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Gas exchange responses of a desert herbaceous perennial to variable sunlight in contrasting microhabitats

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Abstract

Over the course of a day, aridland plants experience a range of incident photosynthetic photon flux (PPF) spanning three orders of magnitude. Rapid photosynthetic responses to changes in PPF have large effects on individual plant carbon gain and water use patterns, hence are important to plant distribution and success. We investigated the response over time of photosynthesis (A), stomatal conductance (g), and inter-cellular CO_2 concentration (C_i) to step changes in PPF in a long-lived aridland perennial that typically occurs in two contrasting microhabitats, shade under shrubs of other species and unshaded inter-shrub spaces. An initial rapid response in A and C_i for plants in both microhabitats occurred after abrupt changes in PPF. This was followed by slower changes in these parameters during the rest of the light or dark period. Stomatal conductance responded more gradually to step changes in PPF. The initial increase in A after a dark cycle was significantly greater for plants under shrubs than for plants in inter-shrub spaces, but other changes in A, g and C_i did not differ. We attribute the similar responses in plants from different microhabitats to natural variations in solar radiation and limited selection for differentiation due to population gene pools dominated by plants in the open. Our results support the hypothesis that variable light regimes select for photosynthetic gas exchange processes that closely track changes in incident PPF. Our data also support the hypothesis that gas exchange responses to variable light regimes in aridland plants minimize trade-offs between carbon gain and water loss.

Keywords: *Cryptantha flava*; Heterogeneity; Photosynthesis; Solar radiation; Water use efficiency

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1. Introduction

Different leaf gas exchange components often differ in the time scale of their responses to changes in incident light. In many species, light induction of the primary carboxylating enzyme, RUBISCO, is necessary before photosynthesis can respond to higher light levels (Chazdon and Pearcy, 1986; Pearcy, 1990). In other plants, stomatal responses lag behind carboxylating responses, temporarily increasing stomatal limitation to photosynthetic carbon gain (Fay and Knapp, 1993; Allen and Pearcy, 2000b). The balance between stomatal and photosynthetic response to light can play an important role not only in the amount of CO_2 that is captured during alternating periods of high and low light, but also in water use patterns. In water-limited habitats, increasing the amount of carbon gained per unit water loss (water use efficiency—WUE) may be an important trait in plant success and distribution (Dawson and Ehleringer, 1993; Ehleringer, 1993).

Knapp and Smith (1991) hypothesized that plants in habitats experiencing high daily sunlight variability should demonstrate rapid recovery in photosynthesis and stomatal conductance after a shading event in order to maximize carbon gain. Conversely, photosynthesis may respond more slowly to changes in insolation in plants native to environments with less variable solar radiation.

Desert ecosystems are noted for their high-light, relatively constant solar regimes (Solar Energy Research Institute, 1981; Knapp and Smith, 1991). Plants growing in inter-shrub spaces in sparsely vegetated, arid communities experience little shading (Forseth et al., 2001), and develop leaf characteristics typical of high-light habitats (Boardman, 1977; Ehleringer et al., 1979). However, many herbaceous perennials and annuals also occur under the canopies of larger shrub species (Aguiar and Sala, 1999; Forseth et al., 2001). Plants in these microhabitats experience lower total light levels and greater variability in light over time periods ranging from seconds to several hours, depending upon the location within the canopy and the height and depth of the shrub canopy (Forseth et al., 2001).

Biochemical and morphological acclimation to the light environment is common in plants (Björkman and Holmgren, 1966; Boardman, 1977; Pearcy and Sims, 1994). Typically, the total light energy received during the day has a greater influence on acclimation than peak levels of photon flux density (PPF; Chabot et al., 1979). However, the timing and duration of sunflecks (brief bursts of light on a ms to s scale) and/or sun patches (longer, minutes to hours exposure) and the pattern of alternation between high and low light are influential in the dynamics of photosynthetic and stomatal responses to changes in light intensity (Chazdon and Pearcy, 1986; Knapp and Smith, 1990b; Allen and Pearcy, 2000a). Individuals of plant species growing in aridland inter-shrub spaces will receive higher and more constant light levels than individuals located under a shrub canopy. Accordingly, these individuals may vary in leaf morphology and biochemistry if acclimation to maximize photosynthetic carbon gain in each microhabitat has occurred. Selection by variable light regimes may also lead to differences in the dynamics of gas exchange processes that act to increase carbon gain and/or WUE. Exceptions to these predictions may occur if the plant species is an obligate sun plant, incapable of adjusting morphologically and biochemically to lower light (Boardman, 1977). Lack of acclimation may also occur if contributions to the population seed pool are limited in individuals growing under shrubs, thereby rendering selection for acclimation to lower, more variable light regimes ineffective.

A significant fraction of native populations of *Cryptantha flava*, a herbaceous perennial in the arid Colorado Plateau of western North America, occurs under shrub canopies (Casper, 1996). Forseth et al. (2001) demonstrated that *C. flava* experiences asymmetric competition for light from the larger, woody perennials in its native habitat. *C. flava* individuals that occur under either rabbitbrush (*Chrysothamnus nauseosus*) or sagebrush (*Artemisia tridentata*) experience lower light levels and concomitant lower photosynthetic rates, growth rates and reproduction than plants occurring in the open (Casper, 1996; Forseth et al., 2001).

Our objective in this study was to investigate the time course of changes in photosynthesis (A), stomatal conductance (g), and inter-cellular CO_2 concentration (C_i) in *C. flava* in response to step changes in PPF. We hypothesized that plants in open, unshaded microhabitats would have more rapid rates of decline and slower rates of recovery of g and A in response to short-term shade events than plants growing in shaded microhabitats. This response pattern would act to conserve water at the expense of reduced carbon gain in this unshaded microhabitat. Additionally, we predicted that gas exchange in plants under shrubs would be characterized by more rapid increases in g after an increase in sunlight, minimizing stomatal limitation of photosynthesis. This would act to maximize carbon gain for plants in shaded microhabitats, at the expense of reduced WUE.

2. Methods and materials

2.1. Study system and species

This research was conducted in June 2001 at a site in north-eastern Utah approximately 15 km N of Vernal, UT. Vegetation is dominated by the woody shrubs *A. tridentata* Nutt. and *C. nauseosus* (Pallas) Britt. and the small tree *Juniperus osteosperma* (Torr.) Little. The study area is characterized by substantial environmental variation, both seasonally and spatially. Annual precipitation averages 215 mm, with a coefficient of variability ranging 50–125% of the mean (Peek and Forseth, 2003). The presence of rock outcrops, soil depth differences, shrubs, variable drainage patterns, and large mammals generate a considerable amount of spatial heterogeneity in water and nutrient availability and solar radiation (Forseth et al., 2001; Peek and Forseth, 2003).

The herbaceous perennial, *Crypthantha flava* (A. Nels.) Payson (Boraginaceae) is associated with sandy soils across the semi-arid Colorado Plateau. *C. flava* can be found growing in open habitats and under shrub canopies of *A. tridentata* and *C. nauseosus*, with no affinity to either habitat (Casper, 1996). *C. flava*'s growth habit consists of a woody caudex supporting several rosettes of nearly vertical leaves. An individual leaf rosette may live for multiple years, but dies after producing a single flowering stalk. Based on leaf cellular structure and photosynthetic characters, *C. flava* has a C_3 photosynthetic pathway. Above-ground vegetative growth begins in late March, flowering begins mid-May and seeds are set by mid-July.

2.2. Data collection and analyses

Incident photosynthetic photon flux (PPF, 0.4–0.7 μm) was measured in the inter-shrub spaces (open) and under shrub canopies using cosine corrected silicon cell quantum sensors built following the design of Biggs et al. (1971) and calibrated against a quantum sensor (Model LI-185, Li-Cor Inc. Lincoln, NE). Sensors were attached to dataloggers (CR-21X, Campbell Scientific, Logan, UT) which recorded readings every 30 s and stored 60 s averages.

Plants were chosen without bias in open microhabitats and under shrub canopies to measure gas exchange responses to step changes in PPF. Open plants were defined as those plants located more than 0.5 m from the nearest shrub, allowing the plant to experience full ambient solar radiation levels throughout the day. Shade plants were classified as those at least 10 cm inside the outer edge of a shrub's canopy, which provided significant shading during the course of the day. We used a LiCor 6400 portable photosynthesis system (LiCor Inc., Lincoln, NE) to record leaf gas exchange, and a LED red/blue light source to control PPF incident on the leaves. Two–three fully expanded leaves were enclosed in the leaf cuvette for the duration of a measurement, which typically lasted 45 min. We held leaf temperature at 32°C, maintained a water mole fraction of 9–15 $\mathrm{mmol\,mol^{-1}}$ depending on initial transpiration rates, and a cuvette CO_2 concentration of 370 $\mu\mathrm{mol\,mol^{-1}}$. Steady-state measurements were made at a PPF of 2000 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ for 5 min followed by alternating periods of 5 min of 200 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ and 8 min of 2000 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ over three cycles. The frequency of high-light/low-light periods were modeled after Knapp and Smith (1989) and chosen to mimic afternoon cumulus cloud cover.

A suite of gas exchange variables was recorded at 30 s intervals for each PPF, including net photosynthesis (A), stomatal conductance (g) and inter-cellular CO_2 concentration (C_i). Photosynthetic and stomatal kinetics were calculated according to Assmann and Grantz (1990). Since A and C_i exhibited biphasic responses, we modeled two components of response for these variables, termed initial increase ($A_\mathrm{initial\ inc}$, $C_{\mathrm{i}_\mathrm{initial\ inc}}$) and increase ($A_\mathrm{inc}$, $C_{\mathrm{i}_\mathrm{inc}}$), and two components of decline, termed initial decline ($A_\mathrm{initial\ dec}$, $C_{\mathrm{i}_\mathrm{initial\ dec}}$) and decline ($A_\mathrm{dec}$, $C_{\mathrm{i}_\mathrm{dec}}$). Stomatal conductance did not show biphasic responses, so we modeled stomatal decline (g_dec) and stomatal increase (g_inc) only. We used linear regression techniques to model the increase and decline of A, g, and C_i for each of the three high-PPF/low-PPF cycles. Initial increase and decline of A were modeled using three data points, the last photosynthetic rate prior to a PPF change, and the first two rates measured after a PPF change. For example for a step decrease in PPF from 2000 to 200 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$, the initial decline in A ($A_\mathrm{initial\ dec}$) was characterized by the last measurement of A at 2000 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ and the first two rates measured at 200 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$. A_inc and A_dec were then modeled using all the rest of the measurements in a given cycle. The resulting variables (slopes) were then analysed using a mixed model ANOVA where the three replicate rates (cycles) per plant were treated as a random effect to control for correlated measurements on the same individual. We used microhabitat (inter-shrub spaces or under-shrub canopies) as a fixed effect to test for differences in $A_{\text{initial inc}}$, $A_{\text{initial dec}}$, A_{inc}, A_{dec}, g_{inc}, g_{dec}, $C_{\text{i}_{\text{initial inc}}}$, $C_{\text{i}_{\text{initial dec}}}$, $C_{\text{i}_{\text{inc}}}$, and $C_{\text{i}_{\text{dec}}}$.

3. Results

On clear, spring days PPF on a horizontal surface can reach up to 2000 μmol m^{-2} s^{-1} at our study site (Fig. 1). Nevertheless, open habitats may experience considerable variability due to clouds during the hours of peak photosynthesis ($\sim$1000 h in Fig. 1). The light regime under shrub canopies is characterized by even more variability than inter-shrub spaces on clear days. Depending upon the position, plants under shrub canopies may experience light levels approaching those in the open, interspersed with periods of diffuse light only (Fig. 1). The timing of sun patches, as well as their duration, is highly variable under these shrubs.

Photosynthesis in both open and shrub habitat plants responded to step decreases in PPF with an initial rapid decrease (Fig. 2a). A biphasic response of A to a step increase in PPF was also evident, with an initial rapid increase, followed by a slower, linear increase until the end of the high-PPF period. Plants in the open had higher photosynthetic rates initially compared to plants under shrub canopies, and A did not decrease as low as that for plants under shrubs during the first low-PPF interval. However, after the first low-PPF interval, A in plants from both microhabitats followed similar response trajectories (Fig. 2).

A biphasic response was not evident in stomatal responses to step changes in PPF (Fig. 2b). As with A, g was initially higher for plants in inter-shrub spaces during the

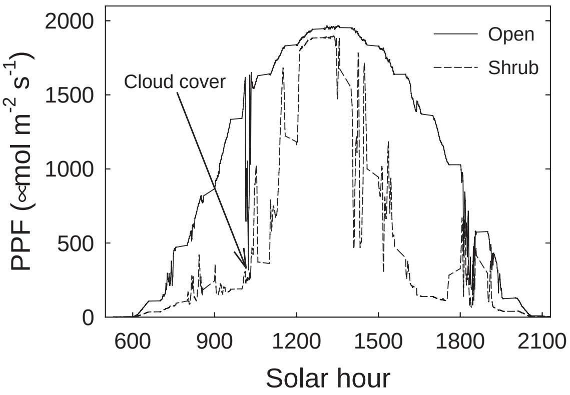

Fig. 1. Representative diurnal courses of PPF for plants in the open and shrub microhabitats. Note the morning cloud cover ($\sim$1000 h) in the open microhabitat and the extreme heterogeneity in light regime for plants under shrub canopies.

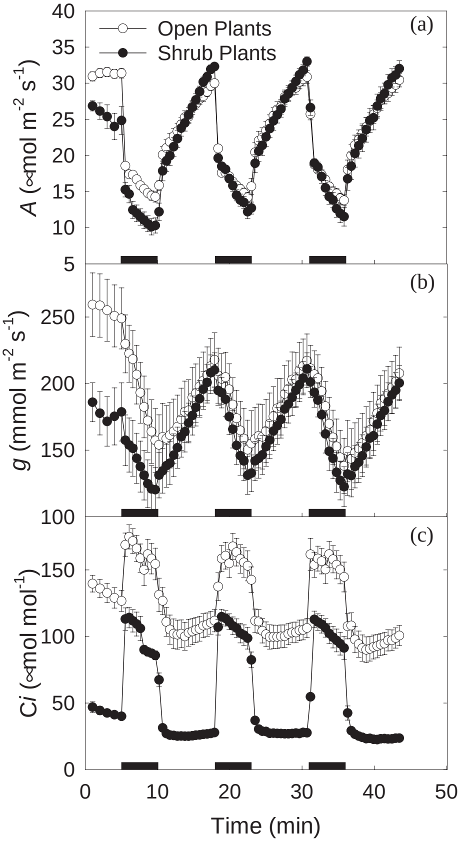

Fig. 2. Mean photosynthetic (A), stomatal conductance (g) and internal CO_2 concentrations (C_i) responses of open and shrub plants to cyclic variation in PPF. PPF varied from 2000 to 200 μmol m^{-2} s^{-1} (shade cycles shown with black bars) in each cycle with data taken every 30 s. Means from six open plants and five shrub plants with their respective standard errors are shown.

first low-PPF period. After this, the response of g to subsequent step changes in PPF was similar for plants in both open and shrub microhabitats.

Intercellular CO_2 concentrations (C_i) exhibited a biphasic response to high–low PPF exposures similar to that for A (Fig. 2c). The beginning of the low-PPF interval was characterized by rapid increases in C_i, followed by a steady decrease for the remainder of the low-PPF period. The subsequent increase in PPF resulted in a rapid decline in C_i followed by a relatively constant C_i for the remainder of the high-PPF cycle, despite a gradual increase in A.

With equal ambient CO_2 concentrations and water vapor differences between the leaf and air, the ratio of A to g can be used as a measure of intrinsic WUE. It may also be used as a parameter to analyse relative rates of response of photosynthesis and stomatal aperture to changes in the environment. The ratio of A to g pooled across all measurements was higher in plants under shrubs than for plants in the

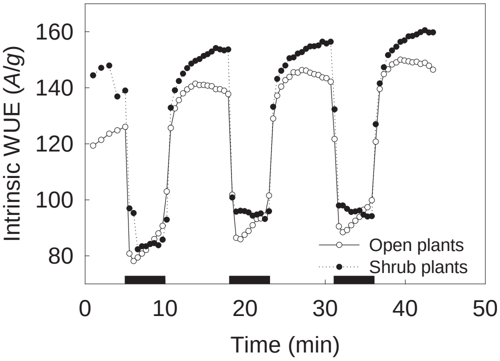

Fig. 3. Intrinsic WUE of open and shrub plants. Data were pooled from means of A and g in Figs. 2a and c. PPF varied from 2000 to 200 μmol m^{-2} s^{-1} (shade cycles shown with black bars) in each cycle with data taken every 30 s.

open (Fig. 3, Student's *t*-test, $p < 0.001$). However, there was no statistical difference due to microhabitat in the response of this parameter to changes in incident PPF. With a step decrease in PPF, A/g decreased rapidly in both open and shrub plants. After the initial drop, A/g increased slowly over the rest of the low-PPF period. With step increases in PPF, A/g increased rapidly in plants of both microhabitats, indicative of a more rapid response in A than in g, and then equilibrated to near-constant values.

The mixed model ANOVA on slope estimates obtained for increase and decline showed a significant difference between plants from different microhabitats for photosynthetic increase, 1.5 ± 0.17 μmol m^{-2} s^{-1} min^{-1} for open plants compared to 2.0 ± 0.19 μmol m^{-2} s^{-1} min^{-1} for shrub plants (Table 1). All other responses of A, g, and C_i were not statistically different between plants from the two habitats.

4. Discussion

Microhabitat had little effect on the gas exchange responses of *C. flava* to step changes in PPF. Plants in inter-shrub spaces and plants under shrub canopies had similar rates of initial increase, initial decline and decline in both A and g (Table 1). Our results are consistent with those of Forseth et al. (2001), who found little photosynthetic acclimation of *C. flava* to shrub microhabitats. In comparison to contrasting ecosystems, our results were more similar to the responses of sub-alpine plants than other desert plants that have been examined. Knapp and Smith (1991) reported that photosynthetic gas exchange in the desert species *Penstemon parryi* and *Ambrosia ambrosioides* did not closely track changes in PPF when compared to sub-alpine plants, which closely tracked changes in PPF. They hypothesized that the variable sub-alpine light regime caused by predictable afternoon cumulus clouds provided a stronger selective pressure for rapid changes in gas exchange. Although the pattern of response in *C. flava* was similar to the sub-alpine species measured by

Table 1
Slope analysis for photosynthesis and stomatal conductance from a linear regression mixed model analysis for the three light/dark cycles shown in Fig. 2

Photosynthesis (μmol m^{-2} s^{-1} min^{-1})				
	$A_{\text{initial dec}}$	A_{dec}	$A_{\text{initial rec}}$	A_{rec}
Open	-12.6 ± 0.96	-1.1 ± 0.25	6.6 ± 1.1	1.5 ± 0.17
Shrub	-13.2 ± 1.1	-1.5 ± 0.28	7.8 ± 1.1	$^{*}2.0 \pm 0.19$
Stomatal conductance (mmol m^{-2} s^{-1} min^{-1})				
	g_{dec}		G_{rec}	
Open	-18 ± 1.7		14 ± 1.5	
Shrub	-16 ± 2.0		11 ± 1.7	
Intracellular CO$_2$ concentration (μmol mol^{-1})				
	$C_{\text{i initial inc}}$	$C_{\text{i drawdown}}$	$C_{\text{i initial dec}}$	$C_{\text{i drawdown}}$
Open	163 ± 5.4	-10 ± 2.2	-122 ± 6.6	-0.5 ± 1.1
Shrub	163 ± 5.4	-12 ± 2.2	-117 ± 6.6	0.1 ± 1.1

Photosynthesis showed a biphasic response of an initial decline ($A_{\text{initial dec}}$), a decline (A_{dec}), an initial recovery ($A_{\text{initial rec}}$) and a recovery (A_{rec}). Stomatal conductance showed smooth transitions between decline (g_{dec}) and recovery (g_{rec}). Means ± SEs are presented with an asterisk denoting significantly different means at $p < 0.05$.

Knapp and Smith (1990a, b), *C. flava* did have slower overall response rates than the sub-alpine species. The slower response in *C. flava* may be due to lower water availability in our semi-arid system compared to sub-alpine habitats, and greater selection for increased WUE. Knapp and Smith (1989) found that gas exchange responses to variable light regimes change in a manner that increases the WUE in plants with reduced water availability compared to those with high water availability.

In contrast to the less variable, high-light habitat of low-elevation deserts such as the Sonoran, considerable variability in solar regime exists in the high-desert habitat of the Colorado Plateau (Fig. 1). The presence of afternoon cumulus clouds generates variability in incident PPF at this site, not unlike sub-alpine habitats (Knapp and Smith, 1990a, b, 1991). Afternoon cumulus clouds occur on approximately 25–45% of the days in May and June (Western Regional Climate Center) in this habitat. This natural variability in solar regime may be one mechanism limiting the degree of differentiation between microhabitats in *C. flava*, resulting in similar gas exchange responses for plants in open and shrub habitats.

Another potential reason for the similarity in photosynthetic responses of plants from open and shrub microhabitats may be that selection for differentiation is limited. The number of flower stalks and seeds set by a plant is positively related to its size (Casper, 1996). Thus, large plants dominate the population seed pool in a particular year. Plants in the open are larger, grow more rapidly, reproduce earlier, and set more seed than do plants under shrubs (Casper, 1996). Thus, the population gene pool may be dominated by individuals growing in open habitats, swamping the contribution of any adaptive genotypes that occur under shrubs.

The biphasic responses that we measured in A in response to sudden changes in PPF are consistent with responses reported in other studies (Fay and Knapp, 1993; Knapp, 1993; Barradas and Jones, 1996). The second phase of the response of A to an increase in PPF is due to a lag in stomatal opening (Knapp and Smith, 1989). This lag acts to increase WUE. Often, large afternoon clouds do not occur singly. Thus, the probability of decreases in PPF interspersed with increases is high. A lag in g following an increase in PPF would result in reduced water loss if subsequent cloud events reduce PPF again. Conversely, the lag in the response of g, relative to A after a decrease in light would improve carbon gain. If the decline phase is interrupted by another high-light event, photosynthesis would be able to increase to a greater extent than if g decreased in concert with A. This same phenomenon occurs in the light regime under the heterogeneous shrub canopies typical of *A. tridentata* and *C. nauseosus*. As the sun moves in an arc through the sky, openings in the canopy allow penetration of high-PPF levels through the canopy at different times of the day (Fig. 1). Large canopy gaps often contain some leaves and branches that cause transient decreases in the PPF penetrating into the canopy, but in general allow longer exposure to high levels of PPF. These decreases will vary in magnitude and timing with the number and degree of clustering of branches in large canopy gaps. In dense portions of the canopy, reduced solar radiation at ground level may be interspersed with short periods of higher light due to smaller canopy openings.

The time frames we used in this study were designed to examine responses to PPF regimes lasting several minutes (sun patches *sensu* Knapp and Smith, 1989) rather than the sunflecks (millisecond to seconds) typical of forested ecosystems (Pearcy, 1990). We felt that these exposure times would be more representative for our Colorado Plateau site where afternoon clouds or open, patchy shrub canopies would be the primary causes of light variation. Plant gas exchange responses to light are strongly influenced by the ambient light regime that leaves develop under. For example Ögren and Sundin (1996) showed complete photosynthetic recovery in less than 1.5 min by mimicking sunflecks after an induced shade period of 2 min. Plants whose distributions span both shaded forest floors and exposed, non-forested sites often show the ability to acclimate their photosynthetic biochemistry and leaf morphology to better exploit these different light regimes (Pearcy and Sims, 1994). In contrast, species restricted to either low light or high light may not have evolved the photosynthetic plasticity to acclimate to different light regimes (Björkman and Holmgren, 1966; Boardman, 1977).

In summary, we attribute similar responses to step changes in PPF in plants from open and shrub habitats to variable light regimes even in inter-shrub spaces and limited selection for acclimation due to population gene pools dominated by plants in the open. Our results support the contention of Knapp and Smith (1990b) that a variable light regime selects for gas exchange responses in plants that closely track changes in incident PPF. The gas exchange responses shown by *C. flava* act both to increase carbon gain and WUE, albeit at different points during cycles of alternating high and low light, minimizing the inherent trade-offs between carbon gain and water loss faced by arid zone plants.

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