Gas Exchange and Reproduction of *Spiranthes vernalis* (Orchidaceae) in a Kansas Tallgrass Prairie

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Abstract. Spring ladies-tresses (*Spiranthes vernalis*) is a spring emergent, summer flowering, geophyte occurring over much of the eastern half of the United States. In northeastern Kansas, it is a rare and subordinate member of upland and lowland, tallgrass prairie, plant communities. At Konza Prairie Research Natural Area in northeastern Kansas, *S. vernalis* is infrequent and found primarily in annually burned or annually mowed sites. In these locations, it emerges into a high light environment and must adjust to ever-decreasing amounts of incident light as the dominant grass canopy forms and closes. Plants growing in prairie with typical canopy cover had a peak CO_2 uptake rate (net photosynthesis) of 22 ìmol m^{-2} s^{-1} in mid-June. When canopy shading was removed in mid-June as a test of this orchid's response to natural canopy removal by grazing, plants showed a significant reduction in CO_2 uptake (8.5 ìmol m^{-2} s^{-1}) within 1 h of canopy removal, but complete recovery of CO_2 uptake to pretreatment levels within 10 d. In late July through August, plants produced scapes supporting 40 ± 5 flowers, which yielded 6 ± 2 mature fruits.

Key words: orchid, photoinhibition, phenology, tallgrass prairie.

Introduction

Studies of vegetation dynamics and plant responses to stress in tallgrass prairie systems typically have concentrated on the effects of fire and grazing on the growth, physiology, and population dynamics of the dominant grasses and forbs (Collins and Barber, 1985; Knapp and Hulbert, 1986; Gibson and Hulbert, 1987; Knapp et al., 1993). Although this effort is important in understanding large scale processes in tallgrass prairie, subdominants such as *Spiranthes vernalis*, which are infrequent or rare, may make a greater contribution to total prairie biodiversity (Freeman and Hulbert, 1985).

Spiranthes vernalis occurs in a wide range of habitats from Atlantic coastal barrier islands to the western margins of tallgrass prairie (Correll, 1950; Duncan and Duncan, 1987; McCaffrey and Dueser, 1990; Kaul, 1986). In the tallgrass prairie of northeastern Kansas, *S. vernalis* grows on uplands beneath a grass canopy (Freeman and Hulbert, 1985). In this environment, plants may be exposed to full sun during the growing season, if the overstory is removed by grazers such as American bison (*Bison bison*) or domestic cattle. Sudden changes from low to high light may lead to photoinhibition and potential damage to photosynthetic pigments (Krause, 1988). Although photoinhibition of photosynthesis and subsequent recovery responses of plants exposed to high light are well documented, most studies of involve agriculturally important species and are conducted under laboratory conditions (Krause, 1988; Liu et al., 1993; Aro et al., 1994). Conversely recovery from photoinhibition in short-statured geophytes such as *S. vernalis* in response to sudden canopy removal is not well documented. Because *S. vernalis* is one of very few species that remain photosynthetically active over much of the growing season, it may be an ideal species for testing responses of short-statured plants to sudden increases in ambient light levels.

The purpose of this study was to 1) quantify seasonal dynamics of CO_2 uptake and stomatal conductance in *S. vernalis*, 2) quantify responses of *S. vernalis* to sudden exposure to full sunlight at mid-season by the removal of canopy shade, and 3) document reproductive characteristics of *S. vernalis* in the tallgrass prairie ecosystem.

Methods

Research was conducted at the Konza Prairie Research Natural Area (KPRNA) near Manhattan, Kansas (39°08'N, 96°35'W). KPRNA undergoes periodic prescribed spring (April) burning, where watershed-sized units (3 to 220 hectares) are burned at 1- to 20-year intervals. Because *Spiranthes vernalis* is much smaller than neighboring grasses and forbs, it is easily located only when in flower. Therefore, study sites on KPRNA were selected after an intensive search for plants beginning in mid-July and continuing until late August of 1992. Of the total 18 *S. vernalis* found, (1) seven plants were located on a shallowly sloped upland site in an annually burned watershed, (2) five were in a lowland area of an annually fall-mowed fire guard between an unburned watershed and a watershed that is annually burned for 3 consecutive years and then left unburned for 3 consecutive years (denoted as 3U3B), (3) two plants were found in separate annually burned *Spartina pectinata* wetlands, (4) three were located on a hilltop in a 10-year burned watershed, and (5) a single plant was located in an upland community in a biennially burned watershed (Figure 1). Plants in the annually burned watershed were scattered over an area of ca. 50 m^2 and may be progeny from a number of parental sources whereas the plants of the mowed fire guard were in a single 0.5 m^2 clump and may represent progeny from a single parent plant. *Spiranthes* may spend as much as 10 years as belowground, corm-like structures. Therefore, the present distribution of plants may be a function of environmental conditions 10 years ago (Wells, 1981). The small upland clump (n=3) also may represent an isolated dispersal. The total sample size is small, but *S. vernalis* is rare on KPRNA (Freeman and Hulbert, 1985).

To quantify the seasonal course of CO_2 uptake (A) and stomatal conductance (g_{wv}), midday A and g_{wv} were measured using a Li-Cor LI 6200 portable gas exchange system (LICOR, Inc., Lincoln, NE). Measurements were made on two mature leaves located in the middle of the leaf cluster at the base of plants. Values for A and g_{wv} for each plant were means of these two measurements. In early May, leaves were exposed to full sunlight (>1500 ìmol m^{-2}
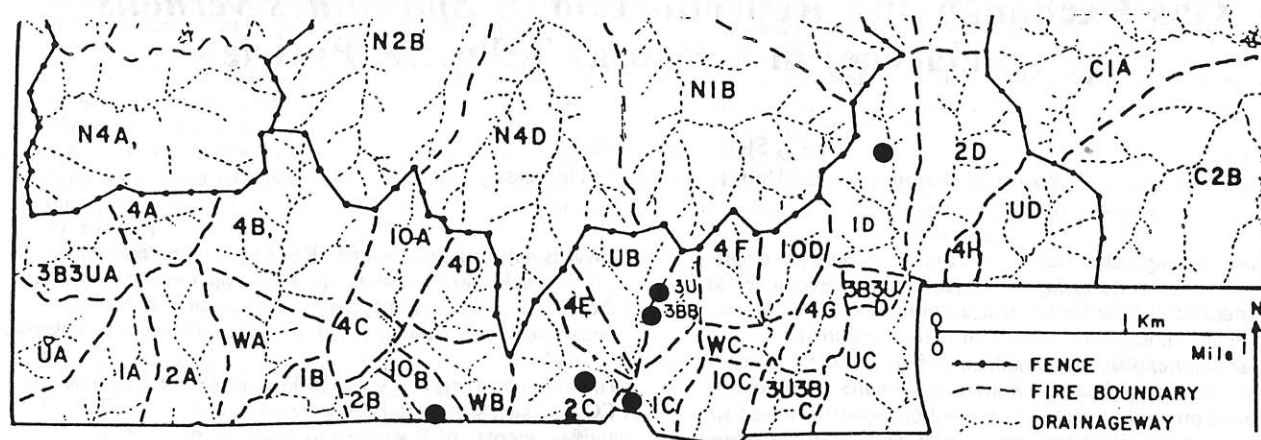
FIG. 1. Map of the southern third of Konza Prairie Research Natural Area indicating the positions (·) of *Spiranthes vernalis* plants or patches described in the text. Two points appear in 3U3BB because one patch of orchids growing in upland is distinct from a single plant growing in a *Spartina pectinata* wetland.

s[-1], photosynthetic photon flux density (PPFD) 0.4 - 0.7 im), but ambient light on *S. vernalis* had been reduced to less than 50 % of full sunlight by late May to early June and to 25 % of full sunlight by late June (Fig. 2). In both 1992 and 1993, air temperatures were between 34 and 36°C and RH between 30 and 45% during field measurements.

To estimate the response of *S. vernalis* to canopy removal, vegetation within an area of 0.25 m² surrounding four plants in the annually burned watershed was clipped to a height of 1 cm in mid and late June. Photosynthetic CO_2 uptake was measured in exposed *S. vernalis* within 1 hour of canopy removal with the Li-Cor 6200. Simultaneous measurements were made on unmanipulated plants in the same annually burned watershed, the two wetlands, and the 10-year unburned upland (n=10). Because inclement weather over northeastern Kansas in the summer of 1993 (with rainfall 25 cm above a 30-year mean; KPRNA weather data, unpubl.), these plants could not be remeasured until 10 days had elapsed following the clipping treatment.

In August and September of 1992 and 1993, I measured heights of mature scapes, flower numbers per scape, initiated fruits, and subsequent mature fruits per scape. Fruits counted as initiated were those that had slightly swollen and remained attached to scapes after flowers had withered. These were visibly different from ovaries, which had fallen away from scapes with withered flowers, and from mature fruits, which were greatly swollen. In order to minimize the effects of elevation and treatment, only the plants of the annually burned watershed were counted. Because sample sizes were small and there were essentially no replicates of any sites where *S. vernalis* grew, this study is best described as mensurative (Hurlbert, 1984) and is meant only as a descriptive study of *S. vernalis* ecology in tallgrass prairie. Where statistical analysis was appropriate, such as with the comparison of plants with canopy removal and without canopy removal, a paired t-test procedure was used at an á=0.05 significance level (Zar, 1984).

Results and Discussion

The seasonal course of net CO_2 uptake (A) (Fig. 2) was typical of an understory geophyte (Yoshie and Yoshida, 1987). The peak A (22.6 ± 1.4 imol CO_2 m² s[-1] (mean ± 1 se); n=15 plants), which occurred in mid-June, was similar to peak rates of C_3 prairie forbs such as *Baptisia leucophaea* (S. Johnson, unpubl. data).

This maximum A was similar to peak A in the tropical, open canopy orchid *Arundinia graminifolia* (15.5 imol m² s[-1]; S. Johnson, unpubl. data). In addition, this rate is higher than peak rates for understory tropical orchids such as *Paphiopedilum armeniacum* (Johnson, 1992; 1993). Seasonal patterns in stomatal conductance (g_{wv}) closely followed A and ranged from 330 ± 53 mmol m² s[-1] in mid-May to 581 ± 38 in late June and to 200 ± 16 mmol m² s[-1] in late August.

Following canopy removal in mid-June, A in exposed plants decreased from 22.6 to 8.5 ± 0.8 imol CO_2 m² s[-1] in 1 h (n=4, Figure 2). Ten days later, A in the exposed orchids had increased to 18.2 ± 1.6 imol CO_2 m² s[-1], whereas A in shaded plants was 17.4 ± 2.6 imol CO_2 m² s[-1] (n=10, Figure 2). Following peak periods of CO_2 uptake, A in plants of both exposed and shaded treatments steadily declined through the rest of the season. The lower CO_2 uptake by exposed plants may have been due to protective mechanisms associated with PSII during photoinhibition (Krause, 1988, Aro et al., 1994, Lovelock et al., 1994). However, other mechanisms such as stomatal closure may have been involved. Stomatal conductance was significantly (p<0.05) reduced in exposed plants 1 h after clipping in mid-June (136 ± 25 mmol m² s[-1] in exposed plants vs 433 ± 73 mmol m² s[-1] in shaded plants, p<0.001) indicating stomatal closure in treatment vs. control plants.

Table 1. Numbers of flowers per scape, initiated fruits, and matured fruits of *Spiranthes vernalis* on KPRNA in 1992 and 1993[*].

Year	No. of flowers	No. of initiated fruits	No. of matured fruits
1992	43.8 ± 3.3	36.1 ± 5.1	4.4 ± 1.9
1993	34.5 ± 5.2	28.6 ± 6.2	8.7 ± 2.3

[*] Flower numbers were counted in early August, initiated fruits in late August to early September, and matured fruits in mid-October of both years of the study. Values represent means ± 1 SE (n=7).
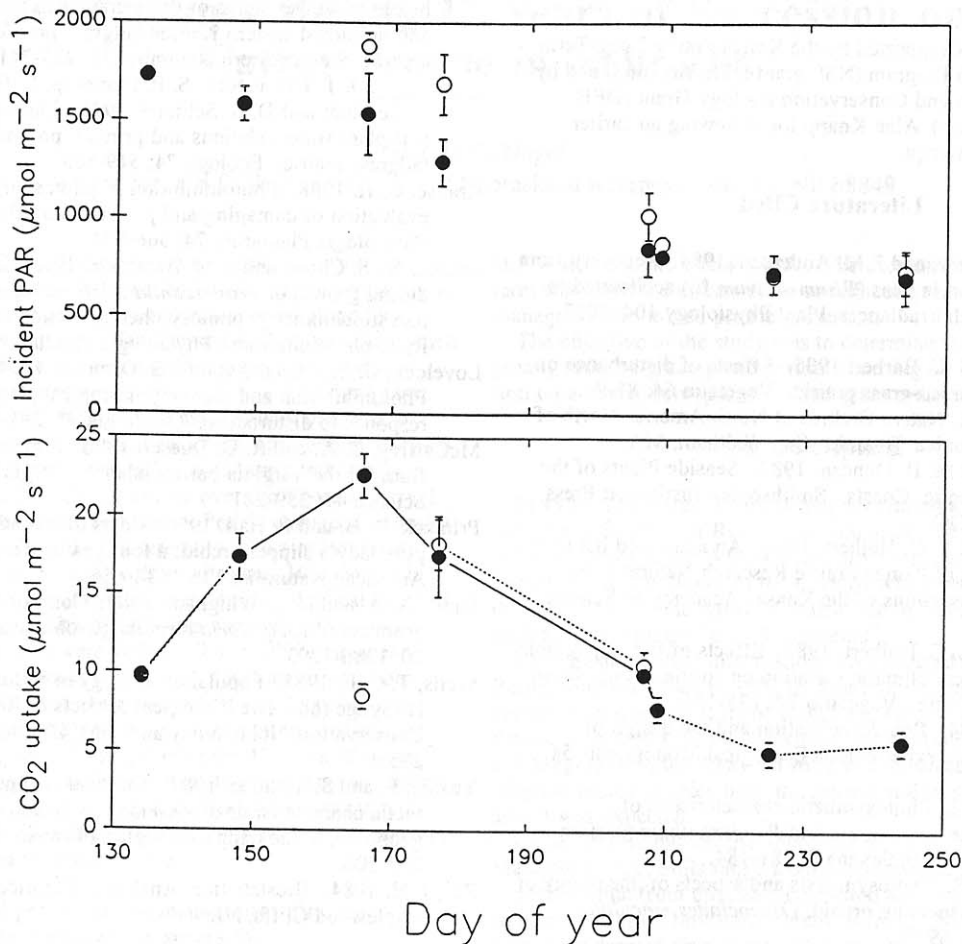
FIG. 2. Incident PAR (top) and CO_2 uptake (imol m^{-2} s^{-1}) for *Spiranthes vernalis* that remained shaded (·) or had shading removed on June 15 and 25 (DOY=166 and 176, °) during the 1993 growing season. Each value is the mean of measurements of three separate leaves on 10 shaded plants and on four exposed plants. Vertical bars indicate one standard error of the mean.

Flower production was higher and fruit production lower in 1992 than in 1993, although the differences between years were not significant (Table 1). The ratio of the number of fruits successfully matured to the initial number of flowers was consistent over the 2 years of the study and may be the maximum number that *S. vernalis* can support successfully (Snow and Whigham, 1989; Primack and Hall, 1990). Although flowering was consisent in plants of the annually burned watershed in 1992 and 1993, large variations in flowering occurred between years in plants at the other locations (Table 2).

Although *S. vernalis* occupies a subordinate position in tallgrass prairie, it is ecologically interesting, because it occurs in a wider range of habitats than do the dominant grasses and most other subdominant forbs. The seasonal course of photosynthetic CO_2 uptake of *S. vernalis* was similar to that associated with many forest understory geophytes. The response to simulated grazing of competitors was a reduction in A immediately following exposure to full sun. Depending on the time needed for recovery of A following exposure, such exposure might affect seasonal CO_2 gain. However, the recovery of *S. vernalis* was fairly rapid and not associated with any visible tissue damage or loss. This may indicate that *S. vernalis* in the tallgrass system is adapted to respond to sudden and lengthy transformations from low to high light that may result when the canopy is grazed away by large vertebrates.

Table 2. Comparison of numbers of *Spiranthes vernalis* which generated flowering scapes in 1992 and 1993.

Location	Number of plants which flowered	
	1992	1993
Annually burned watershed (n=7)[*]	7	7
Biennially burned watershed (n=1)	1	0
3U3B fireguard (n=5)	3	5
S. pectinata wetland (n=2)	2	2
10-year burned watershed (n=3)	3	0

[*] n=number of plants at each location.

Acknowledgements

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