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MICROHABITAT RELATIONS  
OF THE RARE REED BENT  
GRASS, *CALAMAGROSTIS*  
*PORTERI* SUBSP. *INSPERATA*  
(POACEAE), WITH  
IMPLICATIONS FOR ITS  
CONSERVATION<sup>1</sup>

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ABSTRACT

*Calamagrostis porteri* subsp. *insperata* was known from only two extant populations in Ohio prior to the late 1980s. Recent searching has documented more than 80 populations of this rare grass in five states. Although more populations exist than previously believed, the habitat requirements for this subspecies are still unknown. To quantify these requirements, data were collected on photosynthetic photo-flux density (PPFD), air and soil temperature, vapor-pressure deficits (VPD), soil moisture and depth, pH, percent organic matter, and associated species cover from three populations in southern Illinois. Leaf area, predicted total leaf area, and number of tillers per m<sup>2</sup> were measured to ascertain the relationship between vegetative performance and microenvironmental conditions. Detrended Canonical Correspondence Analysis (DCCA) was used to ordinate the samples using the cover of co-occurring species and the environmental variables. Leaf area, predicted total leaf area, and number of tillers were significantly related to the nine environmental variables at all three sites. The vegetative performance of this rare grass in southern Illinois seems to be determined by a complex suite of environmental factors, of which PPFD, VPD, and soil temperature are extremely influential, especially in the spring. The ordination shows that the three populations are distinctly separated, with total predicted leaf area, tiller density, soil moisture, soil temperature, air temperature, and pH being highly correlated to the ordination axes. Habitat modifications resulting in closed forest canopies detrimentally affect the vegetative performance of this taxon.

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Conservation biologists, in attempting to evaluate the causes of endangerment to rare plant species in order to aid in their recovery, have employed ecological research to characterize biotic interactions and habitat requirements (Schemske et al., 1994). In particular, an understanding of the autecology and natural history of rare species is necessary (Brussard, 1991). A number of studies focusing on environmental conditions have led to a better understanding of limiting ecological factors responsible for rarity of endangered species (Gawler et al., 1987; Buchele et al., 1989; Boyd & Hilton, 1994; Vivian, 1967).

Lack of basic ecological information about the former Federal endangered species candidate (FWS, 1993) *Calamagrostis porteri* A. Gray subsp. *insperata* (Swallen) C. W. Greene (Poaceae) poses a problem to conservation biologists and land managers. As conservation measures are appropriately planned for this taxon, there is a need to better understand its microhabitat ecology.

*Calamagrostis porteri* subsp. *insperata* (reed bent grass) was first described from Ohio as *Calamagrostis insperata* (Swallen, 1935). Another Ohio population, three Missouri populations, and one Arkansas population (now believed extirpated) were documented in subsequent years. This grass is now known from more than 80 populations in five states: Illinois, Indiana, Kentucky, Missouri, and Ohio (Campbell et al., 1992; Homoya, 1995; Summers, 1993; Bittner, 1995b). Its habitats are extremely varied but are often located on cool, north-facing sandstone bluff edges and tree-fall gaps in dry-mesic upland forests found in unglaciated areas (Bittner, 1995a). This cool-season, rhizomatous grass rarely flowers and spreads almost exclusively through vegetative growth. It is a tufted perennial that can stand up to 1 m tall. Highly specific flowering conditions, self-incompatibility, and poor fruiting success contribute to the reproductive limitations of several taxa of *Calamagrostis*, including *C. porteri* subsp. *insperata* (Greene, 1980).

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The goals of this study were to determine how microhabitat conditions and ground cover of associated taxa are related to the vegetative performance of *Calamagrostis porteri* subsp. *insperata* in three of the five known southern Illinois populations (as of 1993), to contribute to the general information about this taxon, and to aid in evaluating its endangered status.

## MATERIALS AND METHODS

### STUDY SITES

The five Illinois populations of *Calamagrostis porteri* subsp. *insperata* are located in Pope County, southern Illinois, at Bell Smith Springs Ecological Area and Lusk Creek Canyon Natural Area (Fig. 1). All the populations are within the Shawnee National Forest and are managed by the U.S. Forest Service under prescription 8.2 (to protect, preserve, and enhance the unique scientific, educational, and natural values found within this National Natural Landmark and Ecological Area; USDA, 1992). Only three of the five populations were sizeable enough for the purposes of this research. Two populations were from Bell Smith Springs [BSS1, *Summers* 4774 (MO); BSS2, *Bittner* 347 (ILLS), 348 (SIUC)], and one population was from Lusk Creek Canyon [LC, *Bittner* 350 (ILLS)]. These three populations were estimated to contain between 4000 and 18,000 tillers.

This unglaciated, predominantly forested area lies in the Greater Shawnee Hills Section of the Shawnee Hills Natural Division (Schwegman, 1973). The bedrock consists of massive Pennsylvanian sandstone strata, and the topography is rugged, with many canyons, bluffs, and ravines. The well-drained soils have low organic-matter content, moderate permeability, and moderate available water capacity (USDA, 1975).

The study populations of *Calamagrostis porteri* subsp. *insperata* are located predominantly within the dry-mesic, upland forest community. The habitat of *C. porteri* subsp. *insperata* in these populations is on cool, northwest- and northeast-facing bluff edges and hillsides with high species diversity and many rare, uncommon, and conservative plants (taxa with a high degree of habitat specificity) as associates. Tillers occur in both leaf-litter zones and moss- and lichen-dominated areas within dry-mesic, oak-hickory forests. Within two populations (LC and an unstudied BSS population), dense mats of *Sphagnum* species are present throughout large sections. Springs, intermittent streams, or seeps are also common within the study populations. The dominant overstory species association consists of

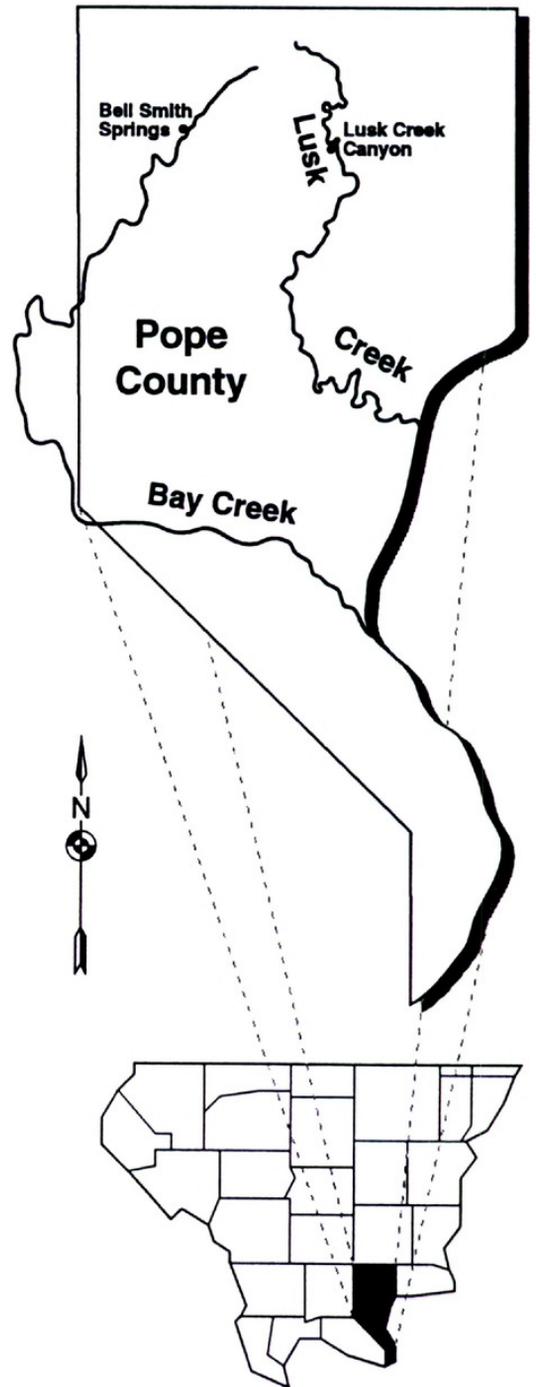


Figure 1. The location of *Calamagrostis porteri* subsp. *insperata* populations at Bell Smith Springs Ecological Area and Lusk Creek Canyon Natural Area in Pope County, southern Illinois.

*Quercus alba* L., *Q. rubra* L., *Q. velutina* Lam., *Carya glabra* (Mill.) Sweet, and *C. ovata* (Mill.) K. Koch (Voigt & Mohlenbrock, 1964).

### FIELD PROCEDURES

In each of the three populations, fifteen 1-m<sup>2</sup> quadrats were located randomly and accepted if they contained tillers of *C. porteri* subsp. *insperata*. An additional four randomly selected 20-m tran-

sects of contiguous 1-m<sup>2</sup> quadrats were established perpendicular to the bluff edge within the BSS1 population (but did not necessarily contain tillers).

The number of tillers in each quadrat was sampled four times during the growing season of 1993 (April, May, July, and September). To calculate mean leaf area per quadrat, the lengths of all the leaves from five randomly chosen tillers, the numbers of leaves per tiller, and an estimated percent of living area per leaf were recorded twice (May and August). A regression developed from leaf tracings of 100 randomly selected leaves was used to predict leaf area from leaf length ( $R^2 = 0.94$ ,  $P < 0.0001$ ). Leaf area was calculated by multiplying the estimated leaf area (predicted from leaf length) by the percent living area per leaf. Mean leaf area per quadrat was calculated by multiplying the number of tillers from the previous month by the mean number of leaves per tiller by the mean leaf area.

Predicted total leaf area per quadrat was calculated by multiplying the mean leaf area for the season by the mean number of leaves per tiller by the mean number of tillers for the season.

Tiller survivorship was determined at each of the three populations by marking new tillers with plastic tags monthly throughout the growing season from April through September in three randomly selected 1-m<sup>2</sup> quadrats per population. Both new tillers and dead tillers (> 50% dead area) were recorded each month.

To determine which factors were related to the microdistribution of *C. porteri* subsp. *insperata*, environmental factors were measured twice a day at monthly intervals (April–September) throughout the growing season from 8:00 to 10:00 A.M. and 2:00 to 4:00 P.M.

At the midpoint of each quadrat, light intensity was measured with a line-quantum sensor, model LI-191SA (LICOR, Lincoln, NB) attached to a data logger (LICOR model 1000). The line-quantum sensor averages photosynthetic photon-flux density (PPFD) through 400–700 nm over 1 m. Total PPFD measurements were made in full sunlight throughout the data-collection period and used as a control. Available PPFD within each quadrat was calculated by dividing values for PPFD in each quadrat by control values to give a total light-intensity value.

Air, soil, and wet-bulb temperatures were collected similarly to PPFD in the individual quadrats, and at 5-m intervals along the transects. The wet- and dry-bulb temperatures were used with barometric pressure obtained from the nearby Carbondale airport weather station (approximately 65 km NE of the study sites) to calculate vapor-pressure deficit (VPD) values according to Cox (1990).

Within each quadrat, morning and afternoon observations of environmental data (PPFD, air, and soil temperature, and vapor pressure deficits) were averaged for each month to obtain six monthly observations. Several transformations were performed to normalize the data according to Sokal and Rohlf (1969). PPFD values were divided by 100 and arcsine transformed prior to analysis ( $\arcsin \sqrt{X * 100}$ ). Vapor pressure deficit values were divided by 10 and arcsine transformed. Soil and air temperature values were log-base 10 transformed.

Soil moisture was measured by collecting soil samples in May and July from each individual quadrat, and in every fifth quadrat within each transect, following the procedures of Bannister (1986). The soil-moisture values were divided by 100, arcsine transformed, and averaged prior to analysis. Soil depth to bedrock was measured in each corner and midpoint for each quadrat with a steel probe, averaged, and log-base 10 transformed prior to analysis. Soil samples, previously dried for soil-moisture measurements, were used to determine the pH using a 1:5 soil-water slurry, and organic content using standard procedures (SPAC, 1992). Soil pH was converted to hydrogen-ion concentration for data analysis.

The canopy cover of all vascular plant species rooted in each quadrat was estimated in July using a modified Daubenmire scale (Abrams & Hulbert, 1987). Moss and lichen cover was recorded, but identification to species was not made. The midpoint values were used for the species-cover data in an ordination, and for total-cover calculations for each sample. Arcsine-transformed midpoint values were used for statistical analysis. The identity of canopy species immediately above each quadrat was also determined; nomenclature follows Mohlenbrock (1986).

#### ANALYTICAL METHODS

The following analyses were performed individually for each of the three populations using SAS, Version 6 (SASI, 1990). Simple and multiple regressions were performed to predict tiller densities, mean leaf area, and total predicted leaf area (performance) from air temperature, soil temperature, vapor-pressure deficit, PPFD, soil moisture, soil depth, pH, percent organic matter, and vegetation cover (environmental). For the simple and multiple monthly regressions, environmental variables (independent variables) from the previous month and the current month were tested against the performance of *C. porteri* subsp. *insperata* (dependent variables) for the current month. Mean variables

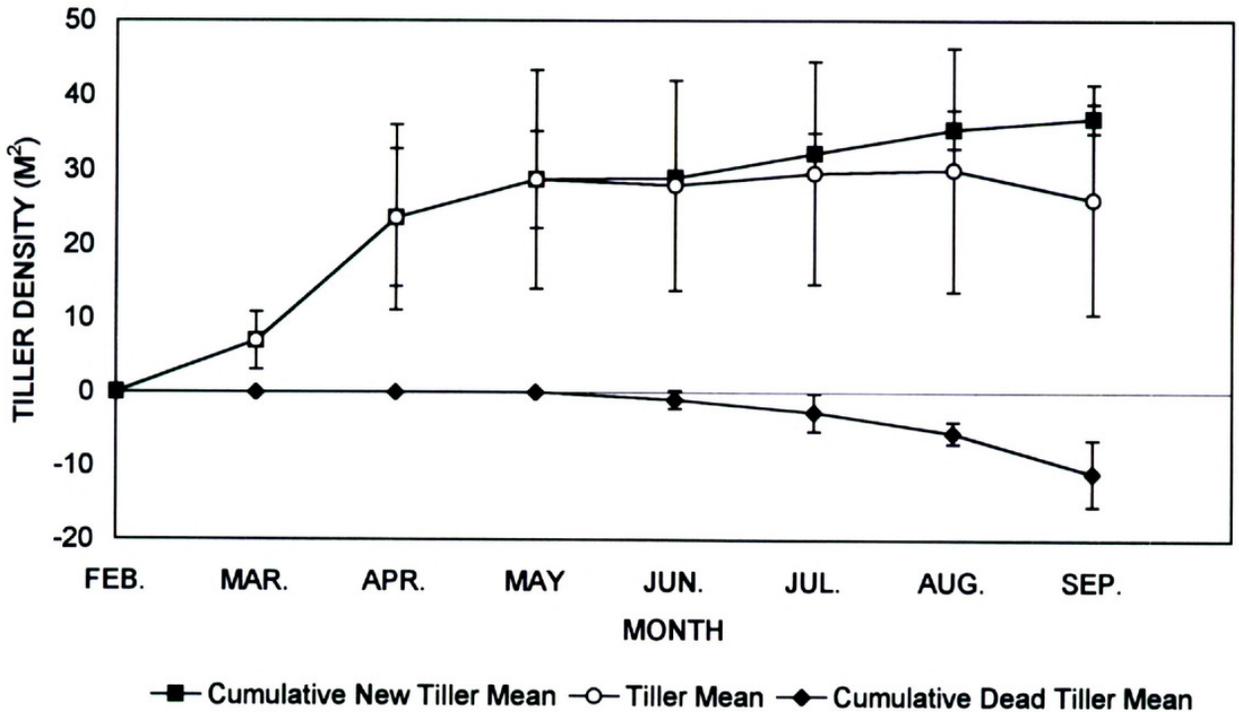


Figure 2. Net tiller density and cumulative number of new and dead tillers of *Calamagrostis porteri* subsp. *insperata* from BSS1, BSS2, and LC from February to September 1993 (mean of nine quadrats from the three sites).

were used for simple regressions. The pair of environmental variables with the lowest probabilities ( $P$ ) for each month and mean were used for the multiple regressions, and for a simple regression of their cross-products, respectively.

Separate one-way ANOVAs were used to compare tiller presence/absence (dependent variable) at BSS1 for each month and mean using the environmental variables (independent variables). Similarly, environmental data from the previous month and the current month were tested against the performance data for the current month.

Detrended Canonical Correspondence Analysis (DCCA) was performed on the cover and environmental data matrices using CANOCO (ter Braak, 1988), in a manner similar to that of Gibson and Looney (1994), to determine the relationships among the 125 quadrats. The ordination was based upon the 59 quadrats that contained tillers of *C. porteri* subsp. *insperata* and from which environmental data were collected. The quadrats for which environmental data were not available were not used to construct the ordination axes, but were held "passive" in the analysis and added subsequently, after the axes were constructed on the basis of their cover data. Rare species were downweighted using the rare-species downweighting option (ter Braak, 1988). Reliability of the results was checked and found to be acceptable using Oksanen and Minchin's (1997) debugged and strict version of DECORANA.

The relationships between the measures of performance for *C. porteri* subsp. *insperata* (i.e., leaf area, predicted area, and tiller density) and the ordination axis-scores were determined using Spearman Rank Correlations (SASI, 1990).

## RESULTS

The highest number of new tillers was produced in April, with March and May yielding the second and third highest number of new tillers, respectively (Fig. 2). New tillers were produced each month, but to a lesser extent from June to September. Cumulative gains leveled off from May to June after a sharp increase. This plateau was followed by a more moderate increase. Mean tiller density remained relatively constant from April to September, with the highest mean in August. No tillers died until June, with the frequency increasing each month thereafter.

The mean percentage PPFD decreased markedly from April to May as the forest canopy closed, lowering the available PPFD on the forest floor to less than 5% (Table 1). Mean monthly temperature of both air and soil increased into the summer, as expected, with a high variation between months. Vapor-pressure deficit monthly means were highest in the late spring and early fall.

Mean tiller densities increased slightly from April to May and generally declined into September (Table 1). Tiller density was highly variable among

Table 1. Monthly means and standard deviations for environmental data and tiller densities in three populations (BSS1 = Bell Smith Springs 1, BSS2 = Bell Smith Springs 2, and LC = Lusk Creek) of *Calamagrostis porteri* subsp. *insperata*. (PPFD = photosynthetic photo flux density, AirT = air temp. (°C), SoilT = soil temp. (°C), VPD = vapor pressure deficit (mm Hg), Tlr = tillers per m<sup>2</sup>; LC and BSS2 have n = 15; BSS1 has n = 95 for PPFD and Tlr and n = 35 for AirT, SoilT, and VPD). No tiller density data collected for any population in June or August.

		April		May		June		July		August		September	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
BSS1	PPFD	71.9	11.8	6.4	5.4	3.3	4.4	2.7	3.8	2.8	1.7	2.6	2.1
	AirT	13.3	1.3	22.3	0.6	26.9	0.8	29.8	0.5	28.4	0.7	21.2	0.4
	SoilT	12.8	0.4	14.9	0.7	18.4	0.8	22.7	0.9	22.1	0.8	18.8	0.5
	VPD	2.3	0.4	2.5	0.4	2.5	0.4	1.1	0.2	0.7	0.2	2.6	0.3
	Tlr	19.3	20.6	20.1	21.1	—	—	21.1	22.2	—	—	13.8	12.6
BSS2	PPFD	53.7	6.9	10.3	10.3	2.8	1.7	2.6	2.6	2.3	2.7	1.5	1.1
	AirT	17.4	0.9	20.2	0.5	29.6	0.5	28.3	0.2	25.6	0.4	20.7	0.3
	SoilT	10.2	0.4	14.7	0.3	18.7	0.4	22.7	0.4	21.8	0.4	17.0	0.6
	VPD	2.2	0.4	2.0	0.2	2.2	0.2	1.2	0.2	1.8	0.2	2.2	0.2
	Tlr	32.0	23.6	45.3	35.1	—	—	41.4	28.5	—	—	27.8	18.0
LC	PPFD	41.4	13.0	6.1	3.9	2.5	2.2	3.3	3.0	6.6	2.2	6.3	5.8
	AirT	24.7	1.8	18.3	0.6	28.4	0.3	30.3	0.2	30.3	0.4	26.9	0.3
	SoilT	9.8	0.5	13.2	0.3	19.3	0.4	22.0	0.5	22.3	0.4	17.8	0.4
	VPD	3.5	0.9	1.6	0.5	2.1	0.2	1.7	0.2	2.0	0.2	3.4	0.3
	Tlr	13.1	17.7	75.7	66.1	—	—	83.0	67.4	—	—	69.2	53.2

samples within the populations, ranging from 0 to almost 240 tillers per m<sup>2</sup>. Mean leaf area declined throughout the year as well, due to leaf senescence. Both leaf area and total predicted leaf area were highly variable within the populations.

Five of the nine environmental variables were significantly different between quadrats with and without tillers of *C. porteri* subsp. *insperata* at different times throughout the year in population BSS1: VPD, air and soil temperature, PPFD, and soil depth (Table 2). Quadrats with tillers present had significantly lower VPD early in the season. Significantly higher soil temperature, air temperature, VPD, PPFD, and deeper soil were observed in quadrats with tillers of *C. porteri* subsp. *insperata* during the second half of the growing season.

Five of the nine environmental variables significantly predicted *C. porteri* subsp. *insperata* performance at BSS1: VPD, PPFD, pH, and soil organic matter (Table 3). VPD was negatively related to leaf area, and PPFD, pH, and organic matter were positively related to tiller density, leaf area, and total predicted leaf area, respectively.

Five of the nine environmental variables at BSS2 significantly predicted *C. porteri* subsp. *insperata* performance: VPD, PPFD, soil temperature, cover, and organic matter (Table 3). Leaf area was negatively related to soil temperature, but positively related to plant cover; tiller density was negatively related to VPD, but positively related to PPFD and

soil temperature; total predicted leaf area was positively related to PPFD; tiller density for two monthly data combinations was positively related to soil temperature and PPFD combined; and mean leaf area was positively related to total cover and negatively related to soil temperature in combination. Predicted total leaf area was positively related to a simple regression interaction between PPFD and organic matter. The regression predicting tiller density in July from PPFD and soil temperature in June had the highest R<sup>2</sup> of all the regressions performed (0.80). Mean leaf area predicted from cover and soil temperature also had a high variance accounted for (R<sup>2</sup> = 0.74).

Five of the nine environmental variables at LC significantly predicted *C. porteri* subsp. *insperata* performance: VPD, PPFD, soil moisture, and soil and air temperature (Table 3). Leaf area was negatively related to soil temperature and positively related to soil moisture individually, combined, and by their interaction. Tiller density was positively related to VPD and PPFD. Total predicted leaf area was positively related to PPFD and air temperature. Mean soil temperature and moisture predicting leaf area accounted for the most variance (R<sup>2</sup> = 0.47).

A total of 113 species associated with *C. porteri* subsp. *insperata* was recorded from the quadrats within the three sites. There were 47 species with a frequency greater than 10% at any site. The woody species (woody vines, seedlings, saplings,

Table 2. ANOVA results from Bell Smith Springs (BSS1) listing significant relationships between the presence/absence of *Calamagrostis porteri* subsp. *insperata* and environmental variables. Given are the probability ( $P$ ), variance accounted for ( $R^2$ ), degrees of freedom (d.f.), mean value (Mean), number of occurrences ( $N$ ), and standard error (s.e.) of each combination of months of measurement. (Environmental variable abbreviations are listed in Table 1. Depth = soil depth (cm), Dep.Var. = dependent performance variable, Ind.Var. = independent environmental variable.)

Month		Ind.Var.	$P$	$R^2$	d.f.	Present			Absent		
Dep.Var.	Ind.Var.					Mean	$N$	s.e.	Mean	$N$	s.e.
May	May	VPD	0.0122	0.18	1/34	2.44	28	0.08	2.91	7	0.10
July	May	VPD	0.0095	0.19	1/34	2.43	27	0.08	2.89	8	0.09
August	May	VPD	0.0095	0.19	1/34	2.43	27	0.08	2.90	8	0.09
July	July	SoilT	0.0308	0.13	1/34	22.89	27	0.19	22.11	8	0.12
August	July	SoilT	0.0308	0.13	1/34	22.90	27	0.19	22.11	8	0.12
August	August	PPFD	0.0003	0.14	1/90	3.18	66	0.23	1.90	25	0.15
August	August	AirT	0.0306	0.13	1/34	28.56	27	0.14	27.90	8	0.15
August	August	SoilT	0.0209	0.15	1/34	22.28	27	0.15	21.60	8	0.08
August	August	VPD	0.0060	0.21	1/34	0.74	27	0.05	0.54	8	0.06
September	August	PPFD	0.0008	0.12	1/90	3.17	65	0.23	1.98	26	0.17
September	August	AirT	0.0113	0.18	1/34	28.60	26	0.18	27.95	9	0.09
September	August	SoilT	0.0488	0.11	1/34	22.27	26	0.16	21.71	9	0.13
September	August	VPD	0.0207	0.15	1/34	0.74	26	0.05	0.60	9	0.06
September	September	PPFD	0.0002	0.14	1/90	2.94	65	0.22	1.63	26	0.51
September	September	SoilT	0.0094	0.19	1/34	18.94	26	0.10	18.44	9	0.11
Mean	Mean	Depth	0.0126	0.07	1/90	28.73	70	2.06	16.80	21	2.54

and shrubs) were, in descending order of dominance, *Parthenocissus quinquefolia* (L.) Planch., *Ostrya virginiana* (Mill.) K. Koch, *Toxicodendron radicans* (L.) Kuntze, *Sassafras albidum* (Nutt.) Nees, *Acer saccharum* Marshall, *Quercus rubra*, *Q. alba*, *Carya glabra*, *Vaccinium pallidum* Aiton, *Fagus grandifolia* Ehrh., *Q. velutina*, and *C. ovata* (mean cover > 2% at any site). The herbaceous vascular and nonvascular species were, in descending order of dominance, mosses, *Polystichum acrostichoides* (Michx.) Schott, *Dichanthelium boscii* (Poir.) Gould & L. G. Clark, and *Luzula multiflora* (Retz.) Lej., (mean cover > 2% at any site).

The first, second, and third DCCA ordination axes cumulatively accounted for 21, 39, and 53% of the variance, respectively (the eigen values were 0.45, 0.41, and 0.30, respectively). Plots from the three sites (BSS1, BSS2, LC) were dissimilar to each other and clearly separated when plotted on DCCA axes 1 and 2 (Fig. 3). Only a small overlap is present between the LC and BSS2 samples. The LC samples had a higher tiller density and a greater predicted total leaf area than those from either BSS site. The two variables with the highest correlation to the first axis were soil temperature ( $r = 0.69$ ) and soil moisture ( $r = 0.53$ ;  $P < 0.05$  for all correlations reported here). The two variables with the highest correlation to the second axis were air temperature ( $r = 0.62$ ) and pH ( $r = 0.53$ ). The variables with the highest correlation to the third axis

were PPFD ( $r = 0.53$ ) and soil depth ( $r = -0.43$ ). Tiller density ( $r = 0.34$ ) and total predicted leaf area ( $r = 0.33$ ) of *C. porteri* subsp. *insperata* were highly correlated ( $P < 0.001$ ) to the second axis, while no measures of performance were significantly related to the first axis.

The species-environmental data biplot shows the environmental variables and species (those with weightings > 50) ordination scores (Fig. 4). *Acer saccharum*, *Luzula multiflora*, *Ostrya virginiana*, *Parthenocissus quinquefolia*, *Quercus alba*, *Sassafras albidum*, *Toxicodendron radicans*, and mosses were highly weighted in the ordination (weight > 100). The LC samples have a higher air temperature and pH. The BSS2 samples have a higher VPD and soil depth. The BSS1 samples have higher organic matter, total cover, PPFD, soil moisture, and soil temperature.

#### DISCUSSION

The habitat conducive to supporting populations of *Calamagrostis porteri* subsp. *insperata* in the Greater Shawnee Hills Section of the Shawnee Hills Natural Division (Schwegman, 1973) of southern Illinois is comprised of high-quality (Grade A or B; White & Madany, 1978), dry-mesic, upland oak-hickory forest and bluff edge communities that have northeast- or northwest-facing aspects.

In determining the microhabitat requirements of

Table 3. Probability (*P*), variance accounted for (*R*<sup>2</sup>), parameter estimate sign (+/-), and the significant independent variables predicting the performance (i.e., tiller density, leaf area, and predicted total leaf area) of *Calamagrostis porteri* subsp. *insperata* in month combinations from BSS1, BSS2, and LC are listed for the simple and multiple regressions. (Environmental variable abbreviations are listed in Tables 1 and 2. SoilMo = soil moisture, Organic = soil organic matter content, Cover = cover of associated species; LC & BSS2: for the simple and cross-product regressions d.f. = 1/13, for the multiple regressions d.f. = 2/12; BSS1: d.f. = 1/63 for PPF, d.f. = 1/27 for Organic and pH, d.f. = 1/26 for VPD.)

Month		Simple regression				Multiple regression					
Dep.Var.	Ind.Var.	Dep.Var.	Variables	Ind.Var.	<i>P</i>	<i>R</i> <sup>2</sup>	Dep.Var.	Variables	Ind.Var.	<i>P</i>	<i>R</i> <sup>2</sup>
<b>Population BSS1</b>											
Aug.	Aug.	Leaf area	- VPD	- VPD	0.0098	0.24	-	-	-	-	-
Sep.	Aug.	Tiller	+ PPF	- VPD	0.0075	0.11	-	-	-	-	-
Mean	Mean	Leaf area	+ pH	-	0.0188	0.19	-	-	-	-	-
Mean	Mean	Pred. area	+ Organic	-	0.0292	0.17	-	-	-	-	-
<b>Population BSS2</b>											
May	May	Tiller	- VPD	- VPD	0.0066	0.45	-	-	-	-	-
July	May	Tiller	- VPD	- VPD	0.0102	0.41	-	-	-	-	-
July	June	Tiller	+ PPF	+ PPF	0.0003	0.64	Tiller	(+)PPF + SoilT	-	0.0001	0.80
July	June	Tiller	+ SoilT	+ SoilT	0.0377	0.29	-	-	-	-	-
July	July	Tiller	+ PPF	+ PPF	0.0033	0.50	Tiller	(+)PPF + SoilT	-	0.0011	0.68
July	July	Tiller	+ SoilT	+ SoilT	0.0052	0.46	-	-	-	-	-
Aug.	July	Leaf area	- SoilT	- SoilT	0.0329	0.30	-	-	-	-	-
Mean	Mean	Tiller	+ PPF	+ PPF	0.0025	0.52	Leaf area	(+/-)Cover + SoilT	-	0.0003	0.74
Mean	Mean	Leaf area	+ Cover	+ Cover	0.0110	0.40	-	-	-	-	-
Mean	Mean	Pred. area	+ PPF	+ PPF	0.0025	0.52	-	-	-	-	-
Mean	Mean	Pred. area	+ PPF * Organic	+ PPF * Organic	0.0309	0.31	-	-	-	-	-
<b>Population LC</b>											
Apr.	Apr.	Tiller	+ VPD	+ VPD	0.0135	0.39	-	-	-	-	-
July	June	Tiller	+ PPF	+ PPF	0.0450	0.27	-	-	-	-	-
July	July	Tiller	+ PPF	+ PPF	0.0486	0.27	-	-	-	-	-
Sep.	Aug.	Tiller	+ PPF	+ PPF	0.0290	0.32	-	-	-	-	-
Mean	Mean	Tiller	+ PPF	+ PPF	0.0434	0.28	Leaf area	(-/+ )SoilT + SoilMo	-	0.0214	0.47
Mean	Mean	Leaf area	- SoilT	- SoilT	0.0287	0.32	-	-	-	-	-
Mean	Mean	Leaf area	+ SoilMo	+ SoilMo	0.0087	0.42	-	-	-	-	-
Mean	Mean	Pred. area	+ PPF	+ PPF	0.0320	0.31	-	-	-	-	-
Mean	Mean	Pred. area	+ AirT	+ AirT	0.0496	0.26	-	-	-	-	-
Mean	Mean	Leaf area	- SoilT * SoilMo	- SoilT * SoilMo	0.0082	0.43	-	-	-	-	-

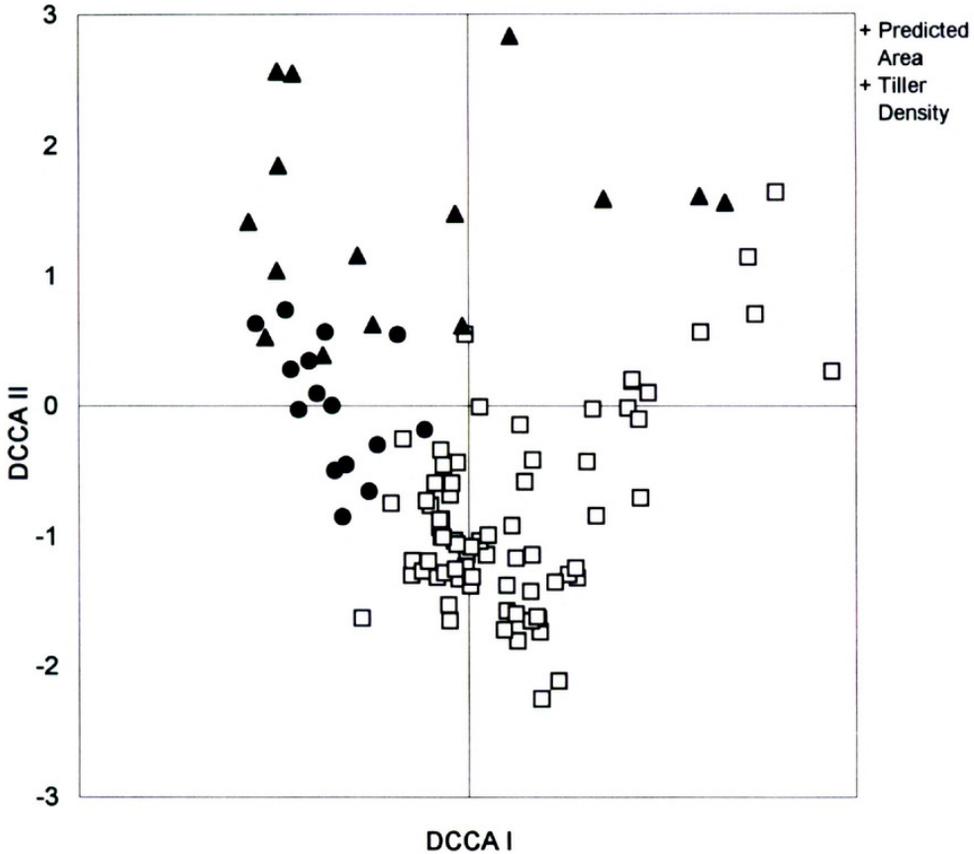


Figure 3. DCCA Axis I and II plot of quadrats containing *Calamagrostis porteri* subsp. *insperata* from sites BSS1 (□), BSS2 (●), and LC (▲). Dependent variables that are significantly ( $P < 0.05$ ) correlated with each ordination axis are listed with their signs on the appropriate axis.

*C. porteri* subsp. *insperata*, we found that vegetative performance is related to a complex suite of environmental factors. All nine environmental variables tested were significantly related at one of the three sites (Table 3). Vapor pressure deficit and PPF were related to the vegetative performance at all three sites. Additionally, vegetative performance was related to air and soil temperature and soil moisture at LC, cover, soil temperature and organic matter at BSS2, and organic matter and pH at BSS1. No single environmental factor seems to be responsible for vegetative performance. Similarly, no single environmental factor is related to the presence or absence of *C. porteri* subsp. *insperata*. Rather, as shown in studies of other taxa (e.g., Gibson & Good, 1987), it is the relative magnitude and importance of these limiting factors that provide an understanding of the subspecies' microhabitat requirements or realized niche.

Although these results show many shared trends between the populations with respect to the environmental variables as significant predictors of vegetative performance, the DCCA ordination shows the sites separated when plotted on two axes. It is clear that the ground cover of associated species and the microhabitat are not similar among the

three sites (at the local level). At a broader level, this is also supported by a review of the literature that shows a wide range of plant associates (and habitats) for *C. porteri* subsp. *insperata* throughout its range (Ambrose et al., 1994; Campbell et al., 1992; Summers, 1993; Bittner, 1995a).

Although soil moisture, soil temperature, air temperature, and pH were highly correlated with the first two axes in the ordination, only 39% of the variance was accounted for. This demonstrates that more factors are involved with distribution and abundance of the associated species than were sampled. Total predicted leaf area and tiller density were both significantly related to the second axis. This was due to the much higher tiller densities and more robust leaves present at the LC population.

Leaf senescence contributed greatly to the decline in leaf area from May to August at each site. Because *C. porteri* subsp. *insperata* grows only on cool, northeast- or northwest-facing slopes, it is possible that there is an upper limiting temperature for growth. Temperature is frequently the main limiting factor for  $C_3$  taxa (Ode et al., 1980; Barnes et al., 1983), such as *C. porteri* subsp. *insperata*. While high soil temperature is related to high per-

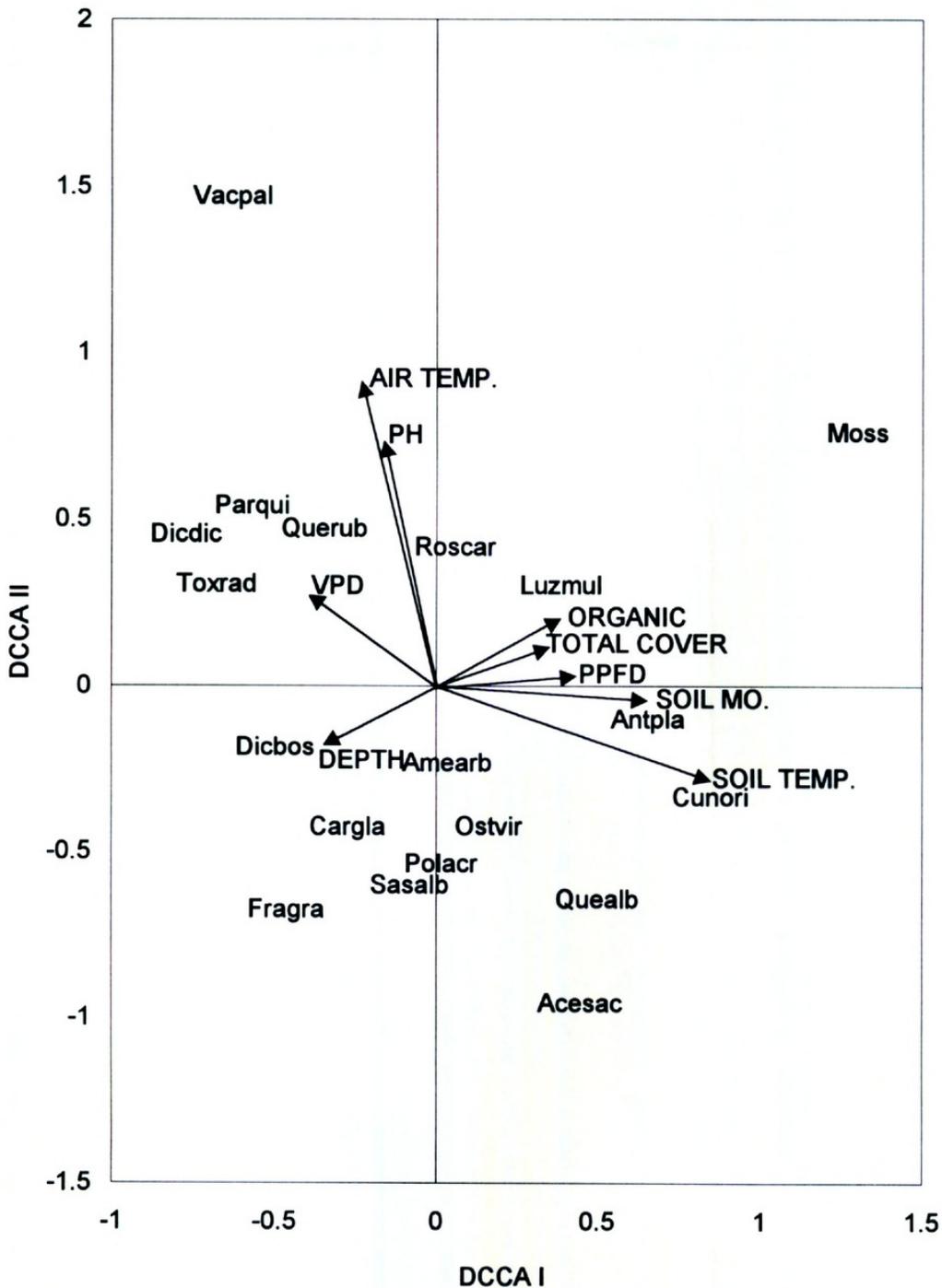


Figure 4. DCCA Axis I and II species cover-environmental variable biplot ordination. Environmental variables and species (those with weightings > 50) coordinates are plotted and labeled on Axes I and II. Acesac = *Acer saccharum*, Amearb = *Amelanchier arborea*, Antpla = *Antennaria plantaginifolia*, Cargla = *Carya glabra*, Cunori = *Cunila organoides*, Dicbos = *Dicanthelium boscii*, Dicdic = *D. dichotomum*, Fragra = *Fagus grandifolia*, Luzmul = *Luzula multiflora*, Ostvir = *Ostrya virginiana*, Parqui = *Parthenocissus quinquefolia*, Polacr = *Polystichum acrostichoides*, Quealb = *Quercus alba*, Querub = *Q. rubra*, Roscar = *Rosa carolina*, Sasal = *Sassafras albidum*, Toxrad = *Toxicodendron radicans*, Vacpal = *Vaccinium pallidum*.

formance early in the growing season, it may contribute to increased leaf senescence later in the season.

*Calamagrostis porteri* subsp. *insperata* seems to exhibit microhabitat selection similar to that of *Calamagrostis canadensis* (Michx.) P. Beauv., a boreal forest understory species. *Calamagrostis canadensis*

exhibits an opportunistic "guerrilla" strategy for clonal foraging that allows the plants to vegetatively locate and exploit the most favorable microhabitats within the population by expanding rhizomes into conditions with warmer soil and higher light, as demonstrated in a glasshouse experiment (Macdonald & Lieffers, 1993). Field observations also doc-

umented that *C. canadensis* allocates resources to its rhizomes for the invasion of favorable microsites (e.g., treefall gaps). Rhizome expansion and exploitation in *C. canadensis* is influenced by soil temperature and cover, rather than PPFD alone (Macdonald & Lieffers, 1993). Tillers of *C. porteri* subsp. *insperata* at population BSS1 were present within the most favorable microhabitats (i.e., quadrats with higher soil temperature and PPFD; Table 2), as in *C. canadensis*.

Observations of tiller production suggest that there are two distinct periods of production, one in the spring and the second in mid to late summer, with the latter considerably lower. The performance of *C. porteri* subsp. *insperata*, especially in the early spring, may be the result of the microenvironmental conditions from the previous year. In *C. canadensis*, mobilization of rhizome carbohydrate reserves for shoot regrowth is responsible for tiller production in the spring (Hogg & Lieffers, 1991), and it is likely that the same is true for *C. porteri* subsp. *insperata*. The second production period may be the result of the photosynthetic output from the current year. The difficulty of understanding the performance of individual tillers is also compounded by the fact that not all photosynthetic products go into tiller production, but some are allocated for rhizome elongation and foraging (Macdonald & Lieffers, 1993).

Unfortunately, the present study was unable to determine the conditions favorable for sexual reproduction due to the low number of flowering tillers. Some states, such as Missouri, have seen prolific but sporadic flowering episodes in some populations (Summers, 1993). No such events have been noted in Illinois. However, from field observations and extrapolations from neighboring samples, inferences can be made to determine the microhabitat conditions most conducive to the production of flowering tillers. Two sterile flowering tillers (inflorescences without reproductive structures) were recorded in 1992, and one in 1993, from the same location (it is unknown if it was the same genet). This location in population BSS1, on a bluff edge under a small canopy gap along a hiking trail, allowed almost full sunlight to reach the tiller from early morning through midday. The northeast-facing aspect at this location allowed the soil and air to be heated by sunlight early in the day and remain warm throughout the day. In contrast, samples at BSS2 and LC had northwest-facing aspects, and did not have soil heated directly by sunlight until midday or the afternoon. Furthermore, soil temperature and PPFD were higher earlier in the year at BSS1 than at BSS2 or LC. These

observations suggest an important role of early-mid growing season soil temperature and light on flowering. Late-season environmental factors may be less important for flowering as suggested by Havens and Holland (1998, this issue), who found no effect on sexual reproductive success from differences in late-season light. The flowering-tiller location was also wet for considerable parts of the year because of the presence of an intermittent stream.

Environmental data were collected for the entire growing season from a quadrat located less than 1 m from the flowering tiller (1993). This same quadrat was the DCCA ordination Axis I right endpoint. Axis I was positively correlated with soil temperature ( $r = 0.69$ ) and soil moisture ( $r = 0.53$ ). These data suggest that there is a very small window of appropriate microhabitat conditions conducive to producing flowering tillers that is dependent on a complex suite of environmental factors including soil temperature, soil moisture, and light. Of course, other environmental and genetic factors not examined may also be related to the ability of this genet to flower.

Establishment of new populations of *C. porteri* subsp. *insperata* via sexual means would be an unlikely event. It is extremely probable that each population consists of a single, fragmented genet. Because *C. porteri* subsp. *insperata* is supposedly self-incompatible (Greene, 1980), successful fertilization would require simultaneous flowering of two genetically dissimilar populations or genets (over 1 km apart at BSS and 50 m at LC). Many plants lack viable pollen (Greene, 1980) or lack sexual structures altogether (Summers, 1993; Bittner, 1995a). Even if fertilization occurs, successful seed production is still not ensured (Greene, 1980). The remote chance of successful sexual reproduction was demonstrated by Havens and Holland (1998) when they hand-crossed four presumably different genotypes and produced only one seed that germinated out of 2000+ fertilized florets examined. Because seed production and suitable habitat are not common, colonization via seed dispersal would be an extremely rare event. Undoubtedly, the infrequency of this occurrence contributes to the rarity of this taxon.

*Calamagrostis porteri* subsp. *insperata* maintains its populations primarily by vegetative means, especially in Illinois. The current populations appear to occupy islands of suitable habitat surrounded by ecologically unsuitable habitat. Therefore, it would be unlikely that a population would be able to expand to new sites via vegetative means, except locally through transport of vegetative fragments.

Two uncommon to rare associated species were

discovered during the course of this study. At LC and an unsampled BSS population, over 10 m<sup>2</sup> were carpeted by *Sphagnum* spp. These areas also contained some of the highest densities of *C. porteri* subsp. *insperata* in southern Illinois. Another associate, *Carex willdenowii* Schuhr, is present in three of the populations. It is listed as an Illinois endangered species and is known from only three counties in the southern part of the state (Herkert, 1991). The presence of these species within suitable habitat might be a good indicator for the presence of *C. porteri* subsp. *insperata* in southern Illinois.

A limitation of the present investigation is that populations throughout the range of *C. porteri* subsp. *insperata* were not studied. Therefore, we are not able to fully document the variable habitats or climates in which this taxon occurs. Additionally, this research was not exhaustive in examining all possibilities that may have affected the rarity of this taxon. Nevertheless, the limiting factors of specificity of habitat, unsuccessful seed production (Greene, 1980; Havens & Holland, 1998), and limited colonization of new habitat are primarily responsible for the few populations present in southern Illinois, and are the most likely reasons why *C. porteri* subsp. *insperata* is rare.

The long-term survival of *C. porteri* subsp. *insperata* in southern Illinois is threatened in several ways. Natural disturbances, such as treefalls, may not create enough favorable microhabitats within extant populations to maintain viable populations indefinitely. Increased forest succession and closure of the tree canopy caused by fire suppression have likely affected this taxon adversely (Bittner, 1995a; Ambrose et al., 1994). Additionally, several populations are extremely small in area (80–120 m<sup>2</sup>), which increases the chances of destruction of a population by a single stochastic event. These actions could eventually degrade or extirpate the current populations. Since it is extremely unlikely that new populations would be produced by either vegetative or sexual means, it is necessary that the existing populations be properly protected and managed to ensure their long-term survival.

Future research is needed to determine the effects of management on vegetative and sexual performance. Summers (1993; in Ambrose et al., 1994) has suggested that canopy gaps should be created within and around the populations to determine how the populations respond to such management. Only a small percentage of the canopy (10–25%) should be removed at first. Summers stated that too much disturbance (e.g., timber cuts) leads to rapid growth from nearby species that outcompete and

choke out *C. porteri* subsp. *insperata*. He further added that prescribed burning should be conducted on an experimental basis and suggested that flowering events may be related to mild disturbance.

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