American Journal of Botany 85(9): 1216–1223. 1998.

CONSEQUENCES OF INCONGRUENCY IN DIURNALLY VARYING RESOURCES FOR SEEDLINGS OF *RUMEX CRISPUS* (POLYGONACEAE)[1]

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The incongruency of diurnally varying resources essential to plants may detrimentally affect plants early in their development as indicated by reduced water use efficiency and carbon gain. Typical diurnal patterns of light and CO_2 availability in a midsized temperate herbaceous or forest gap were simulated in specially designed growth chambers. A sinusoidally varying CO_2 treatment (400 ppm minimum, 800 ppm maximum) approximated the diurnal cycle of CO_2 at the soil surface, while a steady-state CO_2 treatment (600 ppm) with the same average CO_2 concentration provided a control. Crossed with these two CO_2 treatments were two light regimes, one with 3 h of high light (850 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in the morning (west side of a gap), and the other with 3 h of high light in the afternoon (east side). All treatments received baseline low light (55 $\mu mol \cdot m^{-2} \cdot s^{-1}$) for 14 h during the day. *Rumex crispus* was selected as a model species because of its rosette leaves, which grow close to the ground where diurnal CO_2 variation is greatest. The relative timing of diurnal variations in light and CO_2 significantly affected seedling water use efficiency, carbon gain, and morphology. Total biomass, photosynthetic rates, daily integrated carbon, water use efficiency, and leaf area were enhanced by morning exposure to high light. Seedlings that were exposed to peak values of light and CO_2 incongruently, i.e., those plants receiving intense afternoon light with diurnally varying CO_2, were detrimentally affected relative to control plants receiving intense afternoon light with steady-state CO_2. The results of this experiment indicate that the incongruent availability of required resources—such as light and CO_2—can detrimentally affect performance relative to when resources are congruent. These contrasting resource regimes can occur on the east and west side of gaps.

Key words: incongruency of resources; diurnal cycles; gaps; Polygonaceae; *Rumex crispus;* photosynthesis; water use efficiency.

Temporal congruencies in resource availability, which are likely to occur both in herbaceous and forest gaps, have been suggested to affect the growth of plants (Wayne and Bazzaz, 1993; Bazzaz, 1996). Previous studies have indicated that the dynamics of temporally varying resources may be important in determining the structure of certain ecological systems (Seastedt and Knapp, 1993) and may influence rates of succession in old fields (Goldberg and Gross, 1988).

Light environments near the soil surface vary considerably in intensity, duration and temporal availability at different positions within a forest gap (Canham and Marks, 1985; Denslow, 1987; Canham et al., 1990). In tall herbaceous vegetation, such as in old fields, a similar pattern of light variation occurs within gaps (McConnaughay and Bazzaz, 1987). Diurnal movements of direct beam radiation are most significant on the east-west axis of a gap (Bazzaz and Wayne, 1994). In northeastern North America, northwest portions of large gaps receive direct beam radiation 2.0–2.5 h earlier than northeast portions, although both receive similar daily total photosynthetic photon flux density (PPFD) (Canham et al., 1990; Bazzaz and Wayne, 1994; Sipe and Bazzaz, 1995).

Likewise, CO_2 concentrations at various distances above the soil surface have been shown to have distinct diurnal patterns in herbaceous environments (Schwartz and Bazzaz, 1973) and in forest environments (Bazzaz and Williams, 1991; Thomas and Bazzaz, 1993). We have found that empirical measurements of CO_2 profiles in various understory and gap environments at the Harvard experimental forest indicate that peak values of CO_2 in midsummer at or near the soil surface are reached in the early morning, while significantly lower concentrations occur in the early afternoon (P. B. Voss, unpublished data). At opposite sides of a gap, variations in the timing of high light may result in different degrees of temporal incongruency with the diurnal fluctuations of CO_2 (Wayne and Bazzaz, 1993).

This study addressed the question of how the incongruent availability of resources affects plants early in their development. We were specifically interested in the effects of diurnal incongruency of peak values of light and carbon dioxide. We created four treatments simulating the west and east sides of a gap and two controls. In all treatments, plants were exposed to high light for 3 h either in the morning or afternoon and low light the rest of the day, with a total photoperiod of 14 h (see Fig. 1).

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[1] Manuscript received 22 September 1997; revision accepted 19 January 1998.

The authors thank Susan Bassow and Glenn Berntson for help with the physiological measurements and the statistical analyses, and Michal Jasienski, Peter Wayne, Dieter Ramseier, Richard Stomberg, Lesley Hughes, Christine Muth, and Sean Thomas for help with various aspects of the experiment or for useful criticisms of earlier drafts. Part of the research was supported by fellowships from the National Aeronautic and Space Administration and the Mellon Foundation.

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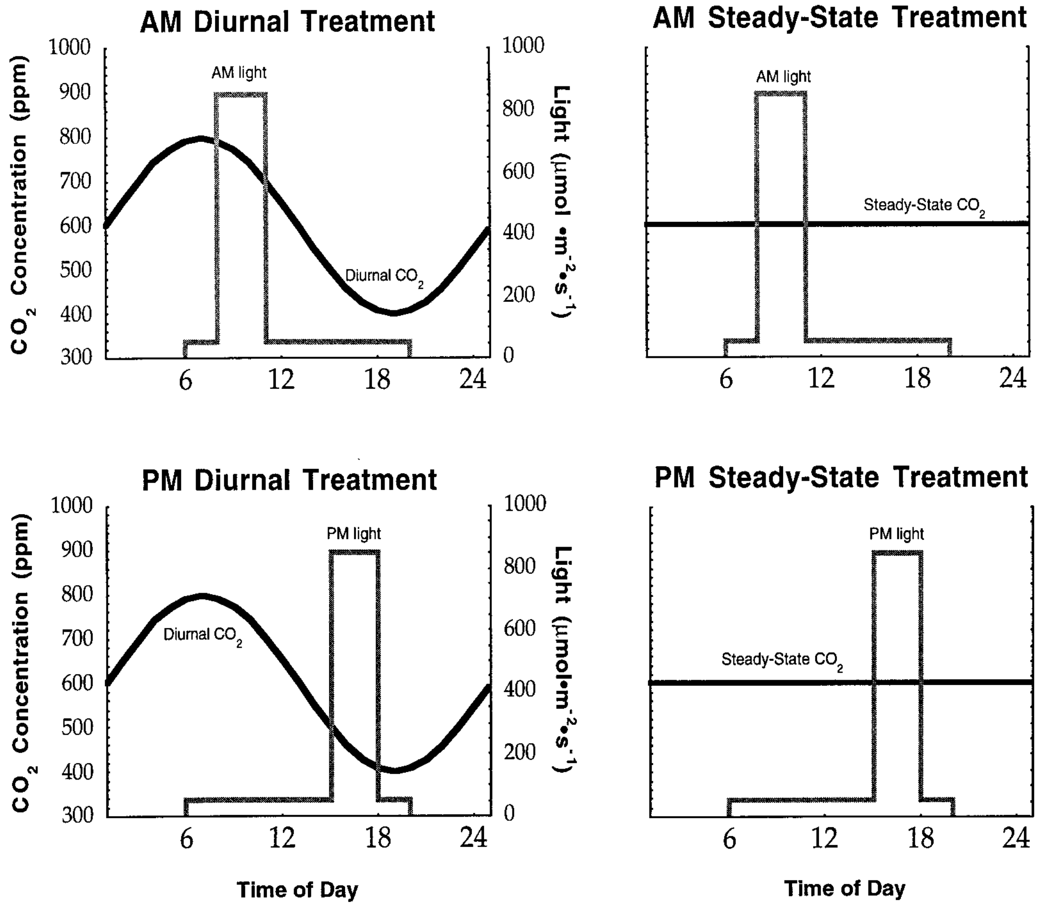

Fig. 1. CO_2 and light treatments: (a) diurnally varying CO_2 and morning high light (AM diurnal), (b) steady-state CO_2 and morning light (AM steady-state), (c) diurnally varying CO_2 and afternoon high light (PM diurnal), and (d) steady-state CO_2 and afternoon high light (PM steady-state).

In two of the treatments, CO_2 concentration followed a sinusoidal curve over a 24-h period reaching a maximum of 800 ppm in the morning and a minimum of 400 ppm in the afternoon. In the control treatments CO_2 concentration was held constant at 600 ppm so that all treatments would have the same mean CO_2 concentration. The first treatment simulated the west side of a gap with peak light in the morning and peak CO_2 in the morning (hereafter called AM diurnal). The second treatment simulated the east side of a gap with peak light in the afternoon and peak CO_2 in the morning (hereafter called PM diurnal). The two control treatments had peak light in the morning and afternoon, respectively, but steady-state values of CO_2 across the day (called AM steady-state and PM steady-state). Using a model species, *Rumex crispus*, an early successional plant which can be found in herbaceous gaps and occasionally in large forest gaps, we tested several predictions: (1) diurnal timing of optimal levels of light and CO_2 will affect carbon assimilation, growth patterns, and water use efficiency of plants; (2) plants that receive high levels of light and CO_2 incongruently will assimilate carbon at lower rates, show reduced growth, and have lower water use efficiency relative to plants which receive resources congruently; and (3) the rank order of performance among the different treatments will be AM diurnal > AM steady-state > PM steady-state > PM diurnal.

The rank order prediction was based on the assumption that congruency of resources is critical to plant performance and that plants in the morning light treatment may show stronger plant performance than the afternoon light treatments due to lower water stress in the morning than in the afternoon. Previous studies have shown that leaf water potential tends to be significantly higher in the morning than in the afternoon (Gallego et al., 1994; Guicherd, 1994; Koch, Amthor, and Goulden, 1994; Von-Willert and Wagner-Douglas, 1994). If significant differences in growth, carbon assimilation, and water use efficiency are found among the different treatments, this suggests that the temporal availability of resources may be as important as the absolute level of resources in influencing success of individuals.

MATERIALS AND METHODS

Experimental design—*Rumex crispus*, an herbaceous species that grows in both herbaceous and forest ecosystems, was selected as a model for study primarily because of its rosette leaf structure. Its leaves grow close to the ground where CO_2 levels are highest and diurnal variations are most extreme. *Rumex crispus* is also documented to respond to CO_2 by altering stomatal conductance and density (Woodward and Bazzaz, 1988) as well as leaf morphology (Thomas and Bazzaz, 1996).

We developed a bench-top environmental control system with four treatments in a fully crossed design of two CO_2 regimes and two light regimes. Treatments were replicated in three blocks with a total of 40 seedlings. Seedlings were exposed either to diurnal fluctuations in CO_2 concentration or to a constant CO_2 concentration. The constant CO_2 treatment was 600 ppm (± about 15 ppm). The diurnal fluctuations followed a sine curve with a mean of 600 ppm, reaching a maximum of 800 ppm at 0600 and a minimum of 400 ppm at 1800 (see Fig. 1). The shape and phase of this diurnal pattern were designed to simulate the forest floor environment at ~1–5 cm above the soil surface at the Harvard Forest in Petersham, Massachusetts, in several sites representative of where *R. crispus* is often found (P. B. Voss and F. A. Bazzaz, unpublished data). The amplitude of our treatment cycle, however, is somewhat larger than the amplitude of a typical diurnal cycle in the field (maximum 600–700 ppm, minimum 370–450 ppm). Given the subtlety of our treatments, we opted to increase this amplitude in order to amplify the potential treatment effect.

Within each of the CO_2 regimes were two light treatments. One group of plants received 3 h of direct light (850 μmol·m^{-2}·s^{-1} high-intensity discharge lamps) in the morning (0800–1100), while the other group received 3 h of direct light in the afternoon (1300–1600). All plants received diffuse light (~55 μmol·m^{-2}·s^{-1}) during the remaining daytime hours. These lower light levels were designed to approximate the understory light conditions at the Harvard Forest (Bazzaz and Wayne, 1994). All four treatments received the same total photosynthetic photon flux density (PPFD) and the same mean CO_2 concentration during daylight hours. Relative humidity (RH) and temperature conditions (25°C, 60–70% RH) were identical for all treatments.

Our system was based on an "open" design in which fresh air was drawn continuously from a roof-top tower (with an intake at 15 m above roof level), humidified, and washed with distilled water, injected with CO_2, and supplied to all chambers. The chambers themselves consisted of acrylic plastic aquariums (25 × 15 × 15 deep). Each pair of these chambers (one diurnal CO_2 and one steady-state CO_2) was placed inside a plastic bin containing circulating water at a controlled temperature. The water circulation and temperature control system was common to all chambers, minimizing the among-treatment variance. Air flowing into each chamber first passed through a 1-m copper pipe immersed in the water bath. This temperature equilibration, in combination with the controlled chamber wall temperature, allowed for excellent environmental control. Air temperature, humidity, and light levels were measured once per minute. While air temperatures drifted above their set points during high-light periods, the effect was common to all treatments, and in many ways is an accurate representation of field conditions.

Because of the complexity of CO_2 control, we created only two CO_2 treatments (diurnal and steady-state), and divided the flow equally among the chambers. CO_2 concentrations were measured every 60 s inside representative growth chambers and were used in feedback loops to control the rate of CO_2 addition to the two airstreams. The time constant (chamber volume/air flow rate) was <4 s, and air was distributed evenly using a bottom plenum. We rotated our CO_2 treatments every 3 d so that the steady-state mixing volume for one period was changed to the diurnal mixing volume during the next. Since each mixing volume remained attached to the same set of six chambers, plants were moved to follow their treatment each time the CO_2 control was changed. This rotation eliminated any potential mixing volume effects. Independent CO_2 and relative humidity measurements using a LI-COR 6200 gas analyzer (LI-COR, Lincoln, Nebraska) confirmed that the CO_2 concentrations in all of the chambers matched the programmed values and that RH was uniform within and across chambers.

Seeds from one population, collected in Cambridge, Massachusetts, were broadcast on the soil surface in 6.0 cm diameter peat pots containing Redi-Earth Peat Lite Mix™ potting soil. All seeds were germinated in the same light and CO_2 conditions (~500 μmols·m^{-2}·s^{-1} and 350 ppm). To improve chances of uniform starting biomass, germinants were thinned to two plants per pot 5 d after planting, and all additional germinants were removed on a daily basis. In two of the blocks, three individuals were placed in each chamber; in one block, four individuals were placed in each chamber. All plants were given a total of 2.77 mg of Peter's Solution (20:20:20 NPK) diluted in 50-mL H_2O aliquots per plant per week.

Physiology and growth—Two weeks after exposing plants to treatment conditions we measured photosynthetic and conductance rates to trace diurnal patterns of carbon assimilation and stomatal control. Using a LI-COR 6200 photosynthesis system, we measured specific leaves for three individuals from each treatment, one from each block, at seven time intervals throughout the day. CO_2 and light levels were carefully monitored during gas exchange measurements to ensure that they matched set treatment values. CO_2 concentrations were within 10 ppm of the set value. The first of three observations from the LI-COR 6200 was used in all cases unless the first observation was faulty. This minimized the problem of declining CO_2 partial pressures within the cuvette during measurements. Care was taken to maintain the leaves in the horizontal plane (the plane in which they were growing) during measurements. This ensured a light environment inside the cuvette within 5 μmol·m^{-2}·s^{-1} of the target value. The measurement at 0700 is missing for one plant each in the AM diurnal and AM steady-state treatments. These two data points were estimated, in order to calculate the integrated measures, by averaging the values for the other two plants in each treatment at that time.

Two days after measuring gas exchange, we harvested individuals from each treatment. All 40 plants were harvested, ten from each treatment. For each plant we measured leaf area in square centimetres using a LI-COR leaf area machine and leaf mass (without petioles), shoot mass, root mass, and total dry biomass in grams.

Statistical analysis—Two-way analysis of variance was conducted to test the effects of CO_2 treatment, light treatment, block, and the interaction of CO_2 and light using Data Desk (Velleman, 1992). Blocks were treated as random factors, and block by factor interactions were not included in the model if there was no significant block effect, according to Bancroft's rules (Bancroft, 1964). Dependent variables included total biomass in grams, specific leaf mass in milligrams per square centimetre, maximum photosynthetic rates (average value during high light in micromoles of carbon per square metre per second), maximum conductance rates (millimoles of water per square metre per second), daily integrated carbon gain (moles of carbon per plant per day), integrated water loss (moles of water per square metre per day), and water use efficiency (WUE) calculated as the ratio of integrated carbon gain to integrated water loss.

RESULTS

Diurnal photosynthesis and conductance—Plants that received intense morning light exhibited significantly higher maximum photosynthetic rates, measured on an area basis, than those that received afternoon light (Table 1, $P < 0.001$). This difference was most pronounced between plants exposed to diurnally varying CO_2 concentrations (congruent vs. incongruent resource availability; Fig. 2). Within the morning light treatments there was no significant difference between the diurnal and steady-state CO_2 treatment ($P < 0.86$). Within the afternoon light treatments, however, plants receiving low CO_2 in the diurnal treatment showed lower photosynthetic rates that were marginally significantly different from the steady-state control ($P < 0.06$). Maximum conductance rates for plants in high morning light and diurnally varying CO_2 were ~45% higher than those of plants in afternoon light with diurnally varying CO_2 during the 3-h high-light period. During low-light periods, however, the afternoon

Table 1. Results of analyses of variance on the effects of incongruency of diurnally varying CO_2 and light. Results are presented for total biomass, leaf area, and specific leaf mass (SLM) ($N = 40$); and maximum photosynthetic rate, maximum stomatal conductance, maximum transpiration, integrated carbon gain, integrated water loss, and integrated water use efficiency (WUE) ($N = 12$). Significance levels are indicated by asterisks ($P \leq 0.001$ ***; $P \leq 0.01$ **; $P \leq 0.05$)*; P values ≤ 0.05 are given in boldface.

Variable	df	MS	*P*
Biomass			
Light	1	0.0056	**0.0008*****
CO_2	1	0.001	0.28
Light × CO_2	1	0.001	0.10
Block	2	0.0002	0.42
Error	34	0.0004	
Photosynthesis			
Light	1	87.32	**0.001*****
CO_2	1	8.12	0.13
Light × CO_2	1	5.85	0.183
Block	2	0.24	0.914
Error	6	2.59	
Integrated carbon gain			
Light	1	5 262 649	**0.0001*****
CO_2	1	172 852	0.10
Light × CO_2	1	146 296	0.13
Block	2	110 840	0.18
Error	6	47 348.8	
Leaf area			
Light	1	172.20	**0.03***
CO_2	1	0.02	0.98
Light × CO_2	1	69.17	0.15
Block	2	16.50	0.60
Error	34	32.03	
Conductance			
Light	1	0.015	**0.01****
CO_2	1	0.00001	0.92
Light × CO_2	1	0.0507	**0.0007*****
Block	2	0.006	0.06
Error	6	0.001	
Integrated water loss			
Light	1	1 174 834	**0.01****
CO_2	1	34 083.3	0.56
Light × CO_2	1	912 396	**0.02***
Block	2	295 850	0.11
Error	6	93 374	
SLM			
Light	1	0.16	**0.01****
CO_2	1	0.15	**0.02***
Light × CO_2	1	0.25	**0.002****
Block	2	0.003	0.89
Error	34	0.02	
Transpiration			
Light	1	10.56	**0.01****
CO_2	1	7.94	0.89
Light × CO_2	1	12.47	**0.02***
Block	2	3.53	0.06
Error	6	0.735	
Integrated WUE			
Light	1	0.87	**0.0005*****
CO_2	1	0.01	0.54
Light × CO_2	1	0.17	**0.02***
Block	2	0.04	0.23
Error	6	0.02	

high-light treatments had much higher conductance rates, with plants exposed to diurnally varying CO_2 showing the highest conductance rates (Fig. 3). This pattern accounts for the highly significant light by CO_2 interaction ($P < 0.0007$). Transpiration rates showed patterns similar to conductance (data not shown).

Total daily carbon gain, water loss, and water use efficiency—Patterns of total daily carbon gain were consistent with patterns of photosynthesis across all of the treatments. For plants receiving morning light, daily integrated carbon gain was higher than for plants receiving intense afternoon light, although there was no difference between steady-state and diurnally varying CO_2 treatments for plants receiving intense morning light. For plants receiving afternoon light and diurnally varying CO_2 integrated carbon gain was lowest and was significantly lower than the steady-state control ($P < 0.04$). The majority of daily carbon gain occurred during the 3-h high-light period, whether it fell in the morning or afternoon, in all of the treatments (Fig. 4a).

Total water loss integrated across the day showed a significant CO_2 by light interaction ($P < 0.02$). Integrated water loss for the morning light treatments was significantly lower than for the afternoon light treatments ($P < 0.01$, Fig. 4). This result was primarily due to the fact that plants receiving high afternoon light showed much higher water loss during the low-light periods (i.e., primarily during the morning) than those receiving high morning light. During the high-light periods, water loss was lower when the diurnally varying CO_2 concentration was greater than the steady-state concentration (congruency of high light and CO_2) and higher when diurnally varying CO_2 was lower than the steady-state concentration (incongruency of high light and CO_2).

Integrated water use efficiency (WUE) showed a significant light effect ($P < 0.0005$) and CO_2 by light interaction ($P < 0.02$, Table 1). WUE was highest in plants receiving high morning light and diurnally varying CO_2 and lowest in plants receiving high afternoon light and diurnally varying CO_2 ($P < 0.0005$). Within the morning high-light treatments, plants receiving diurnally varying CO_2 were not significantly different from the control, but their WUE was significantly lower than the control within the afternoon high-light treatments ($P < 0.04$). Trends in photosynthetic rates, carbon gain, and water use efficiency were consistent with the predicted rank order response of AM diurnal < AM steady-state < PM steady-state < PM diurnal (water loss followed the opposite trend: AM diurnal > AM steady-state > PM steady-state > PM diurnal), although there was no significant difference between the AM diurnal and AM steady-state treatments.

Growth and leaf morphology—Consistent with trends in photosynthetic rates and daily carbon gain, total biomass was highest in plants receiving intense morning light and diurnally varying CO_2 and lowest in plants receiving intense afternoon light and diurnally varying CO_2 (difference of means: $P < 0.0006$, Fig. 4). Analysis of variance for all treatments showed a significant light effect ($P < 0.0008$), but there was no significant light by CO_2 interaction ($P < 1.0$). Specific leaf mass showed a highly significant CO_2 by light interaction ($P < 0.002$).

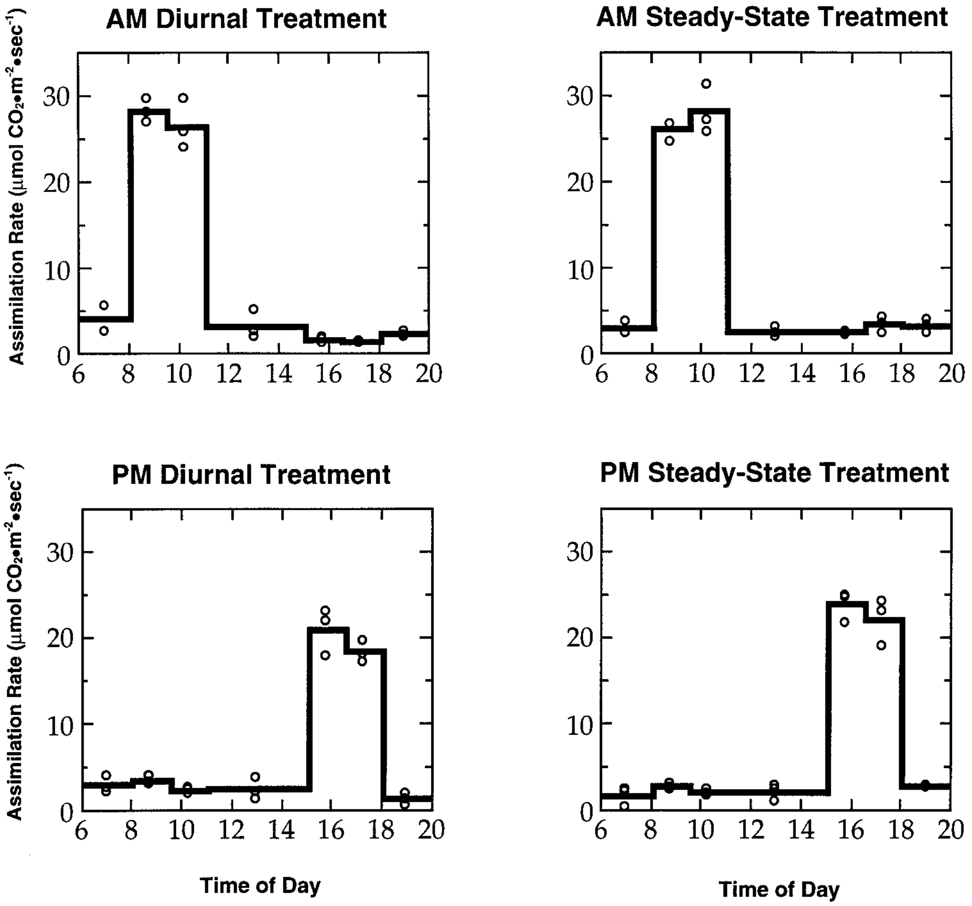

Fig. 2. Diurnal curves of photosynthetic rate for treatments shown in Fig. 1: (a) AM diurnal, (b) AM steady-state, (c) PM diurnal, (d) PM steady-state. Data points are shown for three individuals per treatment measured seven times throughout the day; solid line represents average values.

Specific leaf mass of plants in the AM diurnal treatment were significantly higher than that of plants in the steady-state CO_2 control ($P < 0.0001$); plants in the PM diurnal treatment showed lower specific leaf mass than the PM steady-state treatment, but this difference was not significant. Trends in both biomass rate and specific leaf mass followed the predicted rank order of response: AM diurnal > AM steady-state > PM steady-state > PM diurnal, although differences between individual treatments were not always significantly different.

DISCUSSION

We found that the incongruency of optimal levels of light and carbon dioxide detrimentally affected the physiology and growth of *Rumex crispus* seedlings. Plants receiving peak levels of CO_2 in the morning but peak levels of light in the afternoon performed most poorly in terms of photosynthetic rate, water use efficiency, total biomass, and specific leaf weight, while plants receiving peak levels of CO_2 and light in the morning performed best. While there was no significant difference between CO_2 treatments for plants exposed to intense morning light, for plants receiving intense afternoon light, the diurnally varying CO_2 plants did not perform as well as the steady-state CO_2 control plants. For all parameters measured, there was a significant light effect with plants performing better under intense morning light than under intense afternoon light. This light effect is presumably due to higher leaf water potentials in the morning, although it is possible that it could also be caused by a genetically controlled internal clock. An effect of leaf water potential (not measured) is indicated by high conductance and transpiration rates during low light periods in the morning for both of the afternoon high light treatments. This phenomenon is consistent with previous studies in which the diurnal timing of light availability was varied (Knapp and Smith, 1990; Wayne and Bazzaz, 1993).

Although total light and CO_2 availability across the day were the same in all treatments, plants that received afternoon high light and diurnally varying CO_2 assimilated less daily carbon than plants in other treatments, particularly those in morning high light with diurnally varying CO_2. This is due to the likelihood that plants receiving afternoon high light could not respond to the higher CO_2 levels in the morning, but only to the lower CO_2 levels present during peak light availability. Many studies show higher photosynthetic rates and greater daily integrated carbon gain at higher CO_2 concentrations (Bazzaz, 1990; Poorter, 1993; Ceulemans and Mousseau, 1994). In the afternoon light treatments, the lower carbon gain for the

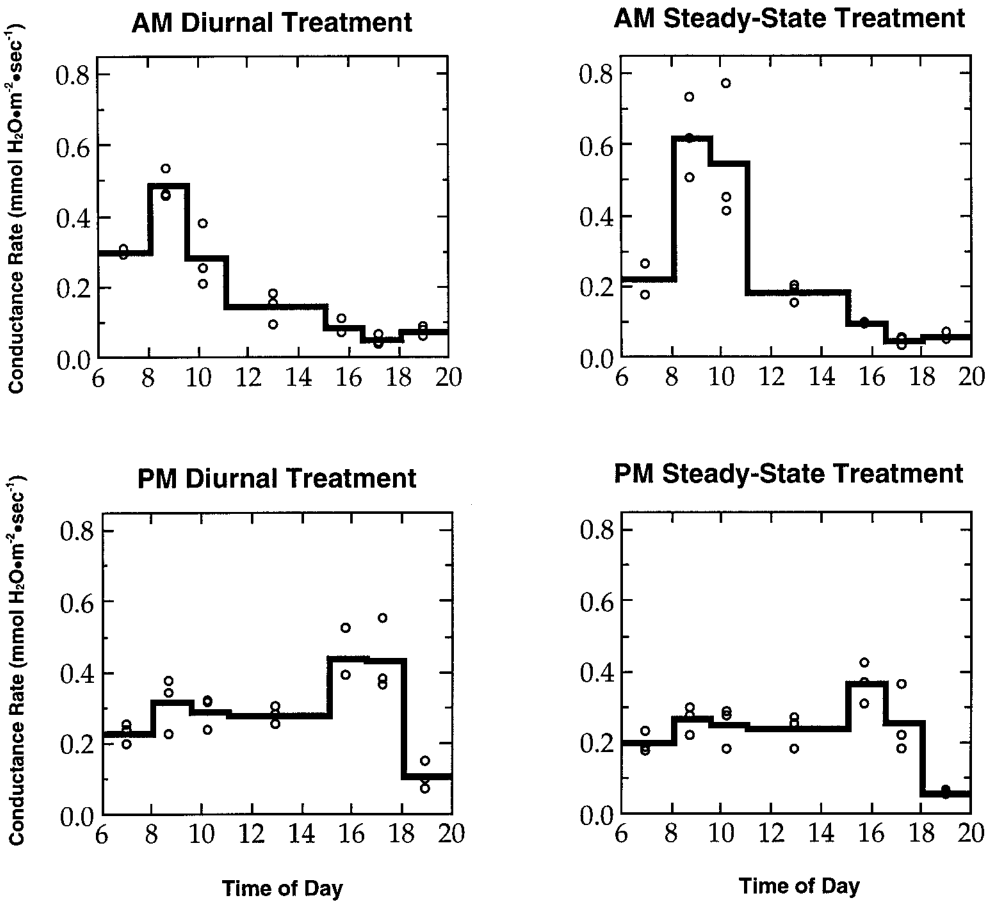

Fig. 3. Diurnal curves of stomatal conductance for all four treatments. Data format is the same as in Fig. 3.

diurnally varying CO_2 treatment relative to the steady-state treatment is consistent with these findings if, in fact, these plants cannot take advantage of peak CO_2 concentrations.

A CO_2-saturation effect is suggested by the fact that higher CO_2 levels within the AM diurnal treatment did not lead to an increase in photosynthetic rate compared with the AM steady-state control. It is possible that plants did not respond to a difference between 600 ppm (steady-state treatment) and 800 ppm (diurnal treatment) in terms of carbon assimilation because they reached their maximum carboxylation capacity at 600 ppm. Despite this phenomenon, conductance and transpiration rates were significantly affected by diurnally varying CO_2 relative to the CO_2 control. This led to an increase in water use efficiency for plants receiving peak levels of light and CO_2 congruently. This is consistent with previous evidence showing that elevated CO_2 reduces stomatal conductance, which leads to reduced water loss (transpiration) and increased water use efficiency (Bazzaz, 1990; Woodward, Thompson, and McKee, 1991; Allen et al., 1994; Diemer, 1994).

Growth and morphological responses—In previous studies, specific leaf mass of herbaceous plants was found to be significantly higher when plants were grown at elevated CO_2 (Bazzaz, Coleman, and Morse, 1990; Garbutt, Williams, and Bazzaz, 1990). In experiments with annuals grown in different light intensities, specific leaf mass also increased (specific leaf area decreased) with increasing light levels (Sultan and Bazzaz, 1993; Ashton and Berlyn, 1994). Our data show a distinct and highly significant difference in specific leaf mass for plants receiving high morning light and diurnally varying CO_2 relative to the other treatments, demonstrating the responsiveness of specific leaf mass to congruency of light and CO_2. Hence, plants may respond to congruent availability of resources in the same way as they would respond to higher total resource levels.

Significant light effects were found for all character responses considered, providing strong evidence that differences in the diurnal timing of light—even with the same total photosynthetic photon flux density and the same variance in intensity, frequency, and duration of light—have important consequences for seedlings and may significantly affect survivorship, particularly in competitive conditions. Conductance, transpiration, daily integrated water loss, and water use efficiency, total leaf mass, and specific leaf mass all showed significant light by CO_2 interactions, suggesting performance was enhanced when peak values of resources were congruent and diminished when they were incongruent. Although conductance and water loss were decreased by the congruency of peak values of CO_2 and light in the morning and increased by the incongruency of peak values of CO_2

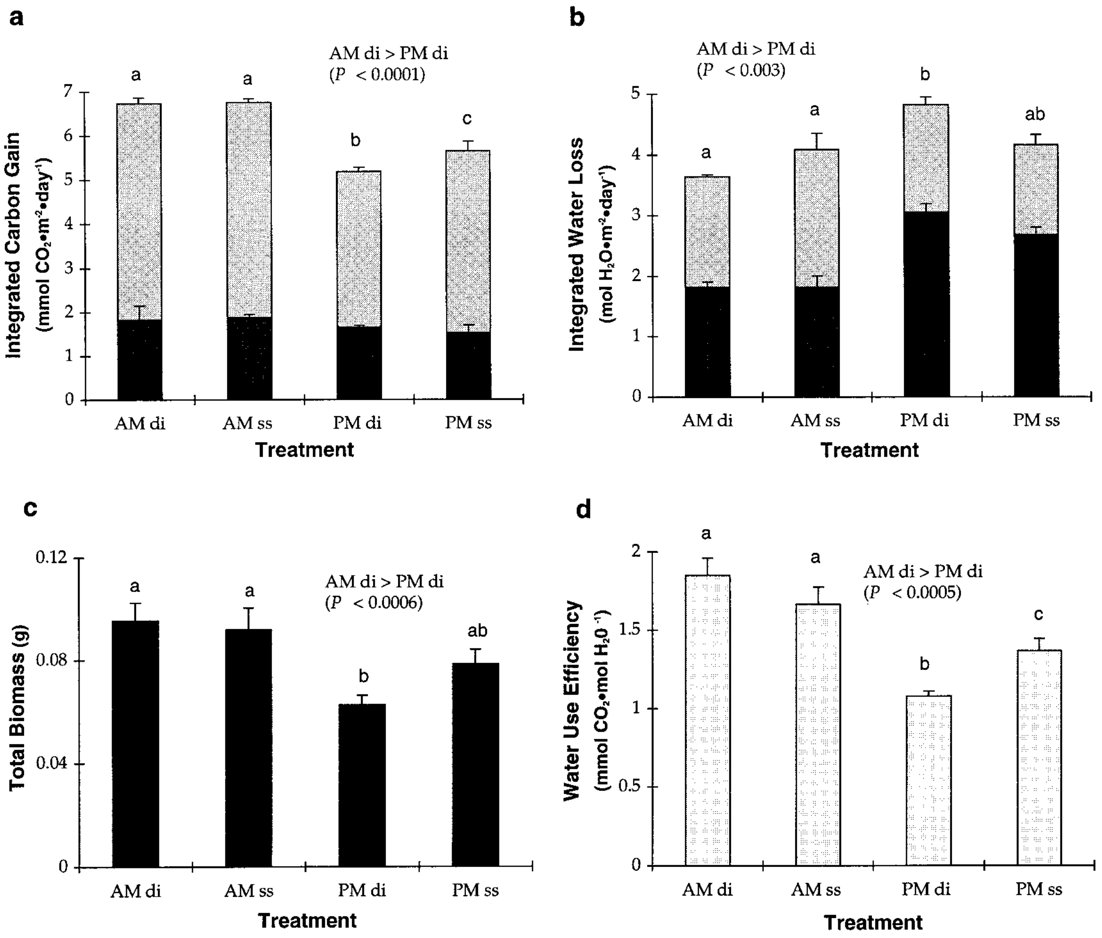

Fig. 4. (a) Integrated carbon gain; (b) integrated water loss; (c) total plant biomass; and (d) water use efficiency (ratio of integrated carbon gain to integrated water loss). In (a) and (b), light and dark bars represent integrated measures during high-light periods (850 μmol photons for 3 h) and low-light periods (55 μmol photons for 11 h), respectively; values are based on averages of Riemann sums of three plants per treatment measured seven times throughout the day. Total integrated values (sum of bars for high- and low-light periods) were used for comparing means of different treatments. For (a–d), error bars are +1 SE of the mean, and letters show differences between treatment means based on Scheffé's post hoc test if $P \leq 0.05$. In addition, probabilities are shown for differences in means of the congruent high-light and high-CO_2 treatment (AM di) and incongruent high-light and high-CO_2 treatment (PM di).

during the afternoon high-light window, photosynthesis and biomass were only affected by the incongruency of peak values of CO_2 and light.

Trends for all of the water-related and morphological character responses were consistent with predicted rank order of performance, even though the treatments were not all significantly different from each other, suggesting that differences in congruencies of high light with optimal CO_2 concentrations, independent of total resource availability, can significantly affect seedling performance. In general, plants were negatively affected by the incongruency of CO_2 and light more than they were affected by the congruency of CO_2 and light.

An important implication of this study is that east and west sides of large gaps, which differ in their diurnal time courses of light availability and CO_2 concentrations, may provide differential advantages for competitively interacting species early in their development. Further investigation is needed to determine whether temporal and spatial heterogeneity in resource availability significantly influences plant performance under field conditions. If so, diurnal variations and congruencies in critical resources may turn out to be important factors in gap partitioning and in the organization of regenerating communities.

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