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Influence of Environmental Factors and Preliminary Demographic Analyses of a Threatened Orchid, Platanthera praeclara

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ABSTRACT.-In 1987, 160 individual *Platanthera praeclara* Sheviak and Bowles were permanently marked on 16 transects on the Sheyenne National Grassland, in southeastern North Dakota. They were located on five sites that represented five management regimes: (1) grazed-rotational; (2) grazed-season long (5.5 mo); (3) ungrazed; (4) ungrazed and burned, and (5) grazed and burned. By 1994, only 4% of the originally marked *Platanthera praeclara* individuals were observed; however, numbers did not differ (P = 0.13) among sites. Beginning in 1990, all *Platanthera praeclara* individuals in belt transects on each site were marked and counted, and demographic data were recorded. Total orchid density differed (P = 0.04) among sites, but not with a consistent pattern among years (P = 0.001). In some years, *Platanthera praeclara* density was positively correlated with surface soil moisture. Preliminary demographic analyses indicate that *Platanthera praeclara* may be short-lived and that absent plants rarely reappear. Cluster analysis indicated that the most common vegetative community supporting *Platanthera praeclara* was dominated by *Poa pratensis L.* and *Juncus balticus* Willd., although *Platanthera praeclara* density on the Sheyenne National Grassland was most highly correlated with cover of *Calamagrostis stricta* (Timm.) Koel.

Introduction

Platanthera praeclara Sheviak and Bowles and its close relative, *P. leucophaea* (Nutt.) Lindl., were once distributed throughout much of the tallgrass prairie in the central United States and southern Canada. However, with the conversion of prairie to cropland and the encroachment of other human development, most of their original habitat has been lost. Concern about the limited number of populations and their relative isolation led to the federal listing of both species as threatened (U.S. Fish and Wildlife Service, 1989). Populations of *P. praeclara* are restricted to the Great Plains States and Manitoba; the three largest populations occur in Minnesota and North Dakota in the United States (Sheviak and Bowles, 1986) and in southern Manitoba in Canada (Catling and Brownell, 1987).

Platanthera praeclara is a perennial herbaceous plant arising from a fusiform tuber. Inflorescences are large and showy, with as many as 20 or more cream-colored flowers arranged on a spike up to 75 cm tall; hawkmoths have been hypothesized as the primary pollinators (Sheviak and Bowles, 1986). Thousands of dustlike seeds are produced each season when extensive flowering occurs. *Platanthera* individuals regenerate vegetatively during the growing season by forming a new primary tuber and perennating bud which develop into the new root system and shoot for the following growing season (Dressler, 1981). In this manner, populations may persist for some time; however, seed establishment is required for recruitment of new individuals (Bowles, 1983). Like many orchids, these species are likely dependent on mycorrhizae during some or all of their life cycle (Sheviak, 1974). A species of *Rhizoctonia* was isolated from *P. praeclara* tubers on the Sheyenne National Grassland (Bjugstad-Porter, 1993).

Platanthera praeclara usually occurs in mesic swales or draws in tallgrass prairie; ideal habitats are subirrigated. Soils are generally Mollisols, and include alluvial soils, subirrigated calcareous, lacustrine soils overlying sand, or fine-textured loess or till with low organic matter content (Bowles, 1983). Associated plant species include *Andropogon* gerardii Vitman. and *A. scoparius* Michx., *Carex* spp., *Panicum virgatum* L. and *Calamovilfa longifolia* (Hook.) Scribn. (Sheviak and Bowles, 1986). It has been hypothesized that disturbances are required to remove competing shrubs and provide open microsites (e.g., regeneration niches) for germination (Bowles, 1983). Such disturbances might include fire and grazing; however, intense disturbances that remove seed heads are detrimental to long-term recruitment (Bowles, 1983).

Platanthera praeclara is thought to be long-lived (Bowles, 1983); however, few data on population trends exist. Demographics of *P. praeclara* are complicated by its erratic flowering and by the fact that a large percentage of plants may remain dormant or vegetative in any given year (Bowles, 1983). The use of transition tables or figures, which contrast current phenological stages with stages in the previous year, are commonly used to summarize life history stages of plants (e.g., Mehrhoff, 1989; McClaran and Sundt, 1992), and this type of demographic analysis is an important first step in understanding whether populations are "self-sustaining," and to evaluate recovery criteria for delisting species ((Schemske *et al.,* 1994). The concept of "half-life" is also used by plant demographers; it is the length of time it would take for half a population of plants, recruited within a given time interval, to die (Hutchings, 1989).

This study was initiated in 198'7 to monitor *Platanthera praeclara* subpopulations on five sites subjected to varying management regimes on the Sheyenne National Grassland, and addresses the following questions: (1) is *P. praeclara* long-lived, and is there a set sequence in life states? and (2) in spite of the erratic life history of *P. praeclara*, do management practices and environmental factors influence population levels? Understanding the role of environmental and demographic stochasticity in its persistence is imperative for plant recovery success (Schemske *et al.,* 1994).

Study Area

The study was conducted in the Sheyenne National Grassland, in southeastern North Dakota. Kuchler (1964) depicted the vegetation of the Sheyenne National Grassland as tallgrass prairie (bluestem prairie and wheatgrass-bluestem-needlegrass) and oak savanna. Big bluestem and little bluestem occur throughout the study area. *Carex lanuginosa* Michx. and *Calamagrostisstricta* (Timm.) Koel. are common in lowland depressions. *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths, *Stipa comata* Trin. & Rupr., *Carex heliophila* Mack. and *Calamovilfa longifolia* grow on uplands.

Platanthera praeclara occurs most often in lowland depressions (swales) associated with the Glacial Sheyenne Delta. The Glacial Sheyenne Delta was formed near the end of the Wisconsin Glaciation as glacial meltwater of the Sheyenne River emptied into Glacial Lake Agassiz and deposited sands, clays and gravels (Baker and Paulson, 1967). The dunelike landscape probably resulted when the receding Lake Agassiz left the area barren and subsequent wind action created dunes. A layer of nearly impervious silt interbedded with clay and sand is responsible for the relatively high water table in the swales (Baker and Paulson, 1967). Mollisols are the most prevalent soils, although Entisols occur on some sites (U.S.

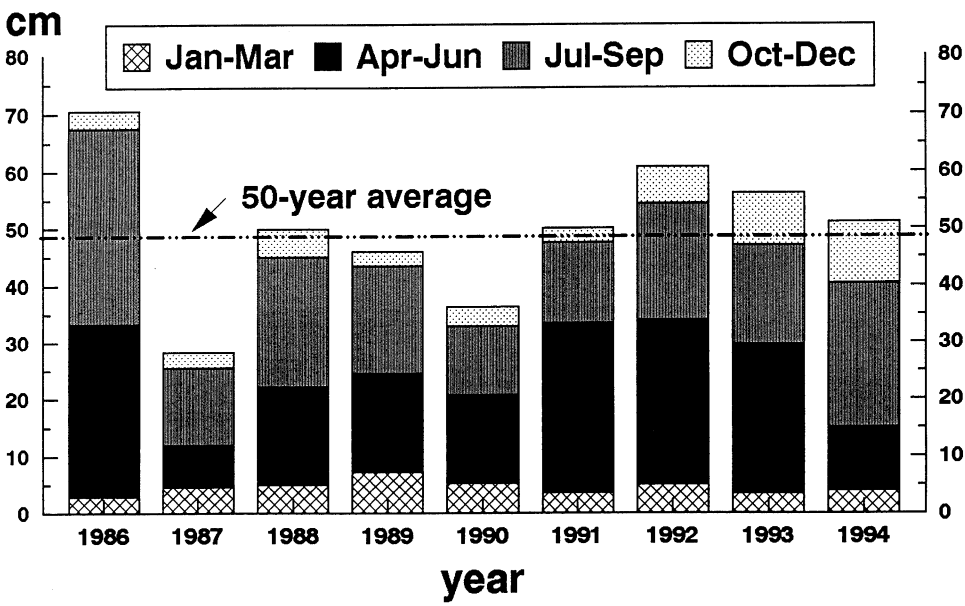

FIG 1.—Total precipitation 1986–1994, by season, at McLeod, North Dakota, near the Sheyenne National Grassland

Soil Conservation Service, 1975). In general, the lowland soils are permeable and poorly drained.

Platanthera praeclara is most often found in the *Carex lanuginosa–Calamagrostis stricta–Juncus balticus* habitat type or in the transition zone between it and the *Andropogon gerardii–A. scoparius–Panicum virgatum* habitat type (Manske, 1980). Recent data suggest that *Poa pratensis* and *Euphorbia esula* L. are other common species in swales supporting orchid populations on the Sheyenne National Grassland (Sieg and Bjugstad, 1994).

The mean annual precipitation on the study area is 49.7 cm, most of which is received during the growing season, April to September (Owenby and Ezell, 1992). Precipitation on the study area was above average in 1986, was below average in 1987, 1989 and 1990, and approximately average in 1988 and 1991 (Fig. 1). Precipitation in 1992, 1993 and 1994 was above average.

METHODS

In 1987, 16 belt transects (10 m wide, 30–80 m long) were established on five separate study sites in areas of orchid concentrations (Bjugstad and Fortune, 1989). The study sites represented five management regimes: grazed-rotational (four transects), grazed-season long (four transects), ungrazed (two transects), ungrazed-burned (three transects) and grazed-burned (three transects). The grazed-rotational site was part of a four-pasture deferred rotation system grazed by cattle twice during the growing season (McNeil, n.d.). The grazed-season long site was grazed for approximately 5.5 mo during the growing season. The ungrazed site consisted of an area along the railroad right-of-way and a small exclosure adjacent to the railroad. The ungrazed-burned site was an exclosure that encompassed three swales supporting *Platanthera praeclara*. This exclosure and the grazed-burned treatment were prescribed burned in April of 1989 and 1993. The grazed-burned site was part of a three-pasture system that was grazed twice during the growing season.

Platanthera praeclara individuals marked in 1987.-A total of 10 flowering *Platanthera praeclara* individuals were permanently marked in 1987 on each of the 16 transects. The transects were laid to best encompass orchid concentration areas. Location of each plant was permanently marked with plastic-coated steel pins located 2 dm towards the outside of the transect from each plant. Individual plants were resurveyed each year during peak flowering (late June through early July), from 1988 through 1994. Data recorded each subsequent year for each *P. praeclara* individual included status (present or absent), height, number of leaves, and life state (vegetative or flowering).

Platanthera praeclara individuals marked 1990-1994.-During the 1st 3 yr of the study, only *Platanthera praeclara* individuals originally marked in 1987 were checked. However, beginning in 1990, all additional *P. praeclara* individuals present in lo-m-wide belt transects were noted and permanently marked. Data on plant status, height, number of leaves and life state were recorded yearly from 1990 through 1994. Status of individual plants included "present," "absent" or "new.": "Absent" plants were those that had previously been observed, but were not present; "new" plants were those that had not been previously observed. We recognize that "new" plants might include some previously absent plants. However, based on the low number of plants that have reappeared aboveground following 1 or more yr of absence, this possibility is minimal.

The occurrence of twin and triplet plants was also noted. In this paper, "ramet" refers to a unit of clonal growth, and a "genet" refers to individuals representing original zygotes (Harper, 1977). Thus, the clone would be a "genet"; and nonclonal individuals, whether vegetative or flowering, would also be termed "genets." Multiple-ramet clones were recognized by the close proximity of the ramets (<3 cm) and movement of one ramet when the other ramet was gently shaken. In another phase of this project, we partially excavated a triple-ramet plant and verified this status.

Realizing the importance of following all life states of *Platanthera praeclara,* but recognizing the difficulty of finding the short vegetative individuals, we initiated a system to maintain quality control on *P. praeclara* counts. Each of two observers counted all *P. praeclara* individuals in a randomly selected 5- by 5-m area on each transect. If counts of the two observers differed by >5%, additional 5- by 5-m sections were counted, until the error rate was <5%. Vegetative *P. praeclara* individuals are more difficult to observe than flowering plants, but low between-observer error rates indicate the high level of accuracy that can be achieved.

Vegetation.-Plant canopy cover was estimated in 1991 and 1992; deep water in many transects in 1993 prevented this sampling. Plant canopy cover was estimated in 30 to 50, 20- by 50-cm quadrats spaced at l-m intervals on the center line of each transect. Cover was estimated by six classes (1 = ≤5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, and 6 = 96-100%) (Daubenmire, 1959). These categorical data were converted to class midpoints for statistical analyses. Variables estimated included total plant canopy cover, litter, bareground, total shrub cover, forb cover, graminoid cover and cover by individual plant species. Great Plains Flora Association (1986) was the authority for plant nomenclature.

Soils.-Soil chemical analyses were conducted in 1988. A total of 160 samples were taken to a depth of approximately 20 cm. One sample was taken within 15 cm of each permanently marked *Platanthera praeclara* individual. A total of five cornposited samples were analyzed from each transect. Each cornposited sample consisted of two spatially distinct samples that were combined in the laboratory. Analyses included particle size distribution (Day, 1965), percentage organic matter (Prince, 1955), pH (McLean, 1982) and calcium content (Lanyon and Heald, 1982). Each organic matter and calcium test was repeated three times and each pH measurement was repeated once; data were averaged.

During the height of the flowering period for *Platanthera praeclara* in 1991, 1992 and 1994, soil moisture was determined gravimetrically. A total of 10 soil moisture samples was taken in each transect: each within 50 cm of the permanently marked *P. praeclara* individual. The soil samples were stratified into four depths: 0-4 cm, 4-8 cm, 8-12 cm, and 12-16 cm. Samples were placed in plastic bags in the field and weighed. Soil moisture was determined gravimetrically by oven drying samples at 100 C for 48 h and reweighing. In 1993, standing water was present in most of the transects, so water depth was recorded in each transect within 10 cm of each of the originally marked *P. praeclara* individuals.

Statistical analyses.- To assess the validity of the assumption that transects were apropriate replications of the five management regimes, the amount of within-site variability was compared to the amount of between-site variability for various site characteristics using a one-factor model of site. If between-site variability greatly exceeds within-site variability, the assumption of transects as replications is suspect. For plant canopy cover, Dyer's (1978) analysis of compositional data using Euclidean distance revealed within- and between-site variability proportions of 0.66 and 0.34, respectively. Using one-factor analysis of variance, organic matter exhibited 0.11 and 0.89 proportions of within- and between-site variability, respectively. This was primarily due to low organic matter content on one site compared to the others. For soil textural fractions, the minimum within-site proportion of variability was 0.73. For calcium and pH, the within-site variability proportions were 0.78 and 0.62, respectively. Since the proportion of within-site variability usually greatly exceeded the proportion of between-site variability, the use of transects as replicates was supported.

Differences among sites in numbers of *Platanthera praeclara* individuals (1988-1994) originally marked in 198'7, density of flowering *P. praeclara* individuals (1990-1994) and total *P. praeclara* density (1990-1994) were analyzed by multivariate repeated measures analysis of variance, using years as the repeated measure (Morrison, 1976; Norusis, 1992a). Examination of plots of the residuals from all analyses did not reveal any substantial departure of these data from normality. Homogeneity of variances was tested with Bartlett-Box F tests for individual years.

Due to a significant site-by-year interaction for total *Platanthera praeclara* density, separate analyses were run for each year to test for differences in total densities among sites. One-way analysis of variance and Tukey's HSD multiple comparison procedure for unequal sample sizes (Spjotvoll and Stoline, 1973) (variables with homogeneous variances) or Welch's test and Dunnett's (1980) T3 multiple comparison procedure (variables with heterogeneous variances) were used to conduct these within-year analyses. Overall Type I error rates were maintained among years with Bonferroni adjustment of significance levels ((x/5), where 5 = number of years (1990-1994) in the overall analysis (Miller, 1981).

Differences among sites in soil texture, pH, organic matter, Ca content and moisture, plus *Platanthera praeclara* heights were tested with one-way analysis of variance (homogeneous variances) or Welch's test (heterogeneous variances). For height data, each year was analyzed separately. As above, Tukey's HSD test (homogeneous variances) or Dunnett's test (heterogeneous variances) were used to separate means. Normality was tested by plotting residuals and homogeneity of variances was tested using the Bartlett-Box F test.

Average 1991-1992 plant canopy cover of 23 major species was used in unweighted pair-groups, using arithmetic averages (UPGMA) cluster analysis (Romesburg, 1984; Norusis, 1992b) to identify major community types. The cosine coefficient (Pielou, 1984; Ludwig and Reynolds, 1988) was used as the similarity measure for separating groups; 95% similarity was used as the point below which clusters were considered distinct. Relationships between vegetative composition and *Platanthera praeclara* density were explored with simple regression analysis. Plant canopy cover (2-yr average) of individual plant species, bare ground, total plant cover, and total cover of graminoids, forbs and shrubs were independent variables; total *P. praeclara* density on each site in 1991, 1992, 1993 and 1994 were dependent variables.

Relationships between transect-level soil parameters and *Platanthera praeclara* density were explored using regression analysis. An analysis of covariance approach allowed inclusion of a site as the first factor to account for coarse-scale differences among sites (Dunn and Clark, 1987). This was necessary because of differences in water depth, soil organic matter content and moisture among sites, which clouded the understanding of the overall role of these variables in influencing *P. praeclara* density. Soil organic matter and soil moisture at four depths in each of 3 yr, plus water depth in 1993 (an approximation of water table depth) were independent variables; total *P. praeclara* density on each site in 1991, 1992, 1993 and 1994 were dependent variables. Regression models using soil texture and other chemical attributes as independent variables did not require inclusion of a site factor, since soil texture and other chemical attributes did not differ among sites.

Results

Platanthera praeclara *marked in 1987*.-Total number of *Platanthera praeclara* individuals displaying aboveground growth differed ($P = 0.002$) among years, but was similar ($P = 0.13$) among sites. Of the 160 *P. praeclara* individuals originally marked in 1987, 88 individuals, or 55% reappeared aboveground in 1988. In 1989, 1990, 1991, 1992, 1993 and 1994, the number of marked *Platanthera praeclara* that showed aboveground growth was 28%, 16%, 11%, 13%, 11% and 4% respectively (Table 1). Nearly two thirds of the 160 *P. praeclara* individuals marked in 1987 were present for only 1 (35%) or 2 (30.6%) yr. Only two of the 160 P. *praeclara* individuals marked in 1987 have reappeared aboveground in every subsequent year; four have been observed in 7 out of 8 yr, four have been observed in 6 of the 8 yr, and six have been observed in 5 yr. Three years is the longest any individual has been absent before reappearing aboveground again.

Platanthera praeclara *individuals marked between 1990-1994*.-The total number of *Platanthera praeclara* individuals observed on the 16 transects ranged from 82 in 1991 to 583 in 1993 (Table 2). Most ('73%) of the *P. praeclara* individuals observed during the 5 yr were in the vegetative life state; and in each year between 1991 and 1993, over 60% of the P. *praeclara* individuals observed were new ones. The exception was in 1994, when only 33% were new.

The percentage of a given cohort (only new *Platanthera praeclara* individuals in that year) that reappeared the following year ranged from a high of 73% for the 1991 cohort to only 15.9% for the 1993 cohort (Fig. 2). Fifty seven percent of the 1991 cohort was present in 1993; only 14% of the 1992 cohort was present in 1994.

Only one individual *Platanthera praeclara* was present every year between 1990 and 1994; 10 were present in 4 consecutive yr; two were present in 4 nonconsecutive yr. A total of 46 *P. praeclara* individuals were present in 3 consecutive yr between 1990 and 1994; four were present in 3 nonconsecutive yr. Single ramets from one tuber were most common; however, six sets of double ramets were observed in 1992; 33 sets of double ramets and six sets of triple ramets from one tuber were observed in 1993; and 22 sets of double ramets and six sets of triple ramets were observed in 1994.

The transition matrix for *Platanthera praeclara* for the 5 yr does not reveal a set sequence in life states (Table 3). For example, 24% of the vegetative *P. praeclara* individuals in 1990

TABLE 1.—Number of permanently marked *Platanthera praeclara* reclocated on five sites on the Sheyenne National Grassland, 1987–1994

Site	Year															
	1987		1988		1989		1990		1991		1992		1993		1994	
	No.	(%)	No.	(%)	No.	(%)	No.	(%)	No.	(%)	No.	(%)	No.	(%)	No.	(%)
Grazed-rotational	40	(100%)	18	(45%)	12	(30%)	10	(25%)	1	(3%)	3	(8%)	1	(3%)	0	(0%)
Grazed-season long	40	(100%)	30	(75%)	6	(15%)	2	(5%)	6	(15%)	8	(20%)	7	(18%)	0	(0%)
Ungrazed	20	(100%)	13	(65%)	8	(40%)	1	(5%)	3	(15%)	2	(10%)	1	(5%)	0	(0%)
Ungrazed-burned	30	(100%)	15	(50%)	13	(43%)	8	(27%)	7	(23%)	9	(30%)	7	(23%)	6	(20%)
Grazed-burned	30	(100%)	12	(40%)	5	(17%)	4	(13%)	0	(0%)	0	(0%)	2	(7%)	1	(3%)
Total (%)	160	(100%)	88	(55%)	44	(28%)	25	(16%)	17	(11%)	22	(13%)	18	(11%)	7	(4%)

TABLE 2.—Life states of marked *Platanthera praeclara* individuals, 1990–1994. Numbers in parentheses are numbers of "new" *Platanthera praeclara* individuals, or ones not previously observed on the study area

	Vegetative		Flowering		Total	
Year	No.	(No. new)	No.	(No. new)	No.	(No. new)
1990	74	(53)	13	(9)	87	(62)
1991	78	(48)	4	(3)	82	(51)
1992	191	(129)	28	(10)	219	(139)
1993	433	(353)	150	(68)	583	(421)
1994	49	(10)	104	(40)	153	(50)

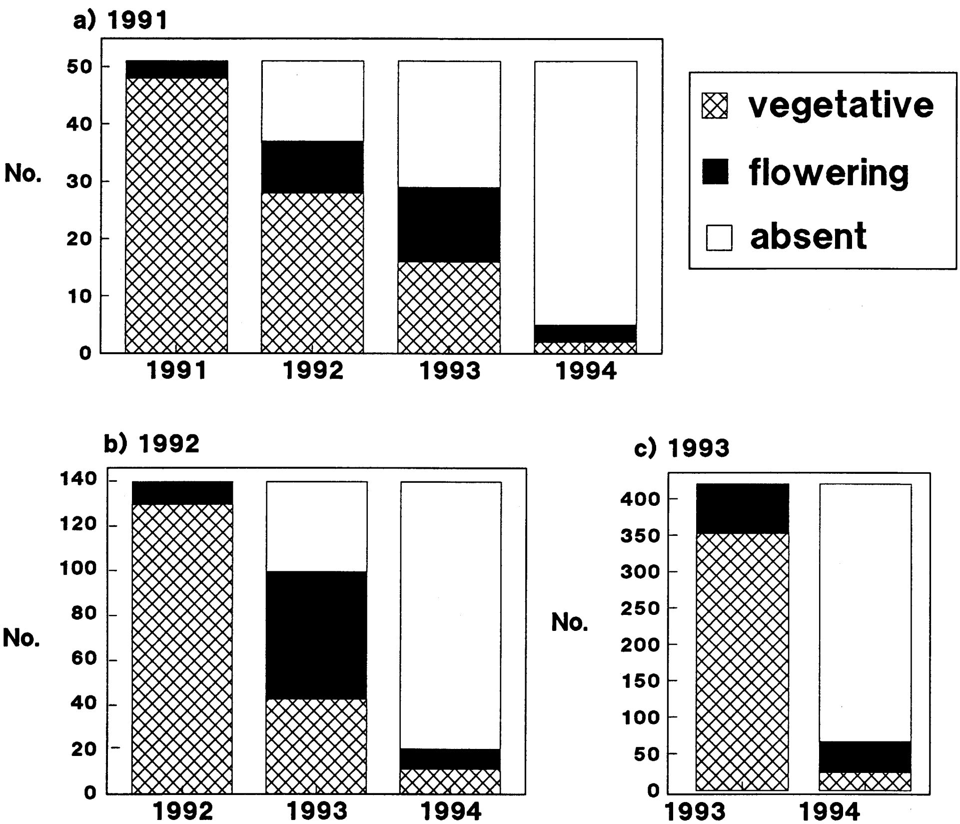

FIG 2.—Number of new *Platanthera praeclara* individuals, by life state, in (a) 1991, (b) 1992, and (c) 1993 and the life state (or absence) of these individuals in subsequent years

TABLE 3.-Composite transition matrix for *Platanthera praeclara*, 1990-1994

Life state in 2nd year	Life state in 1st yr of period				Period
	Vegetative	Flowering	Absent 1 yr	Absent 2 yr	
Vegetative	0.24	0.15			1990-1991
	0.54	0.50	0.12	0.17	1991-1992
	0.32	0.25	0.14	0.10	1992-1993
	0.06	0.07	0.03	0.00	1993-1994
Flowering	0.00	0.08			1990-1991
	0.20	0.00	0.02	0.04	1991-1992
	0.36	0.43	0.05	0.00	1992-1993
	0.09	0.16	0.01	0.00	1993-1994
Absent 1 yr	0.76	0.77			1990-1991
	0.26	0.50			1991-1992
	0.32	0.32			1992-1993
	0.85	0.77			1993-1994
Absent 2 yr					1990-1991
			0.86		1991-1992
			0.82		1992-1993
			0.96		1993-1994
Absent 3 yr					1990-1991
				0.86	1991-1992
				0.90	1992-1993
				1.00	1993-1994

were also vegetative in 1991; none flowered in 1991 and 76% were absent. In contrast, 32% of the vegetative *P. praeclara* individuals in 1992 were vegetative in 1993; 36% flowered in 1993, and 32% were absent. Although sample sizes for flowering *P. praeclara* individuals were small (<30) in 1990, 1991 and 1992, flowering *P. praeclara* either flowered again the following year, reappeared as vegetative individuals, or were absent (Table 3).

Further, once absent, few *Platanthera praeclara* individuals reappeared the following year (Table 3). Of 66 *P. praeclara* individuals that were absent in 1991, 86% were also absent in 1992. Of 22 absent in 1992, 82% were absent the following year, and of 70 absent *P. praeclara* individuals in 1993, 96% were absent in 1994. An average of 88% of the *P. praeclara* individuals that were absent in 1 yr between 1991 and 1993 were also absent the following year. For *P. praeclara* individuals absent 2 yr, an average of 92% were absent the 3rd yr.

Flowering *Platanthera praeclara* individuals ranged from an average height of 24.6 cm in 1992 to 51.5 cm in 1994; the tallest observed was 74.9 cm. Heights of flowering *P. praeclara* individuals differed ($P = 0.01$) among sites only in 1 yr, and then only between two sites; heights on the remaining sites were similar ($P > 0.11$). Height of vegetative *P. praeclara* individuals ranged from an average of 11.7 cm in 1990 to 24.0 cm in 1994, and differed ($P < 0.03$) among sites in 1992, 1993 and 1994; however, there was no consistent trend in height relative to site. Vegetative *P. praeclara* individuals generally had one or two leaves; flowering *P. praeclara* individuals averaged between 10.3 and 15.6 leaves per plant.

Platanthera praeclara density averaged 1.1, 1.2, 2.8, 6.8 and 1.6 plants/100m^2 in 1990, 1991, 1992, 1993 and 1994, respectively. A maximum density of 18 plants/100m^2 was observed in one transect in 1993. Total *P. praeclara* density (both flowering and nonflowering individuals) differed among sites ($P = 0.04$) and among years ($P = 0.005$); but a significant ($P = 0.001$) site **X** year interaction was observed (Fig. 3), which biases the main effect tests

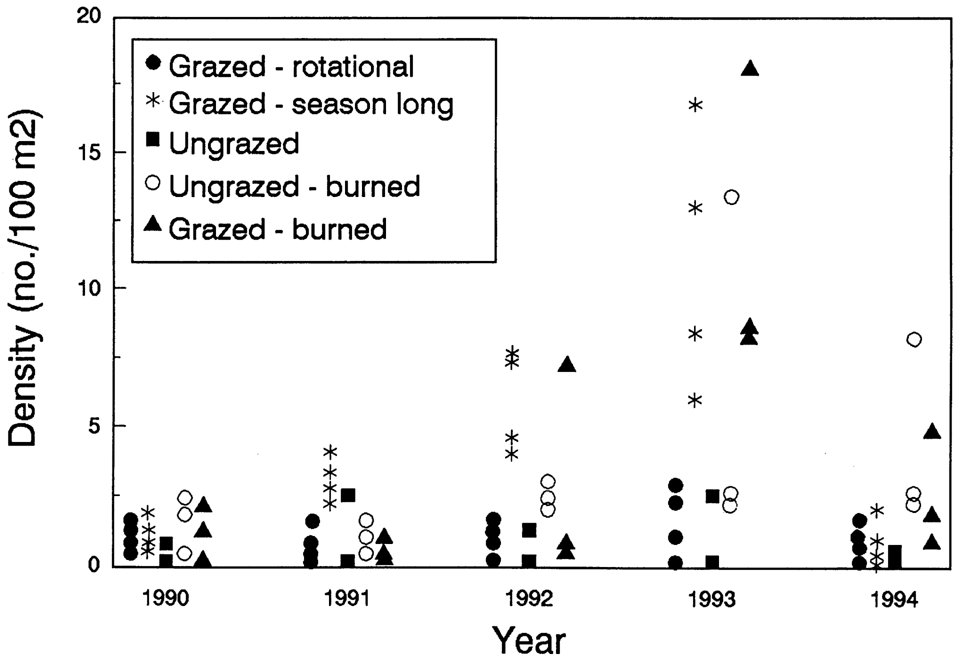

FIG 3.—Total *Platanthera praeclara* density (no./100 m^2) in 1990–1994, on five study sites. Density for individual transects are shown

of sites and years. Individual year analyses of *P. praeclara* densities did not reveal any significant ($P > 0.1$) differences among sites in any year. When only flowering *P. praeclara* individuals were considered, average densities ranged from a low of 0.4 plants/100m^2 in 1991 to 1.74 plants/100m^2 in 1993. The maximum density of flowering *P. praeclara* individuals in one transect was 7.6 plants/100m^2. Density of flowering *P. praeclara* individuals did not differ ($P = 0.12$) among sites, but varied ($P = 0.02$) among years.

Plant canopy cover.—Transects supporting *Platanthera praeclara* populations were diverse vegetatively, and this diversity was not necessarily related to the various management regimes. Cluster analysis identified four plant communities associated with *P. praeclara*: (1) *Poa pratensis/Juncus balticus*; (2) *Carex* spp./*Dichanthelium wilcoxianum* (Vasey) Freckmann; (3) *Salix* spp./*Calamagrostis stricta* and (4) *Salix* spp./*Anemone canadensis* L. (Table 4). The first community included over half of the transects; all sites except the ungrazed and grazed season-long sites were represented. Community 2 included one transect from the grazed (rotational) and one from the grazed season-long. Community 3 included three grazed season-long transects, and community 4 consisted of the two ungrazed transects.

Density of *Platanthera praeclara* in 1991 and 1992 was positively correlated ($P < 0.01$) with cover of *Calamagrostis stricta* ($r = 0.70$ and 0.73, respectively) and negatively correlated ($P < 0.1$) with total plant canopy cover ($r = -0.58$ and -0.44, respectively). *Platanthera praeclara* density in 1991 was negatively correlated ($r = -0.73$, $P < 0.001$) with *Poa pratensis* cover and positively correlated with *Salix* spp. cover ($r = 0.61$, $P < 0.01$). *Platanthera praeclara* density in 1993 was significantly correlated ($P \leq 0.08$) with cover of *Calamagrostis*

TABLE 4.—Two-year average plant canopy cover ($\bar{x} \pm$ SE) of major plant species in plant communities supporting *Platanthera praeclara* populations, identified by cluster analysis. Plant nomenclature follows Great Plains Flora Association (1986)

Category / Species	Plant community: Popr/Juba[1] (n = 9)	Carex/Diwi[2] (n = 2)	Salix/Cast[3] (n = 3)	Salix/Anca[4] (n = 2)
Total cover	92.5 ± 0.5	88.5 ± 3.1	86.7 ± 1.8	88.0 ± 2.2
Litter cover	95.4 ± 0.7	93.2 ± 1.2	97.2 ± 0.2	89.9 ± 4.1
Bare ground	0.5 ± 0.2	1.5 ± 0.7	0.4 ± 0.3	4.7 ± 2.1
Total forb cover	32.5 ± 2.8	35.7 ± 10.5	36.8 ± 1.6	66.9 ± 0.4
Ambrosia psilostachya	4.0 ± 2.0	5.7 ± 0.4	7.1 ± 1.7	5.5 ± 5.5
Anemone canadensis	2.9 ± 1.2	1.1 ± 0.01	7.8 ± 3.4	12.9 ± 3.6
Aster simplex	3.6 ± 1.3	1.0 ± 0.3	2.5 ± 0.8	0.7 ± 0.2
Euphorbia esula	5.7 ± 3.4	0.1 ± 0.1	7.4 ± 6.8	10.1 ± 9.1
Euthamia gramnifolia	0.2 ± 0.4	2.6 ± 0.9	5.9 ± 1.8	7.3 ± 6.7
Fragaria virginiana	6.2 ± 3.0	11.6 ± 10.0	3.4 ± 1.7	0.3 ± 0.3
Solidago canadensis	1.1 ± 0.6	2.9 ± 1.1	10.9 ± 1.5	4.4 ± 2.1
Total graminoid cover	80.7 ± 1.4	70.8 ± 6.1	50.8 ± 2.6	28.3 ± 6.3
Calamagrostis stricta	1.6 ± 0.4	7.9 ± 2.7	19.3 ± 1.2	1.3 ± 0.5
Carex spp.[5]	6.9 ± 1.0	30.4 ± 10.2	11.2 ± 3.1	10.7 ± 2.8
Dichanthelium wilcoxianum	2.9 ± 1.4	17.9 ± 1.9	3.1 ± 0.8	1.7 ± 1.6
Juncus balticus	12.6 ± 2.2	3.8 ± 1.9	8.8 ± 2.0	0.2 ± 0.1
Panicum virgatum	8.1 ± 2.3	14.3 ± 11.8	7.9 ± 3.5	6.5 ± 1.0
Poa pratensis	47.5 ± 5.2	8.7 ± 6.8	1.5 ± 0.5	4.0 ± 2.5
Spartina pectinata	7.9 ± 2.4	0.9 ± 0.6	0.7 ± 0.6	1.2 ± 1.0
Total shrub cover	11.1 ± 3.3	6.0 ± 4.9	33.0 ± 11.9	23.3 ± 13.5
Salix spp.[6]	8.9 ± 2.9	5.3 ± 5.2	26.4 ± 6.5	16.2 ± 14.3

[1] *Poa pratensis/Juncus balticus*
[2] *Carex* spp./*Dichanthelium wilcoxianum*
[3] *Salix* spp./*Calamagrostis stricta*
[4] *Salix* spp./*Anemone canadensis*
[5] Includes *Carex lanuginosa, C. granularis* and *C. brevior*
[6] Includes *Salix exigua* and *S. bebbiana*

stricta (r = 0.64) and litter cover (r = 0.45). No other significant correlations between average *P. praeclara* density and plant canopy cover were observed.

Soil chemistry and physical properties.—With the exception of organic matter and gravimetric moisture, the soils associated with the 16 transects were relatively similar. The percentage of sand, silt and clay did not differ ($P > 0.4$) among sites (Table 5). Average percent sand on the five study sites ranged from 74.7 to 81.1; percent silt ranged from 7.5 to 9.8 and percent clay ranged from 11.4 to 16.1. Organic matter percentages generally ranged from 4.1 to 4.6%; however, on the study site grazed season-long, the organic matter was significantly lower ($P < 0.01$), averaging only 1.7%. Soil pH and Ca content did not differ ($P > 0.2$) among study sites. Average soil pH ranged from 7.6 to 8.2 and average Ca ranged from 2758 to 3828 ppm. *Platanthera praeclara* density was not significantly correlated ($P > 0.1$) with soil textural or chemical attributes measured in this study.

Soil moisture.—Soil moisture content was higher in 1992 than in 1991, and was higher yet in 1994. However, the same general trends were observed in all 3 yr. Three-year average soil moisture differed among sites ($P = 0.01$); soil moisture was lower on the grazed season-

TABLE 5.—Average ($\bar{x} \pm$ SD) soil chemical characteristics and texture on 16 transects on five sites, 1988

Site	Organic matter (%)	pH	Ca (ppm)	Soil texture Sand (%)	Silt (%)	Clay (%)
Grazed-rotational	4.6 ± 0.7[b]	7.6 ± 0.6	3540 ± 823	74.7 ± 6.9	9.8 ± 2.3	15.6 ± 4.9
Grazed-season long	1.7 ± 0.6[a]	8.2 ± 0.1	3496 ± 167	76.1 ± 4.6	8.5 ± 1.9	15.4 ± 3.0
Ungrazed	4.1 ± 0.9[b]	8.1 ± 0.1	3828 ± 778	74.8 ± 5.6	9.1 ± 3.3	16.1 ± 3.8
Ungrazed-burned	4.5 ± 0.3[b]	7.7 ± 0.3	3364 ± 864	77.7 ± 4.5	8.0 ± 1.6	14.3 ± 3.8
Grazed-burned	4.4 ± 0.5[b]	7.8 ± 0.2	2758 ± 790	81.1 ± 2.3	7.5 ± 1.3	11.4 ± 1.2

[a,b] Significantly different ($P < 0.01$) among sites

long site than on all other sites ($P < 0.01$) (Fig. 4). Soil moisture also differed among depths on the five sites. Soil moisture on season-long grazed sites was lower ($P = 0.03$) than on ungrazed sites in surface samples; lower than both grazed-burned ($P = 0.01$) and ungrazed-burned ($P = 0.06$) sites at intermediate depths; and lower ($P < 0.01$) relative to all sites but ungrazed at the 8–12 cm depth.

Based on regression analysis, density of flowering *Platanthera praeclara* individuals in 1991 was correlated ($r = 0.48$, $P = 0.06$) with surface soil moisture in 1991. Further, total *P. praeclara* density in 1992 was positively correlated ($r = 0.70$, $P < 0.01$) with surface soil moisture the previous year and with surface soil moisture in 1992 ($r = 0.50$, $P = 0.05$). *Platanthera praeclara* density in other years was not significantly ($P > 0.1$) correlated with soil moisture.

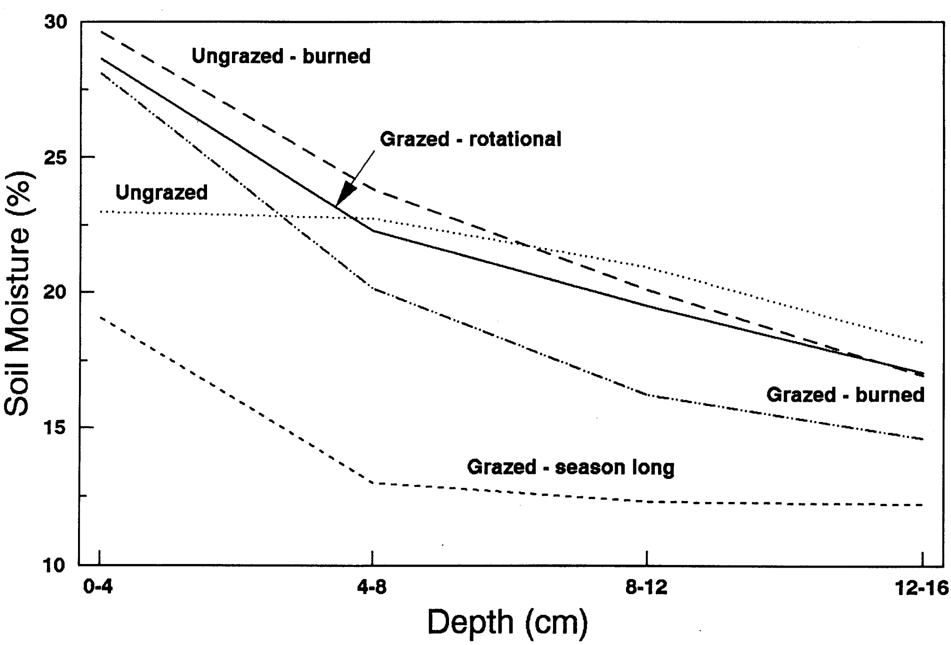

FIG 4.—Three-year average (1991, 1992, 1994) gravimetric soil moisture (%) at four depths on five sites. Flooding of the study area in 1993 prevented sampling soil moisture

In 1993, soils in the majority of the transects supporting *Platanthera praeclara* populations had standing water, and hence were saturated. In 1993, water depth during the height of the *P. praeclara* flowering season ranged from 0 to 17.8 cm; water was deeper ($P < 0.01$) on the grazed season-long site (13.2 cm ± 2.0 SE) than on the grazed-rotational (2.8 ± 1.7), grazed-burned (2.0 ± 2.0), and ungrazed-burned sites (0.3 ± 0.3), and similar to depth on the ungrazed site (5.2 ± 5.2 cm). Water depth was not significantly correlated ($P > 0.1$) with density of *P. praeclara* in any of the 5 yr.

DISCUSSION

The low number of originally marked *Platanthera praeclara* individuals that reappeared aboveground in subsequent years suggests that this plant is short-lived, or is capable of longer periods of dormancy than previously observed. Based on 1-yr aboveground reappearance rates of between 24 and 73% in this study, it appears that *P. praeclara* could have a half-life as short as 1–3 yr. Such a short half-life is relatively uncommon for most orchid species, although half-lives of as short as 0.5–4.3 yr have been documented for a few species (*see* Hutchings, 1989, p. 104–105). These initial estimates will need to be tested with additional data in subsequent years; most survivorship curves are developed from at least 10 yr of data (Menges, 1986). Further, droughty conditions in the 1st 4 of 7 yr of our study, followed by flooding in 1993, may have reduced survival and/or increased dormancy rates beyond levels that could be expected under optimum periods.

A predictable sequence in the life states of *Platanthera praeclara* is not yet apparent. A high percentage of both flowering and vegetative *P. praeclara* individuals failed to appear aboveground the following year; some flowered in consecutive years; and some remained vegetative in consecutive growing seasons. Gregg (1991) failed to detect a fixed sequence of life states in *Cleistes divaricata* (L.) Ames, and proportions of ramets making particular life state transitions varied among populations and years. Ramet numbers and transition proportions were affected by 2 drought yr.

Many orchid species have erratic flowering habits (Curtis and Greene, 1953; Wells, 1967), and for *Platanthera,* flowering may be related to precipitation (Bowles, 1983). Bowles *et al.* (1992) reported that flowering *P. leucophaea* individuals were present 89% of the time in wet sites, but less than 40% of the time in relatively dry sites. Bowles (1983) suggested that nonflowering in *P. leucophaea* may reflect inadequate moisture conditions the previous growing season, since flower bud initiation takes place during the development of the new tuber and perennating bud in the season preceding flowering. Drought stress during the active growth of *Herminium monorchis,* a European orchid, adversely affected flowering and had a carry-over effect the following year (Wells, 1981). Numbers of flowering *P. praeclara* individuals in our study were lowest in years with low precipitation. The increase in percentage of plants that flowered in 1993 (25%) and 1994 (68%) in our study relative to previous years (5–15%) indicated the importance of moisture in initiating flowering. In addition to high rainfall (Bowles, 1983), fire may stimulate flowering in *P.* (Sheviak, 1974; Currier, 1982).

The only consistent trend during this period of observation is that once absent, the probability of an orchid remaining absent was 82–100%. Similar probabilities of remaining absent (80%) were observed for *Ophrys sphegodes* (Hutchings, 1989). Few *Platanthera praeclara* individuals reappeared after being absent in our study; the remainder may be dead. Three to 4 yr is the maximum dormancy period for many orchid species (Falb and Leopold, 1993; Mehrhoff, 1989; Calvo, 1990). Hutchings (1989, p. 106) called dormancy in *Ophrys sphegodes* "the surest route to an early grave." It appears the same can be said for *P. praeclara,* at least during these years of highly variable moisture conditions.

Duration of our study is too short for a quantitative examination of the relationship between precipitation and *Platanthera praeclara* numbers across years, since total counts are available only for 5 yr. However, high numbers of *P. praeclara* corresponded to years of above average precipitation. The large number of *P. praeclara* individuals observed in 198'7 also followed a year of above-normal precipitation. The positive correlations of *P. praeclara* densities with surface soil moisture content provided additional evidence of the importance of moisture in both the current growing season and in the previous growing season in maintaining orchid populations.

The wide variation in *Platanthera praeclara* density among years makes any assessment of the effects of management regimes suspect, particularly since flowering and aboveground growth might be sporadic processes highly influenced by environmental factors. The significant site X year interactions are further indication that adverse climatic conditions confounded response of *P. praeclara* to various management regimes. Currier (1982) discovered a colony of 50 *P. praeclara* individuals along the Platte River in Nebraska, in an area that had been grazed season-long for 50 yr. The year the plants were discovered, the area was burned in April, cattle grazing was delayed until **15** July, and moisture was abundant (Currier, 1982). The absence of, or inconsistent statistical differences in *P. praeclara* density or height among sites in our study is likely attributable to the sporadic aboveground growth and flowering behavior of *P. praeclara* in response to highly variable moisture conditions.

Average densities of <0.01 plants/m^2 observed in this study are common for *Platanthera praeclara,* although densities of up to 1.12 plants/m2 have been reported on the Sheyenne National Grassland (Bowles, 1983). Bowles (1983) postulated that seasonal mowing, grazing and burning on the Sheyenne National Grassland reduced competition and enhanced colonization by *P. praeclara.* However, the absence of any differences in *P. praeclara* densities among management regimes observed in our study to this point fails to support this theory. Research involving experimental manipulation is necessary to gain a better understanding of the influence disturbances such as fire, grazing and mowing on *P. praeclara* populations.

Of the four plant communities identified by cluster analysis in which *P. praeclara* populations occurred, the most common type was dominated by *Poa pratensis* and *Juncus balticus.* Other dominant species in this type included *Panicum virgatum* and *Spartina pectinata; Fragaria virginiana* Duchn. and *Euphorbia esula* were major forbs. The three other types included two or three transects each, and varied from one dominated by *Carex* spp. and *Dichanthelium wilconianum* to two salix-dominated types. Two of these community types included transects from three management regimes: grazed-rotational, grazed-burned and ungrazed-burned; the two other groups were made up of transects from only one management regime each.

In spite of the large contribution of *Poa pratensis* to the vegetative composition of the transects, regression analysis indicated that *Platanthera praeclara* density in 1 yr was negatively associated with cover of this species. Although causal factors for this relationship were not explored, the sod-forming nature of *Poa pratensis* may inhibit *P. praeclara* germination and establishment. The positive relationship of *P. praeclara* densities with *Salix* cover is counter to previous work that suggests that shrub encroachment might degrade orchid habitat (e.g., Bowles, 1983). Early spring or early autumn cutting reduced shrub cover and increased density and flowering of *Cypripedium candidum* Muhl. ex Willd. (Curtis, 1946). However, experimental removal of shrubs did not enhance numbers of *C. candidum* (Falb and Leopold, 1993). Perhaps at the levels of *Salix* cover observed on the Sheyenne National Grassland, competition is relatively low. Negative correlations with total plant canopy cover and positive association with litter cover suggest *P. praeclara* may do best in areas of reduced competition, but requires some litter cover. Based on regression analysis, *Calamagrostis stricta* is the best indicator of *P. praeclara* habitat on the Sheyenne National Grassland.

With the exception of organic matter content, physical and chemical properties of soils were similar among sites. The extremely low organic matter content on the season-long grazing site is unusual, and may be attributed to the occurrence of Entisols in some transects on this site (U.S. Soil Conservation Service, 1975), which tend to be low in organic matter (Boul *et al.,* 1980). This low organic matter content may also explain the lower soil moisture content on this site compared to other sites. However, the greater water depth on the grazed season-long site is evidence of a higher water table on this site, compared to other sites.

These preliminary demographic analyses of *Platanthera praeclara* subpopulations on the Sheyenne National Grassland indicate that this plant may not always be long-lived. Menges (1986, p. 16) suggested that data from two field seasons can be used to make preliminary analyses, but cautioned that "these predictions are only as good as that time period is typical of the future." The true demographic picture of *P. praeclara* will likely emerge only after several more years of intensive monitoring. In addition to continuing to monitor plants already marked, a new monitoring program will begin on the Sheyenne National Grassland in 1995. The plan is to replicate four treatments (burned, burned/grazed, not burned/grazed, not burned/not grazed) over a variety of soil types. In addition, experimental manipulations using fire, grazing and mowing are needed to examine the role of regeneration niches in the establishment of *P. praeclara.*

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