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Photosynthetic temperature responses of co-occurring desert winter annuals with contrasting resource-use efficiencies and different temporal patterns of resource utilization may allow for species coexistence

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ABSTRACT

A mechanistic understanding of population dynamics requires close examination of species' differences in how physiological traits interact with environmental variation and translate into demographic variation. We focused on two co-occurring winter annual species (*Pectocarya recurvata* and *Plantago insularis*) that differ in photosynthetic resource-use efficiency and demographic responses to environmental variation and covariation between temperature and water availability. Previous work showed that *Pectocarya* has higher water-use efficiency and nitrogen allocation to light-driven dynamics of the Calvin cycle (J_{max}:$V_{C_{max}}$) than *Plantago*, which is often associated with enhanced electron transport capacity at low temperatures and better light harvesting capacity. These traits could enhance *Pectocarya* photosynthesis during reliably moist but cool, cloudy periods following precipitation. We acclimated plants to low and high temperatures and then measured gas exchange across a 30 °C temperature range. As predicted, optimal temperatures of photosynthesis were lower for *Pectocarya* than *Plantago*. Additionally, *Pectocarya* experienced greater respiratory carbon loss than *Plantago* at higher temperatures (every 1 °C increase beyond 24 °C increased the ratio of carbon loss to gain 9% and 27% in cold and warm-acclimated plants, respectively). These differential patterns of photosynthetic optimization and assimilation in response to differing rainfall distributions may have important implications for population dynamic differences and species coexistence.

1. Introduction

Examining interspecific differences in physiological traits can illuminate the link between environmental variation and demographic variation and thereby contribute to a mechanistic understanding of population and community dynamics (McGill et al., 2006). In dryland ecosystems, precipitation exerts a dominant influence on most biological processes, from short-term responses such as plant photosynthetic activity to longer-term demographic responses such as growth, survival and recruitment (Barron-Gafford et al., 2012; Huxman et al., 2004; Schwinning and Sala, 2004). Functional trait differences that underlie plant response to precipitation may explain within-year and between-year resource partitioning among coexisting species (Chesson et al., 2004; Novoplansky and Goldberg, 2001). For example, species differences in physiology or phenology may cause species-specific patterns of resource-use in response to the same precipitation event, or they

Abbreviations: A_{net}, steady-state photosynthesis (μmol CO_2 m^{-2} s^{-1}); A_{max}, maximum photosynthetic rate (μmol CO_2 m^{-2} s^{-1}); F_o, initial fluorescence when dark-adapted; F'_o, initial fluorescence when light-adapted; F_m, maximum fluorescence when dark-adapted; F'_m, maximum fluorescence when light-adapted; F_s, steady state light-adapted fluorescence signal; F_v, variable fluorescence level when dark-adapted = (F_m − F_o); F'_v, variable fluorescence level when light-adapted = (F'_m − F'_o); F_v/F_m, maximum quantum yield of photosystem II; F'_v/F'_m, light-adapted PSII yield; J_{max}, maximum electron transport rates; NPQ, non-photochemical quenching = $[(F_m - F'_m)/F'_m]$; qP, photochemical quenching = $[(F'_m - F_s)/(F'_m - F'_o)]$; R_d, respiration after 5 min in complete darkness (μmol CO_2 m^{-2} s^{-1}); T_{acc}, acclimation temperatures (°C); T_{leaf}, leaf temperature (°C); T_{meas}, measurement temperatures (°C); T_{opt}, optimal temperature of photosynthesis (°C); $V_{C_{max}}$, carboxylation capacity; WUE, water-use efficiency; Δ, leaf carbon isotope discrimination (ppm).

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may enable species to take advantage of precipitation sequences of differing magnitudes and timing. Most examinations of biological responses to precipitation have focused on the direct effects of increased soil moisture, but a more complete understanding will require investigation of the sensitivity of resource gain to co-varying environmental factors such as light availability and temperature.

Precipitation in deserts typically falls in discrete events that may be clustered in space and time, and patterns of event clustering determine the amount of resources and the duration of their availability (Huxman et al., 2004; Noy-Meir, 1973; Reynolds et al., 2004). Monthly precipitation is highly variable between years, with some years experiencing consistent precipitation across a growing season, while others have predominance of early- or late-season rain (Noy-Meir, 1973, Fig. 1a). Temperature exhibits far less *inter*-annual variation than precipitation, but desert plants experience a wide range of temperatures within a growing season (Fig. 1b). Thus for a winter annual plant, early-season precipitation occurs when temperatures tend to be low, but late-season precipitation occurs when atmospheric temperatures tend to be high. Therefore, if species differ in temperature sensitivity, then they might differ in seasonal dynamics of carbon uptake during and after rain events. Additionally, storm events themselves change resource availability by temporarily reducing light and atmospheric temperature and by stimulating nutrient mobilization (Cui and Caldwell, 1997; Woodhouse, 1997). In the Sonoran Desert, periods following winter rainfall are significantly cooler than pre-storm periods for an average of three-five days (Huxman et al., 2008, Fig. 1c and d). These short periods of time following precipitation events may contribute disproportionately to plant seasonal carbon gain (Huxman et al., 2004), yet they may coincide with low-temperature and low-light limitations for some species. Therefore, enhancing photosynthesis under these conditions could allow species to better exploit this resource-rich window of opportunity.

Photosynthetic carbon assimilation is strongly affected by temperature, but many species exhibit a remarkable ability to adjust photosynthetic processes to altered growth temperatures (Berry and Björkman, 1980). Temperature acclimation of photosynthesis and respiration can allow plants to maintain relatively constant rates of net CO_2 exchange as daily temperatures change across the growing season. Desert plants have played an important role in the development of our understanding of photosynthetic adaptations to temperature (e.g., Lange et al., 1974; Mooney et al., 1978; Nobel et al., 1978). Yet many comparative studies have often focused on adaptive differentiation between geographic regions or on long-lived perennials that must withstand extremes of temperature and drought. Annual species constitute over half the flora of the Sonoran Desert (Shreve and Wiggins, 1964), and winter annuals, in particular, present an opportunity to examine the photosynthetic temperature responses of species that begin growth during times of relatively low temperature but face increasingly hot and dry conditions toward the end of their life cycle (Forseth and Ehleringer, 1982; Seemann et al., 1986; Werk et al., 1983). As such, we used a pair of winter annuals to examine how species' differences in physiological traits might interact with temperature variation to translate into demographic variation over time.

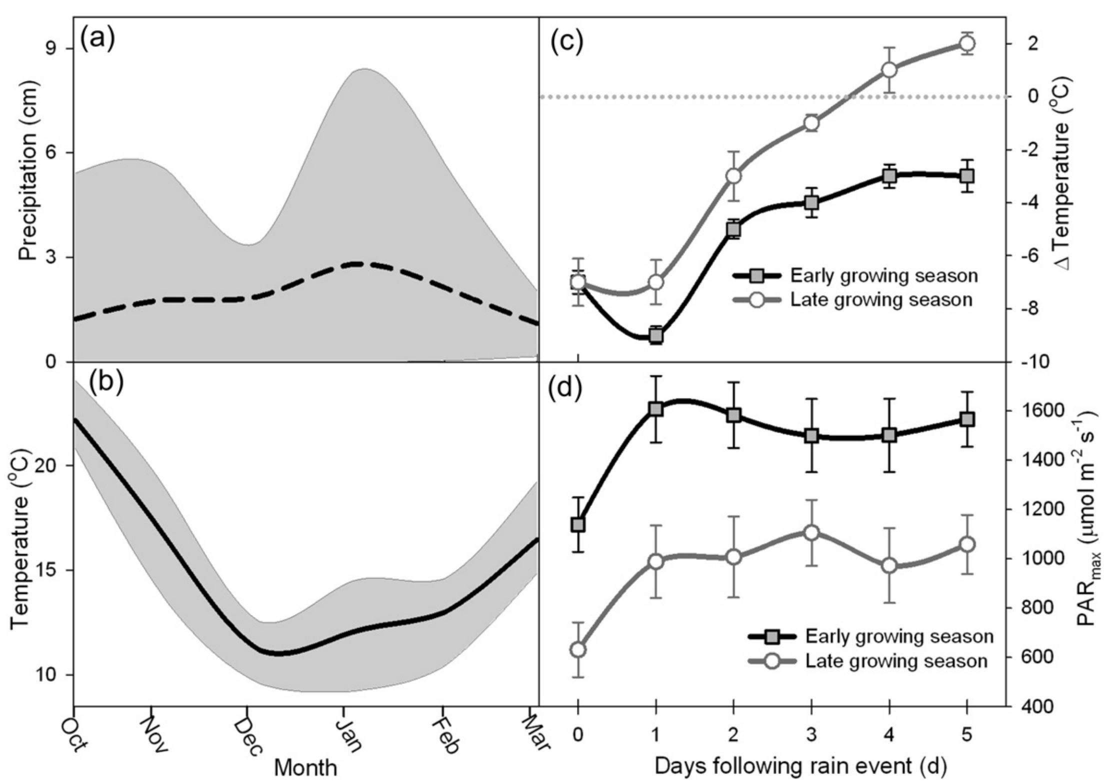

Fig. 1. Microclimatic data from the winter growing season of the Sonoran Desert that illustrate inter- and intra-annual covariation between precipitation, temperature, and photosynthetically active radiation. (a) Mean total monthly precipitation (cm) and (b) mean monthly temperatures (°C) across 2002–2011 are shown within the shaded region indicating the longer-term average (1982–2007; solid line). (c) Relative changes in atmospheric temperature (Δ Temperature; °C). Averaged across all precipitation events between 2002 and 2011, 24-h temperature was reduced by mean 7.0 ± 0.67 °C. Temperatures remained significantly lower than pre-event conditions for five days within the early growing season (Oct–Dec) and three days within the late growing season (Jan–Mar), highlighting seasonal variation in the influence of precipitation on other micrometeorological variables. (d) Average maximum photosynthetically active radiation (PAR_{max}) for the five days after all rain events ($d = 0$) from within the early (Nov–Dec) and late (Feb–March) from 2006 to 2012. PAR_{max} decreased from pre-event levels an average of 27 ± 3% in the early growing season and 39 ± 4% in the late growing season on the days of precipitation events but recovered to pre-event levels within one day, regardless of growing season period. Vertical bars represent one standard error of the mean.