxidanthera brevifolia* Wells) contributed 249 (25%) of the total number of occurrences extant in 1999, while the state threatened *Eupatorium resinosum* Torr. *ex* DC and state candidate *Tofieldia glabra* Nutt. each contributed 105 (10.4%) and 96 (9.6%) occurrences, respectively (Table 1).

Of the 1,268 rare plant occurrences, 1,181 burned at least once, and these experienced an average of 2.38 fires during the study period. Fire frequency was highest where rare plants colonized, lower where they persisted, and lowest where they went extinct (Figure 2).

Effects of Fire Frequency on Temporal Responses

There were statistically significant differences in the proportions of persistence, colonization, and local extinction of rare plant occurrences in response to fire frequency when examined across all species (P=0.0005, $X^2_{0.05\ (10\ df)} = 31.42$, contingency table analysis). Deviations between expected and observed frequencies were greatest for persistent occurrences.

Using logistic regression, we examined extinction and colonization in response to fire frequency. We chose to contrast extinction and colonization because these are the most dynamic processes and differed the most with respect to fire frequency. Colonizations significantly increased and extinctions declined as a function of fire frequency at P= 0.0009 (Figure 3). Between fire frequencies of four and five

Table 1. List of rare flora, mean fires 1991-99, mean stem number 1998–99, total occurrences in 1991–93 and 1998–99, temporal responses, and state status. Botanical nomenclature follows Kartesz (1994). State statuses (Amoroso 1999) are abbreviated as follows: E=Endangered, T=Threatened, SR=Significantly Rare, SC=Special Concern, C=Candidate, and W1=Watch list.

Scientific Name	Mean Fires 1991–99	Mean Stem No. 1998–99	Total Pop. 1991–93	Persistence	Extinction	Colonization	Total Pop. 1998–99	State Status
Agalinis aphylla (Nutt.) Raf.	1.3	26.7	2	1	1	1	2	SR
Agalinis obtusifolia Raf.	1.5	5.0	2	1	1	0	1	W1
Amorpha georgiana var. *georgiana* Wilbur	1.9	55.6	30	26	4	3	29	E
Astragalus michauxii (Kuntze) F.J. Herm	2.1	10.7	88	69	19	18	87	T
Carex tenax Chapman	1.0	200.0	1	1	0	0	1	C
Cladium mariscoides (Muhl.) Torr.	2.0	535.0	5	5	0	0	5	SR
Danthonia sericea Nutt.	2.6	161.8	18	16	2	1	17	SR
Dionaea muscipula Ellis	3.8	89.2	9	9	0	1	10	C-SC
Eriocaulon texense Koern.	2.8	30.0	4	4	0	1	5	C
Eupatorium resinosum Torr. *ex* DC.	2.0	93.1	136	99	37	6	105	T-SC
Gaillardia aestivalis (Walt.) H. Rock	3.3	16.9	5	2	3	2	4	C
Gallactia mollis Michx.	3.0	4.8	7	4	3	0	4	C
Gnaphalium helleri var. *helleri* Britt.	1.6	26.1	5	2	3	2	4	SR
Kalmia cuneata Michx.	2.5	115.2	25	22	3	2	24	E-SC
Lilium iridollae Henry	2.7	0.5	12	2	10	10	12	T
Lindera subcoriacea B.E. Wofford	2.6	40.8	64	55	9	5	60	E
Muhlenbergia torreyana (J.A. Schultes) A.S. Hitchc.	2.0	100.0	1	1	0	0	1	E
Nestronia umbellula Raf.	1.5	541.9	25	23	2	2	25	W1
Parnassia caroliniana Michx.	3.4	92.9	3	2	1	4	6	E
Phaseolus polystachios (L.) B.S.P.	2.4	8.2	86	61	25	6	67	C
Physalis lanceolata Michx.	1.8	15.5	11	5	6	2	7	W1
Polygala grandiflora Walt.	2.1	48.5	7	5	2	1	6	SR
Pyxidanthera brevifolia Wells	2.2	2.0	255	238	17	11	249	E
Rhynchospora macra (C.B. Clarke) Small	2.5	125.2	10	8	2	0	8	E
Rhynchospora oligantha Gray	2.1	36.7	12	11	1	0	11	C
Ruellia ciliosa (Pursh) R.W. Long	3.0	12.5	1	0	1	1	1	C
Solidago gracillima Torr. and Gray	1.8	50.8	6	6	0	0	6	SR
Solidago pulchra Small	3.0	0.0	1	0	1	0	0	E
Solidago verna M.A. Curtis	1.9	59.8	17	14	3	2	16	T
Stylisma pickeringii var. *pickeringii* (Torr. *ex* M.A. Curtis) Gray	1.4	283.4	58	53	5	5	58	E
Tofieldia glabra Nutt.	2.5	8.3	145	79	66	17	96	C
Tridens carolinianus (Steud.) Henr.	2.4	21.5	43	29	14	1	30	C
Warea cuneifolia (Muhl. *ex* Nutt.) Nutt.	2.0	2.5	4	1	3	0	1	C
Xyris chapmanii Bridges and Orzell	2.1	31.2	26	21	5	5	26	C
Xyris elliottii Chapman	3.0	0.0	1	0	1	0	0	C
Xyris scabrifolia Harper	2.2	8.0	24	16	8	10	26	C
			1149	**891**	**258**	**119**	**1010**	

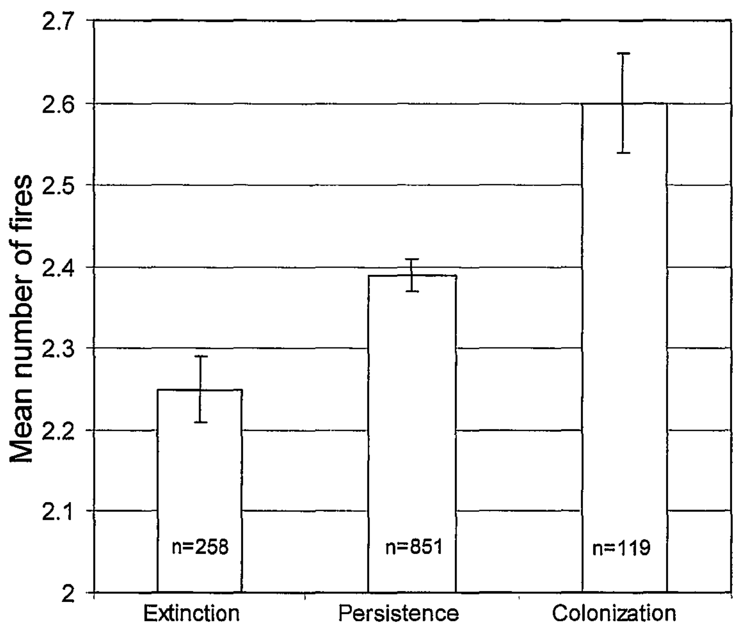

Figure 2. Mean number of fires incurred for occurrences of rare species representing each temporal state, during the period 1991–99.

each increased with increasing fire frequency at $P = < 0.0541$ and $P = 0.0360$, respectively, while those of dicots declined. We found no statistically significant relationships between the responses of persistence and colonization of legumes versus nonlegumes, woody versus herbaceous species, and annuals versus perennials to fire frequency (Table 2, right side).

Changes in Stem Number and Area Occupied as a Function of Fire Frequency

We hypothesized that increased fire frequency increases both stem number and area occupied for persistent rare plant occurrences over time. There were statistically significant effects of fire frequency on changes in mean stem number during the period 1991–99 at $P = 0.0023$. Stem number increased by an average of 24.5 stems across all observations. Fifty percent of the observations were at or near

times during the 9-y period, the proportions of colonizations and extinctions were equal (Figure 3).

Effects of Fire Frequency on Functional Groups

We used logistic regression to test fire frequency effects on functional groups by classifying occurrences into one of two mutually exclusive functional groups and assigning a 1 to the functional group of interest and a 0 to the contrasting functional group. Colonized and persistent occurrences were pooled and chosen for this analysis as these represent successful occurrences present in 1999. Proportions of monocot occurrences increased while proportions of dicot occurrences declined with increasing fire frequency, significant at $P = < 0.0001$ (Table 2, left side). We found no statistically significant relationships between proportions of legumes versus nonlegumes, woody versus herbaceous species, and annuals versus perennials as a function of fire frequency (Table 2, left side). We then evaluated separately functional group persistences and colonizations as functions of fire frequency. Proportions of monocot colonizations and persistences

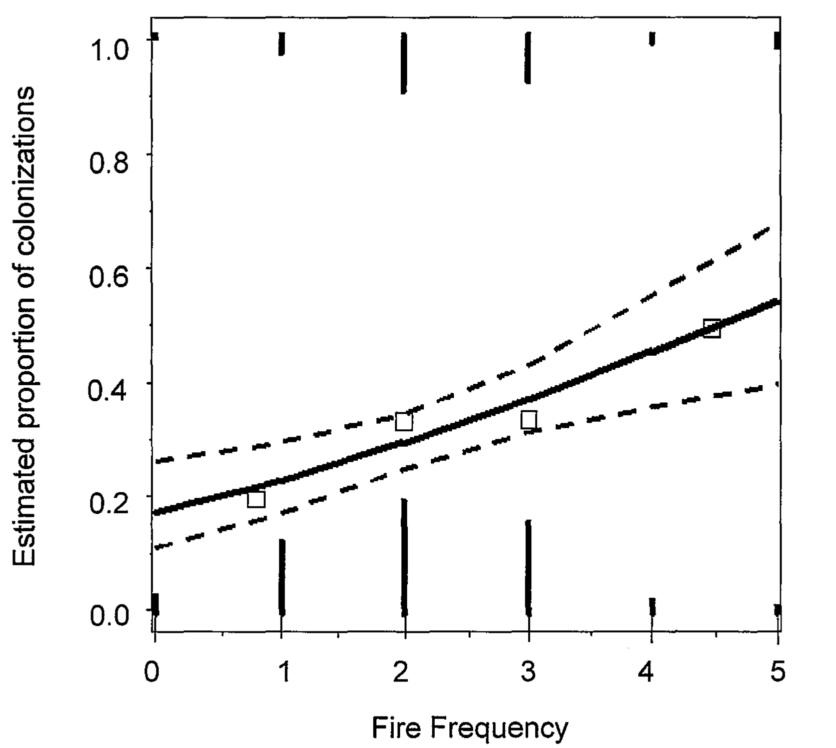

Figure 3. Proportions of colonizations (n=119), assigned a value of 1, contrasted with extinctions (n=258), assigned a value of 0, as a function of fire frequency and as estimated by logistic regression. The broken lines represent the 95% confidence bands on each side of the fitted logistic relation. The arrow represents equilibrium of colonizations and extinctions at fire frequencies of four and five times during the 9-y period. The relative numbers of colonizations and extinctions at each fire frequency are depicted as bars across the top and bottom of the graph, respectively. The relationship was significant at $P = 0.0009$, $X^2_{0.05(1)} = 11.06$.

Table 2. Tests for fire frequency as a predictor of functional group proportions and persistence and colonization proportions using logistic regression.

Pairs of Functional groups	Per.-Col. Combined (n = 1010)	Persistence (n = 891)	Colonization (n = 119)
Monocot vs. dicot	P = < 0.0001	P =0.0036	P =0.0541
	X^2 = 15.32	X^2 = 8.50	X^2 = 3.71
Legume vs. non-legume	P = 0.7397	P = 0.8037	P = 0.5825
	X^2 = 0.11	X^2 = 0.06	X^2 = 0.30
Woody vs. herbaceous	P =0.4656	P = 0.9827	P = 0.2370
	X^2 = 0.53	X^2 = 0.00	X^2 = 1.40
Annual vs. perennial	P = 0.3735	P = 0.3649	P = 0.3001
	X^2 = 0.54	X^2 = 0.82	X^2 = 1.07

zero change, with high variability in changes in stem number at low fire frequencies and little variability in changes in stem number at high fire frequencies. There were statistically significant effects of fire frequency on changes in average area occupied at P = <0.0001. Area occupied exhibited a mean decline of –0.24 ha across all observations during the 9-y period. As was the case with changes in stem number, 50% of the observations were at or near zero change, with high variability in changes in area occupied at low fire frequencies and little variability in changes in area occupied at high fire frequencies.

Persistence versus Local Extinction as a Function of Population Size

We hypothesized that extinctions of rare plant occurrences would decline and the persistence of occurrences would increase with increasing stem number and area occupied. We chose to contrast persistence versus extinction as these occurrences differed the most in population size. The proportions of local extinctions declined and the proportions of persistent occurrences increased significantly as a function of stem number (P = 0.0002, Figure 4) and area occupied (P = < 0.0001, Figure 5). Occurrences that went locally extinct had the smallest stem numbers and occupied relatively small areas, while those of persistent occurrences had the largest stem numbers and occupied the largest areas (Figure 6). Small occurrences were disproportionately represented among extinctions. Of the rare plant occurrences that went extinct, 175 (71.1%) had 1–10 stems, and 164 (64.0%) occupied an area of 1 m^2.

DISCUSSION

We were able to assess with reasonable accuracy the extinction and persistence of rare plant occurrences. Return visits to occurrences recorded during the initial survey are likely to be accurate; either the occurrence was present or not. Like Harrison et al. (2000), we found that the majority of the species we studied were perennials. This is an advantage when censuses are infrequent, because occurrences of longer-lived species have greater intrinsic stability (Ricklefs 2001). Perhaps our least reliable data are those for colonizations. Psuedo-colonizations could exist if any occurrences were missed during the 1991–93 survey and then discovered during the 1998–99 survey. However, given the length of the initial survey and the highly trained botanists conducting the survey, missing existing plant occurrences was minimized to the maximum extent possible.

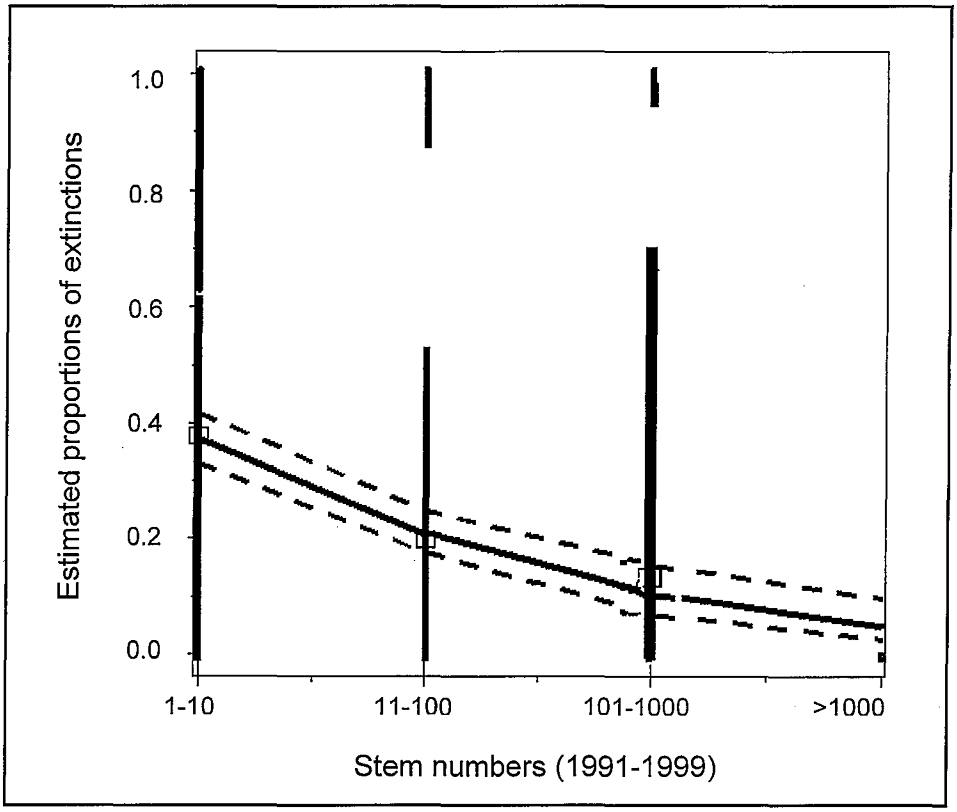

Figure 4. Proportions of extinctions (n=246), assigned a value of 1, contrasted with persistences (n=605), assigned a value of 0, as a function of stem number and as estimated by logistic regression. The broken lines represent the 95% confidence bands on each side of the fitted logistic relation. The relative numbers of extinctions and persistences are depicted as bars across the top and bottom of the graph, respectively. The relationship was significant at P = 0.0002, $X^2_{0.05(1)}$ = 13.83.

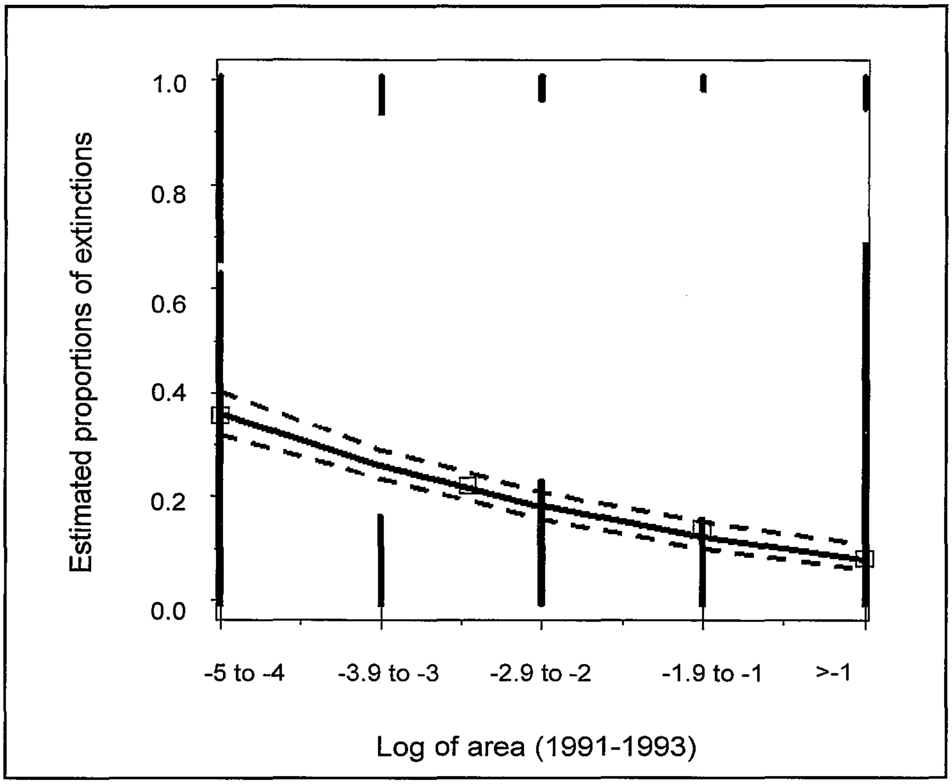

Figure 5. Proportions of extinctions (n=258), assigned a value of 1, contrasted with persistences (n=885), assigned a value of 0, as a function of the log of area and as estimated by logistic regression. The broken lines represent the 95% confidence bands on each side of the fitted logistic relation. The relative numbers of extinctions and persistences are depicted as bars across the top and bottom of each graph, respectively. The relationship was highly significant at P = <0.0001, $X^2_{0.05(1)}$ = 84.10.

Fire frequency effects were apparent in the data for both colonization and extinction across species. Extinctions declined and colonizations increased with increasing fire frequency. There were statistically significant effects of both area occupied and stem number on the persistence and extinction of rare flora; extinctions declined and persistences increased with increasing area occupied and stem number.

Although most occurrences in this study were burned during the period 1991–99, there were more than twice as many extinctions as colonizations. For long-term stability of the number of occurrences of rare species, extinctions must be offset by colonizations. Our evidence suggests that the rate of colonization balances the rate of extinction at fire frequencies of between four and five times during the 9-y study period (Figure 3). Occurrences that went locally extinct burned the fewest number of times while extinctions declined to 50% among occurrences that burned between four and five times during the 9-yr. period (Fig. 3). This indicates that increased fire frequency is warranted in areas across the reservations with infrequent fire and points to a fire return interval of approximately 2 y for balancing rates of extinction and colonization.

Among the pairs of functional groups examined, monocots and dicots varied significantly in response to fire. The proportions of monocots increased with increasing fire frequency, as did monocot colonizations and persistences, when examined individually. The reverse was true for dicots. It is plausible that monocots are more sensitive to fire and more responsive to the open conditions created by frequent fire than are other functional groups. This may be particularly true for the four perennial grasses considered in our study. Seeds of perennial grasses are light and require openings for seedling establishment. Persistent pappus-like hairs and awns aid in dispersal to new seedbeds created by fire. Infrequent fire encourages encroaching woody vegetation, thus eliminating open areas for seedling establishment (Keeley 1981).

There were declines in area occupied and increases in stem number among rare plant occurrences in response to fire frequency, but gains and losses were small. Fifty percent of the observations were at or near zero change in both stem number and area. A case may be made for reduction in the fluctuation of stem number and area as a means of stabilizing occurrences of rare plants. Across the range of fire frequencies, occurrences exhibited the least change in stem number and area at the highest fire frequencies, suggesting that burning every 2 y would be sufficient to minimize volatility. Thus, we propose that 2 y be considered the minimum fire return interval for rare vascular flora in this longleaf pine–wiregrass ecosystem. This fire return interval is in the mid-range of a presettlement fire regime of 1–3 y reported by Frost (1998) for the southeastern coastal plain of the United States, where 50% to 90% of the landscape probably burned that frequently and in which many rare, fire-dependent plant species appear to require a 1- to 3-year fire return interval.

In contrast to the small variation in stem number and area at the highest fire frequencies were large spikes of both stem number and area gained at zero fire frequency. These large gains in stem number and area were primarily attributable to *Stylisma pickeringii* var. *pickeringii* (Torr. *ex* M.A. Curtis) *Gray* and *Pyxidanthera brevifolia*. Large, densely populated areas of *Stylisma pickeringii* var. *pickeringii* are common in physically disturbed areas, such as roadsides and human dominated areas that are subject to frequent mechanical disturbance and that have low to no canopy cover. This appears to be indicative of the species' ability to proliferate under a disturbance regime other than fire, as long as competition for light is reduced. Small, widely scattered clumps of *Pyxidanthera brevifolia* are also contained within xeric sandhill communities that were not burned during the time frame of this study. The

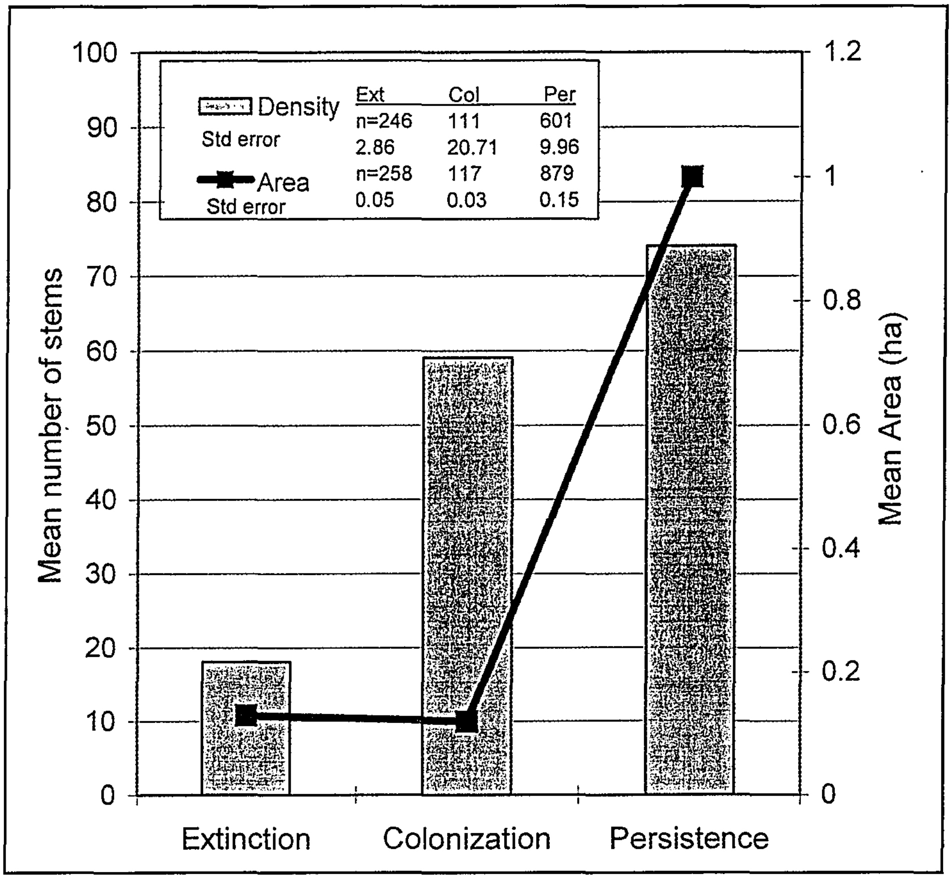

Figure 6. Mean population size of temporal responses. Values for extinction and persistence are based on 1991–93 data and values for colonization are based on 1998–99 data.

xeric sandhill communities are characterized by a sparse canopy and shrub layer, minimal ground litter and large areas of open sand. In contrast to communities that contain *Stylisma pickeringii* var. *pickeringii*, these areas are not subject to frequent mechanical disturbance. Persistence under these conditions is similar to that seen in some rare Florida scrub endemics adapted to fire cycles of 10 to 40 y. The persistence of these endemics is highly correlated with open sand conditions and is independent of fire (Hawkes and Menges 1995).

Extinctions declined and the persistence of rare plant occurrences increased with increasing population size (Figure 4 and 5). Is there a minimum population size that best promotes the persistence of rare plant occurrences? We found that 236 (96.0 %) of all extinctions occurred in the two smallest stem classes of 1–10 and 11–100 stems, suggesting that extinctions would be greatly reduced if a minimum population size in excess of 100 stems could be achieved for occurrences of rare plant species in this landscape. The finding that the average population size for persistent occurrences in 1991–93 was 74.0 (Figure 6) stems and rose to 98 stems in 1998–99 also supports our recommendation for minimum population size. Although not addressed in this study, a spatial analysis of the potential metapopulation structure of each rare species to include the variables of population size, location, and the distances among them will further enlighten our understanding of the dynamics of extinction, colonization, and persistence and could serve to direct future management efforts.

This study is a first step in elucidating the effects of prescribed fire as a management tool for rare vascular flora associated with the longleaf pine–wiregrass ecosystem. There are few studies in the literature that address the temporal responses of rare flora to fire frequency and few studies in the plant literature that address extinction and persistence as a function of population size.

The relationships among the three temporal states are complex and there are differences among species in their responses to fire. Despite the fact that this study involved multiple species with a diversity of life forms, life histories, and environmental relations, strong signals of effects of fire frequency and population size on temporal responses were apparent.

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LITERATURE CITED

Amoroso, J. 1999. Natural Heritage Program list of the rare plant species of North Carolina. North Carolina Natural Heritage Program, Raleigh, N.C.

Brewer, J.S., and W.J. Platt. 1994. Effects of fire season and herbivory on reproductive success in a clonal forb, *Pityopsis graminifolia*. Journal of Ecology 82:665-675.

Brockway, D.G., and C.E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. Forest Ecology and Management 96:167-183.

Daniels, R.B., H.J. Kleiss, S.W. Buol, H.J. Byrd, and J.A. Phillips. 1984. Soil systems in North Carolina. N.C. Agricultural Research Service, N.C. State University, Raleigh.

Engle, D.M., M.W. Palmer, J.S. Crockett, R.L. Mitchell, and R. Stevens. 2000. Influence of late season fire on early successional vegetation of an Oklahoma prairie. Journal of Vegetation Science 11:135-144.

Fischer, M., and J. Stöcklin. 1997. Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-1985. Conservation Biology 11:727-737.

Frost, C.C. 1995. Presettlement fire frequency regimes in southeastern marshes, peatlands, and swamps. Pp. 39-60 *in* Susan I. Cerulean and R. Todd Engstrom, eds., Fire in Wetlands: A Management Perspective. Tall Timbers Fire Ecology Conference Proceedings, No. 19. Tall Timbers Research Station, Tallahassee, Fla.

Frost, C.C. 1998. Presettlement fire frequency regimes of the United States: a first approximation. Pp. 70-81 *in* Teresa L. Pruden and Leonard A. Brennan, eds., Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription. Tall Timbers Fire Ecology Conference Proceedings, no. 20. Tall Timbers Research Station, Tallahassee, Fla.

Garnier, L.K., and I. Dajoz. 2001. The influence of fire on the demography of a dominant grass species of West African savannas, *Hyparrhenia diplandra*. Journal of Ecology 89:200-208.

Gilpin, M.E., and M.E. Soulè. 1986. Minimum viable occurrences: processes of species extinctions. Pp. 19-34 in M.E. Soulè, ed., Conservation Biology: The Science of Scarcity and Diversity. Sinauer, Sunderland, Mass.

Glitzenstein, J.S., W.J. Plat,t and D.R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecological Monographs 65:441-476.

Hardin, E.D., and D.L. White. 1989. Rare vascular plant species associated with wiregrass (*Aristida stricta*) in the Southeastern United States. Natural Areas Journal 9:234-245.

Harrison, S., J. Maron, and G. Huxel. 2000. Regional turnover and fluctuation in occurrences of five plants confined to serpentine seeps. Conservation Biology 14:769-779.

Hawkes, C.W., and E.S. Menges. 1995. Density and seed production of a Florida endemic, *Polygonella basiramia*, in relation to time since fire and open sand. American Midland Naturalist 133:138-148.

Hawkes, C.W., and E.S. Menges. 1996. The relationship between open space and fire for species in a xeric Florida shrubland. Bulletin of the Torrey Botanical Club 123:81-92.

Heyward, F. 1939. The relation of fire to stand composition of longleaf pine forests. Ecology 20:287-304.

Kartesz, J.T. 1994. Synonymized Checklist of the Vascular Flora of the United States, Canada and Greenland. 2nd Ed. Timber Press, Portland, Ore.

Keeley, J.E. 1981. Reproductive cycles and fire regimes. Pp. 231-277 in Fire Regimes and Ecosystem Properties. General Technical Report WO-26, U.S. Department of Agiculture, Forest Service, Washington, D.C.

Kirkman, L.K., M.B. Drew, and D. Edwards. 1998. Effects of experimental fire regimes on the occurrence dynamics of *Schwalbea americana* L. Plant Ecology 137:115-137.

Kush, J.S., R.S. Meldahl, and W.D. Boyer. 2000. Understory plant community response to season of burn in natural longleaf pine forests. Pp. 32-39 *in* W. Keith. Moser and Cynthia F. Moser, eds., Fire and Forest Ecology: Innovative Silviculture and Vegetation Management. Tall Timbers Fire Ecology Conference, Proceedings No. 21. Tall Timbers Research Station, Tallahassee, Fla.

Lamont, B.B., P.W. Swanborough, and D. Ward. 2000. Plant size and season of burn affect flowering and fruiting of the grasstree *Xanthorrhoea preissii*. Austral Ecology 25:268-272.

Leslie, M., G.K. Meffe, J.L. Hardesty, and D.L. Adams. 1996. Conserving biodiversity on military lands: a handbook for natural resource managers. The Nature Conservancy, Arlington, Va.

Menges E. 1991. Seed germination percentage increases with population size in a fragmented prairie species. Conservation Biology 5:158-164.

Menges, E.S., and J. Kimmich. 1996. Microhabitat and time-since-fire: effects on demography of *Eryngium cuneifolium* (Apiaceae), a Florida scrub endemic plant. American Journal of Botany 83:185-191.

Menges, E.S., and N. Kohfeldt. 1995. Life history strategies of Florida scrub plants in relation to fire. Bulletin of the Torrey Botanical Club 122:282-297.

Ouborg, N.J. 1993. Isolation, population size and extinction: the classical and metaoccurrence approaches applied to vascular plants along the Dutch-Rhine-system. Oikos 66:298-308.

Platt, W.J., G.W. Evans, and M.M. Davis. 1988. Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. Oecologia 76:353-363.

Quintana-Ascencio, P.F., R.W Dolan, and E.S. Menges. 1998. *Hypericum cumulicola* demography in unoccupied and occupied Florida scrub patches with different time-since-fire. Journal of Ecology 86:640-651.

Ricklefs, R.E. 2001. The Economy of Nature. 5th Ed. W.H. Freeman and Company, New York.

Russo, M.J., B.A. Sorrie, B. van Erden, and T.E. Hippensteel. 1993. Rare and endangered plant survey and natural area inventory for Fort Bragg and Camp Mackall Military Reservations. Unpublished report, DOD Contract M67004-91-D-0010, The Nature Conservancy, Carrboro, N.C., and N.C. Natural Heritage Program, Raleigh.

Schafale, M., and A. Weakley. 1990. Classification of the natural communities of North Carolina, Third Approximation. North Carolina Natural Heritage Program, Raleigh, N.C.

Sparks, J.C., R.E. Masters, D.M. Engle, M.W. Palmer, and G.A. Bukenhofer. 1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. Journal of Vegetation Science 9:133-142.

Van treuren, R., R. Bijlsma, W. van Delden, and N. J. Ouborg. 1993. The effects of population size and plant density on outcrossing rates in locally endangered *Salvia pratensis.* Evolution 47:1094-1104.

Walker, J. 1993. Rare vascular plant taxa associated with the longleaf pine ecosystems: patterns in taxonomy and ecology. Pp. 105-125 *in* Sharon M. Hermann, ed., The Longleaf Pine Ecosystem: Ecology, Restoration and Management. Tall Timbers Fire Ecology Conference, Proceedings No. 18. Tall Timbers Research Station, Tallahassee, Fla.

Walker, J., and R.K. Peet. 1983. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. Vegetatio 55:163-179.

Westemeier, R.L., J.D. Brown, and S.A. Simpson. 1998. Tracking the long-term decline and recovery of an isolated population. Science 282:1695-1698.

Widen, B. 1993. Demographic and genetic effects on reproduction as related population size in a rare, perennial herb, *Senecio integrifolius* (Asteraceae). Biological Journal of the Linnean Society 50:179-195.