

DYNAMICS OF A THREATENED ORCHID IN FLOODED WETLANDS

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Abstract: One of the three largest metapopulations of the western prairie fringed orchid (*Platanthera praeclara*) occurs on the Sheyenne National Grassland, in southeastern North Dakota. Our study was initiated in 1993 to quantify the effect of flooding on individual orchid plants. In 1993, 66 plants (33 flowering and 33 vegetative) growing in standing water were permanently marked; their status was checked at the end of the growing season in 1993 and in subsequent growing seasons (1994–1996). Most (70%) of the flowering plants persisted through the 1993 growing season. Those that did not were shorter ($P = 0.001$) and had a higher percentage of their stalk submerged through the growing season ($P < 0.02$). Only one vegetative plant persisted through the 1993 growing season. The ability of flowering plants to persist in standing water was attributed to their greater height which allowed some portion of the plant to remain above the water and produce photosynthates needed to produce next season's shoot bud and immature root system. Flowering plants persisted through the first growing season with as much as 75% of their stalk submerged in water. In 1994, only four plants reappeared; in 1995 only one plant reappeared aboveground. None of the plants that did not persist through 1993 reappeared in 1994 or 1995. By 1996 none of the marked plants were observed aboveground. Although flooding is detrimental, especially to the survival of vegetative plants, its impact must be viewed in a larger context and include data from several years. It is likely that flooding creates suitable moisture conditions on higher landscape positions, provides an important mechanism for seed dispersal, and is one of several natural catastrophic events that plays a significant role in perpetuating these wetland systems and associated species.

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The western prairie fringed orchid (*Platanthera praeclara*) is a federally listed threatened plant species found in wetlands of the tallgrass prairie west of the Mississippi River (U. S. Fish and Wildlife Service 1996). One of the three largest metapopulations of the orchid occurs on the Sheyenne National Grassland in the southeastern corner of North Dakota (U. S. Fish and Wildlife Service 1996). The climate in this region is erratic and is characterized by periods of both severe droughts and periodic flooding.

The western prairie fringed orchid is a perennial plant characterized by erratic aboveground growth and flowering. Periods of high orchid numbers, usually linked with above-average precipitation, are followed by years when the orchids have seemingly disappeared (Bowles et al. 1992). The life history of the orchid includes two distinct life states. Vegetative plants on the study area average up to 24 cm tall, usually have 1 or 2 leaves, and remain vegetative throughout the growing season; flowering plants develop a hollow flowering stalk early in the growing season that has

numerous leaves (> 10) and average up to 52 cm tall (Sieg and King 1995).

The western prairie fringed orchid was thought to be a long-lived species, with erratic flowering patterns and periods of dormancy (Bowles 1983). However, recent demographic data collected on the Sheyenne National Grassland during a period that included a drought and episodic flooding suggest that most plants live three years or less, and once absent, the odds of remaining absent are 80% or better (Sieg and King 1995). The orchid regenerates 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, Wolken 1995). In this manner, populations may persist for some time. However, seed establishment is required for recruitment of new individuals (Bowles 1983).

The association between soil moisture and growth and flowering of the orchid has been documented. Densities of flowering orchids on the

Sheyenne National Grassland were positively correlated with soil moisture in the current year, and total orchid density was correlated with soil moisture in the current and previous year (Sieg and King 1995). However, the dynamics of orchid populations in flooded wetlands are undocumented. Severe flooding on the Sheyenne National Grassland, beginning in 1993 and continuing to a lesser extent through 1996, afforded us the opportunity to assess the impacts of standing water on the persistence of western prairie fringed orchids. The purpose of this study was to determine if orchids that were partially or totally submerged persisted through the 1993 growing season, and if they reappeared aboveground in 1994 and in subsequent years. We were also interested in determining what variables were most useful in predicting survival of orchids in flooded conditions.

STUDY AREA

The study was conducted in the Sheyenne National Grassland, in southeastern North Dakota. The National Grassland encompasses 27,244 ha, and is managed by the United States Forest Service. Kuchler (1964) depicted the vegetation of the Sheyenne National Grassland as tallgrass prairie; however, the "Sandhills Prairie" terminology of Barker and Whitman (1989) is more accurate. Big bluestem (*Andropogon gerardii*) and little bluestem (*Andropogon scoparius*) occur throughout the study area. The western prairie fringed orchid occurs most often in lowland depressions ("swales") associated with the Glacial Sheyenne Delta. 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). Woolly sedge (*Carex lanuginosa* Michx.) northern reedgrass (*Calamagrostis stricta* (Timm.) Koel.), and Baltic rush (*Juncus balticus* Willd.) are common in lowland depressions where the orchid occurs (Sieg and Bjugstad 1994, Sieg and King 1995). Blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths), needle-and-thread (*Stipa comata* Tm. & Rupr.), sun sedge (*Carex heliophila* Mack.), and prairie sandreed (*Calamovilfa longifolia* (Hook) Scribn. grow on uplands.

The mean annual precipitation on the study area is 497 mm, the major portion of which is received during the growing season months of April to September (U. S. Department of Commerce 1973). Precipitation on the National Grassland was above average in 1992 (608 mm), 1993 (561 mm), 1994 (510 mm), 1995 (602 mm), and 1996 (549 mm). As

a result, the National Grassland was severely flooded in 1993 and some swales where the orchid commonly occurs remained flooded in 1994, 1995, and 1996. Although records on flooding on the National Grassland are not available, the Sheyenne River at Lisbon, N. D., has exceeded flood stage 10 times since 1975; four of these dates were since 1993; flooding occurred twice in 1996 (Fig. 1). Eight of these occurrences (80%) were from March to May (National Weather Service unpublished data, on file at the National Weather Service Office, Grand Forks, ND 58203-0600).

METHODS

In order to assess persistence of orchids through periods of flooding, our goal was to randomly select a minimum of 2 vegetative and 2 flowering orchids in each of a total of 15 flooded swales on six sites (Fig. 2). The other criteria was that the water depth at each plant location was at least 5 cm at some point during the growing season. Therefore, we permanently marked and mapped the locations of a total of 66 orchids (33 flowering and 33 vegetative plants) in early July 1993. In addition to recording the life state of each plant, we also measured plant height, number of leaves, number of flowers (for flowering plants), and water depth for each marked plant.

We quantified persistence by revisiting marked orchids late in the orchid growing season (mid-August) in 1993. In addition to assessing orchid health and survival, we again measured water depth at each plant. We visited the marked locations and measured water depth (if standing water was present) during the peak of flowering (mid-July) in 1994, 1995 and 1996 to determine if the orchids reappeared in subsequent growing seasons.

Statistical Analyses

Flowering and vegetative plants were analyzed separately. For each life state, plants were divided into one of two groups: "alive" - those that persisted through the 1993 growing season or "dead" - those that did not persist through the growing season. "Dead" plants included orchids whose aboveground portions were present but severely decomposed, and those whose aboveground portions were entirely rotted off.

Only 1 vegetative plant persisted through the growing season; therefore, we were not able to analyze characteristics of "alive" and "dead" vegetative plants. However, sample sizes for these two persistence classes were adequate to compare characteristics of "alive" and "dead" flowering plants.

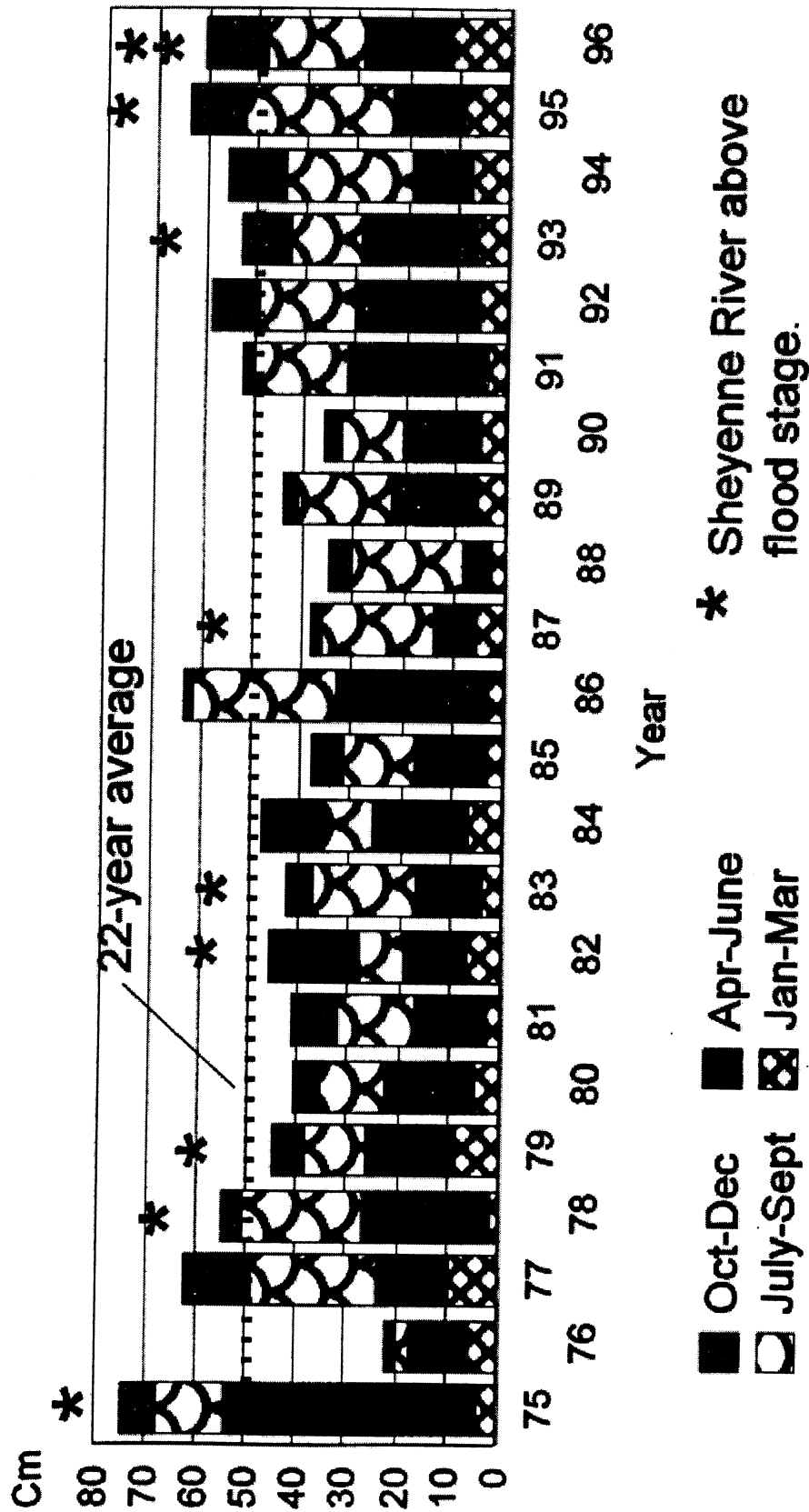


Fig. 1. Total annual precipitation, by season 1975-1996, for Lisbon, North Dakota, near the Sheyenne National Grassland, plus years with one or more times when the flow in the Sheyenne River at Lisbon exceeded flood stage (National Weather Service unpublished data, on file at the National Weather Service Office, Grand Forks, ND 58203-0600).

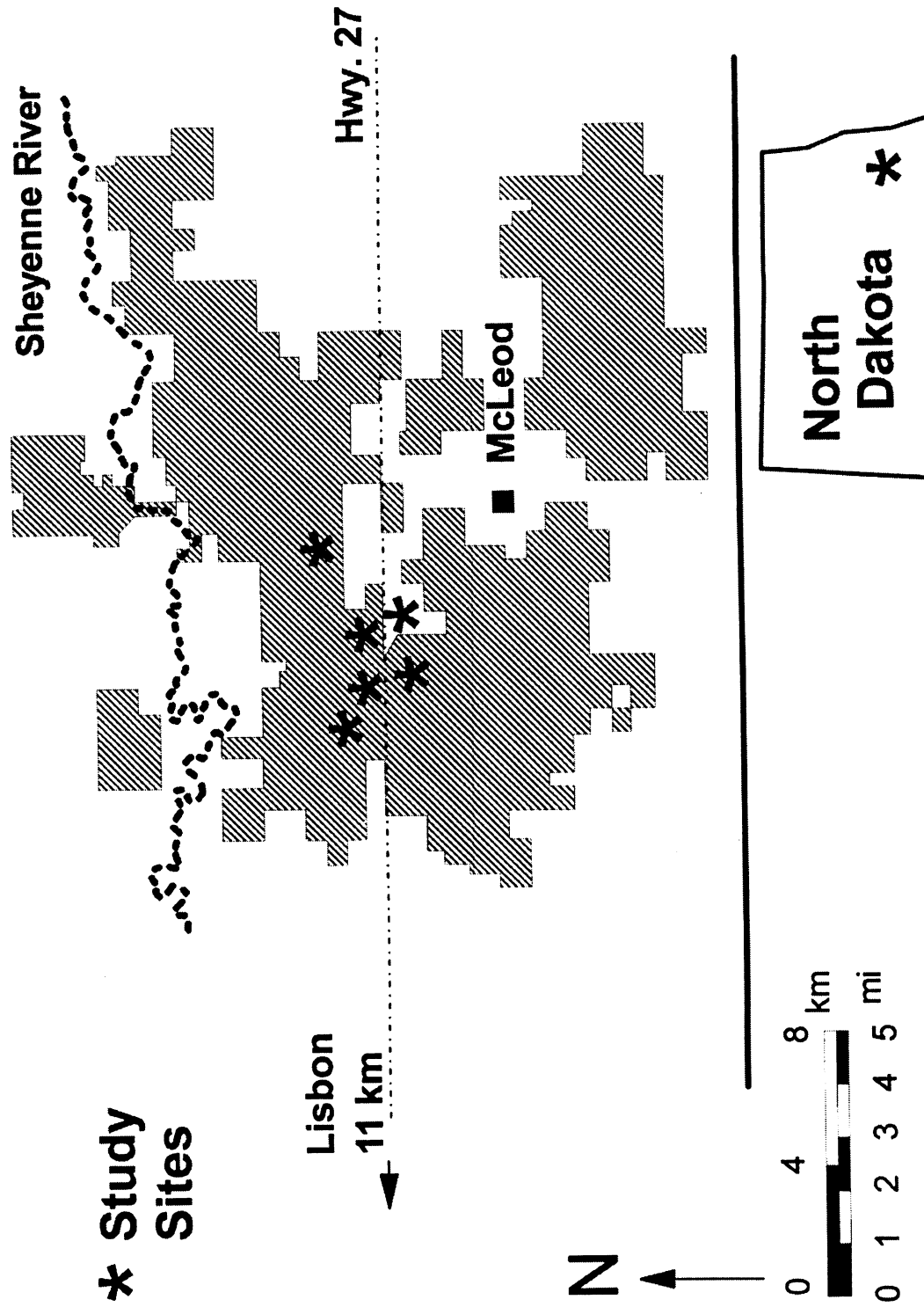


Fig. 2. Location of the study sites on the Shenyenne National Grassland in southeastern North Dakota.

Independent samples t-tests were used to compare differences between heights and percentages of “alive” and “dead” flowering plants that were submerged in July and August 1993 (Statistical Product and Service Solutions 1997). We also used t-tests to compare water depths in July and August 1993 between “alive” and “dead” flowering orchids. The assumption that variances were homogeneous was tested with Levene’s test (Milliken and Johnson 1984). Differences between variables with heterogeneous variances were analyzed with heterogeneous variance t-tests for independent samples (Statistical Product and Service Solutions 1997). Variables that had heterogeneous variances ($P < 0.05$) included June water depth, average water depth, plant submergence percentage in September, and average percentage submergence).

RESULTS

Flowering Orchids

Plant Height. -Of the 33 flowering plants, 23 (70%) persisted through the 1993 growing season. “Alive” flowering orchids were significantly ($t = 3.875$, $df = 31$, $P = 0.001$) taller than “dead” plants (Table 1). Flowering orchids that survived through the 1993 growing season averaged 50 cm tall, with a range of 30 to 77 cm. Flowering orchids classified as “dead” at the end of the 1993 growing season averaged 32 cm tall, and ranged in height from 14 to 46 cm tall.

Water Depth. -Standing water was present in the swales throughout the summer. Water depth in June ($t = -0.428$, $P = 0.6$) and September ($t = -1.12$, $P = 0.3$), and average water depth ($t = -0.826$, $P = 0.4$) did not differ significantly between persistence classes of flowering plants. In June, water depth averaged 19 cm for “alive” plants and 21 cm for “dead” flowering plants (Table 1). The maximum water depth we recorded in June was 43 cm. In September, water depth averaged 22 cm and 26 cm, respectively, for “alive” and “dead” flowering plants; but, we measured water up to 46 cm deep. Average water depth through the growing season was 20 and 24 cm for “alive” and “dead” flowering plants, respectively.

Plant Submergence. -In spite of similar water depth for the two persistence classes of flowering orchids, percentage of the plant that was submerged in water differed significantly between “alive” and “dead” plants in June ($t = -2.802$, $P = 0.009$) and in September ($t = -2.660$, $P = 0.02$), and the overall average percent submergence also differed ($t = -3.067$, $P = 0.001$) between the two persistence classes for flowering plants (Table 1). Percentage

submergence in June averaged 35% for “alive” plants, with a maximum of 73%, compared to 66% for “dead” plants, with a maximum of 100%. The percentage of “alive” plants that was submerged in September averaged 43%, with a maximum of 75%, compared to 91% submergence for “dead” plants, with a maximum of 100%. The average percentage submergence through the growing season was 40% for “alive” plants and 78% for “dead” plants.

Vegetative Orchids

Only one vegetative orchid persisted through the 1993 growing season. This plant averaged 23 cm tall and was found in water that averaged 6 cm deep in June (Table 2). By the end of the growing season, the water was < 1 cm deep. “Dead” vegetative orchids averaged 19 cm tall, and occurred in water that averaged 15 cm in June and 18 cm in September. The percentage submergence for “dead” vegetative plants averaged 90% in June and 100% in September. In some cases, we found little of the plant by the middle of August 1993. All of the submerged plants had some partially rotted leaves; some plants were totally rotted.

Subsequent Growing Seasons

Of the 23 flowering plants that persisted through the 1993 growing season, only three reappeared aboveground in 1994 (Table 3). The average percentage of submergence for these three plants in August 1993 was 28%, compared to an average submergence of 45% for the 20 plants that survived through 1993 but did not reappear in 1994. Two of the flowering plants returned as vegetative plants in 1994 and 1 flowering plant returned as a flowering plant in 1994. The one vegetative plant that persisted through 1993 reappeared as a vegetative plant in 1994. By the time we revisited the marked plants in 1994, other swales on the study area remained flooded, but standing water was not present at the marked orchid locations.

In 1995, we found only one of the originally marked orchids, and in 1996 none of the originally marked orchids appeared aboveground. Standing water was again present in most swales in both July 1995 (ranging from an average of 4.0 to 18.8 cm deep) and July 1996 (ranging from an average depth of 0 to 33.0 cm) on these study sites when we checked marked orchids in July. None of the 42 plants that did not persist through the 1993 growing season reappeared in the three subsequent growing seasons.

Table 1. Average plant height ($\pm$ SE), water depth in June and September, and percentage submergence of plants in June and September, plus overall average water depth and average percentage submergence for 33 flowering western prairie fringed orchids occurring in flooded swales, by their status (alive or "dead"^a) at the end of the growing season in 1993.

	Alive (n=23)	"Dead" ^a (n=10)
Plant height (cm)	49.5 $\pm$ 2.6 ^b	32.4 $\pm$ 3.1 ^c
June water depth (cm)	18.8 $\pm$ 3.1 ^c	20.9 $\pm$ 3.6 ^c
June plant submergence (%)	35.2 $\pm$ 4.9 ^c	65.5 $\pm$ 12.0 ^b
September water depth (cm)	21.5 $\pm$ 2.4 ^c	26.0 $\pm$ 2.7 ^c
September plant submergence (%)	42.7 $\pm$ 3.8 ^c	91.1 $\pm$ 17.8 ^b
Average water depth (cm)	20.1 $\pm$ 2.7 ^c	23.5 $\pm$ 3.0 ^c
Average plant submergence (%)	38.9 $\pm$ 4.0 ^c	78.3 $\pm$ 14.0 ^b

^a"Dead" plants were those whose aboveground portions were present, but severely decomposed, or whose aboveground portions were entirely rotted off.

^{b,c}Means followed by different superscripts are significantly different ($P < 0.05$).

Table 2. Average ($\pm$ SE) plant height, water depth in June and September, and average percent plant submergence in June and September, plus overall average water depth and average percent plant submergence for 33 vegetative western prairie fringed orchids occurring in flooded swales, by their status (alive or "dead") at the end of the growing season in 1993.

	Alive (n=1)	"Dead" ^a (n=32)
Plant height (cm)	22.5 $\pm$ 0	19.4 $\pm$ 1.3
June water depth (cm)	6.1 $\pm$ 0	14.9 $\pm$ 2.0
June plant submergence (%)	27.1 $\pm$ 0	78.3 $\pm$ 9.2
September water depth (cm)	0.1 $\pm$ 0	17.9 $\pm$ 1.8
September plant submergence (%)	0.4 $\pm$ 0	100.6 $\pm$ 13.1
Average water depth (cm)	3.1 $\pm$ 0	16.4 $\pm$ 1.8
Average plant submergence (%)	13.8 $\pm$ 0	89.5 $\pm$ 10.4

^a "Dead" plants were those whose aboveground portions were present, but severely decomposed, or whose aboveground portions were entirely rotted off.

DISCUSSION

This study provides evidence that flooding on the Sheyenne National Grassland differentially affects vegetative and flowering western prairie fringed orchids. Seventy percent of the flowering orchids persisted through the 1993 growing season, compared to only 3% of the shorter vegetative plants. The low rate of persistence of vegetative plants was attributed to their short stature and absence of a hollow seed stalk. The greater height of flowering orchids and lower percentage of their total height that was submerged increased the odds that some portion of the plants was above the water and thus able to photosynthesize. Further, their hollow stems provided a likely conduit for oxygen to the roots. The development of pore space in the cortical tissues is an adaptation in wetland vascular plants that allows oxygen to diffuse from the aerial parts of the plant to the roots to supply root respiratory demands (Mitsch and Gosselink 1993).

For flowering plants, those that persisted through the 1993 growing season were taller and had a smaller percentage of their total height submerged. Our evidence (Wolken 1995) suggests that the western prairie fringed orchid is similar to species such as the little green orchid (*P. hyperborea*) (Currah et al. 1990) in that successful development of the mature plant, flowers, fruits and storage tissue depends on the photosynthetic gains of the new foliage (Pate and Dixon 1982). Present photosynthates also contribute to the formation of next season's shoot bud and immature root system (Currah et al. 1990). Taller

flowering plants with a greater portion of their biomass above the water would be more likely to produce adequate photosynthates for completion of their seasonal development.

Yet, many orchids that did survive through 1993 failed to reappear in subsequent growing seasons. Only 13% of the flowering plants that survived through the 1993 growing season reappeared in 1994, and only one of these plants reappeared in 1995. Demographic data collected on the Sheyenne National Grassland between 1990 and 1994 indicated that the percentage of marked plants that reappeared the following year ranged from a high of 73% for the 1991 cohort to only 16% for the 1993 cohort (Sieg and King 1995). This variation in reappearance rates is likely influenced by environmental conditions both the first year and in subsequent years. The exposure to environmental stresses such as flooding may have a carry-over effect in subsequent growing seasons (Bowles et al. 1992, Falb and Leopold 1993, Lesica and Steele 1994). Environmental stresses or damage in a previous season during which carbohydrate reserves and perennating tissues were formed, or during the beginning of the current growing season when adequate conditions dictate the growth and survival of a new plant, were thought to be cues that influenced the reappearance of plants during a growing season (Epling and Lewis 1952, Stoutamire 1974, Pate and Dixon 1982, Davies et al. 1983, Mehrhoff 1989).

Another factor that certainly influences the survival of flooded plants is the timing and duration

Table 3. Presence the second growing season (1994) of 33 vegetative and 33 flowering western prairie fringed orchids occurring in flooded swales, by their status (alive or "dead"^a) at the end of the growing season in 1993.

Life state	Status at end of 1993	n	Presence in 1994	
			Present (life state) ^b	Absent
Vegetative	alive	1	1 (V)	-
	"dead"	32	0	32
Flowering	alive	23	3 (2V, 1F)	20
	"dead"	10	0	10

^a"Dead" plants were those whose aboveground portions were present, but severely decomposed, or whose aboveground portions were entirely rotted off.

^bV = vegetative; F = flowering

of the flooding. In 1993, the swales remained flooded through the growing season, in response to high summer precipitation. In fact, the water depth increased through the growing season in many swales, and this was 1 of only 2 times that the flow in the Sheyenne River at Lisbon exceeded flood stage after May (2 August); the only other time this occurred since 1950 was on 1 July 1975 (National Weather Service unpublished data, on file at the National Weather Service Office, Grand Forks, ND 58203-0600). It is likely that plants would be more likely to persist, and flowering plants more likely to produce seeds, in years when the flooding occurs early in the growing season and then subsides.

For the plants whose aboveground portions perished, the question remains if the plants can survive belowground. Although the prairie fringed orchids, like many species of orchids, are known for their erratic dormancy patterns (e. g. Hutchings 1989), few data are available on the long-term impacts of flooding or other stresses on survival of individual plants. In an effort to assess if aboveground absence was due to dormancy or death, we excavated 10 orchids in 1994 that were present and precisely marked in 1993, and absent aboveground in 1994. We removed a 40-cm diameter by 20-cm deep plug of soil around the location of each absent orchid and carefully searched for any evidence of the 1993 dormant root system, and found no evidence of any recognizable root system tissue where any of the ten 1993 orchids were originally marked (Wolken 1995). Demographic data collected between 1987 and 1994 on the Sheyenne National Grassland indicate that once orchids disappear, the odds of reappearing aboveground the following year are < 20% (Sieg and King 1995). Therefore, it is unlikely that the plants that did not reappear in 1994 or in subsequent years will reappear aboveground in the future.

Although this paper documents that flooding has a detrimental effect on the persistence of some individual orchids occurring in the wettest portions of the landscape, we do not suggest that flooding over the last 4 years has destroyed the metapopulation of the western prairie fringed orchid on the Sheyenne National Grassland. To the contrary, we observed high numbers of orchids on the Grassland in 1993 and in subsequent years (Sieg and King 1995). However, we have documented a shift in the metapopulation. Swales that supported orchids during a drought in the early 1990's have been flooded and devoid of orchids since 1993; yet the presence of orchids on higher

landscape positions have resulted in a net increase in orchid numbers on the National Grassland beginning in 1993 (Sieg and King 1995).

Although flooding may result in low persistence rates especially for vegetative plants, flooding also creates habitats with suitable moisture conditions higher on the landscape and then serves to disperse orchid seeds to these habitats. The dust-like seeds of orchids are among the smallest known in the plant kingdom; because of their minute size (from 0.07 to 0.4 mm across and from 0.11 to 1.97 mm in length), we know relatively little about their germination ecology (Rasmussen 1995). The minute size and inflated air-filled testa make orchid seeds well equipped for wind dispersal, but the water-repellent lipid layer, buoyancy and rough surface enable them to float on the surface of water (Rasmussen 1995). Flooding functions to concentrate and deposit seeds of wetland plants along drift lines (Mitsch and Gosselink 1993).

Therefore, to appreciate the complete and complex role of flooding on the life history and distribution of the western prairie fringed orchid and other wetland species, data from both individual plant and landscape levels are needed. Floods and droughts are catastrophic events that play a significant role in both modifying yet perpetuating these wetland systems and their associated species (Mitsch and Gosselink 1993). Further, long-term data sets that incorporate the impacts of droughts, fires and human influences are needed to fully understand the population dynamics of this threatened plant species.

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