

SHORT COMMUNICATION

## Photoperiod and photosynthetic capacity in *Lotus scoparius*

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**Abstract.** Leaves of *Lotus scoparius* Nutt., a Mediterranean-climate shrub, exhibited higher photosynthetic capacities when grown under winter (10/14 h, day/night) than summer (14/10 h) photoperiods, even though total daily photon irradiance was higher under summer photoperiods. Photosynthetic dependence on natural variations in photoperiod, such that activity was higher under photoperiods associated with expected precipitation, may be a more dependable environmental parameter than total irradiance in temperate habitats with winter–spring precipitation patterns and where seasonal cloudiness may cause total daily irradiance levels to be highly variable.

**Key-words:** *Lotus scoparius*; photoperiod; photosynthetic capacity; Mediterranean climate; photosynthesis; leaf nitrogen content; day-length.

Plants vary in their photosynthetic capacities in ways that contribute to efficient performance under differing environmental conditions. Modification of photosynthetic capacity in response to immediate environmental conditions such as total daily irradiance (Björkman & Holmgren, 1963; Boardman, 1977; Chabot, Jurik & Chabot, 1979; Björkman, 1981), water status (Hsiao, 1973; Hanson, 1982), and/or mineral nutrition (Medina, 1970; Field, 1983) are well known. In some ecosystems, however, seasonal cues such as photoperiod, rather than immediate resource levels, may be the more useful indicators of environmental quality. Mediterranean-type climate ecosystems are one such example, where mild winter temperatures would permit growth at this time of the year, but where photosynthetic activity during the summer is limited by highly seasonal droughts (DiCasteri & Mooney, 1973).

In Mediterranean climates, natural photoperiod, as opposed to total daily irradiance, may represent the best indicator of future environmental conditions. Precipitation, and thus growth, in these habitats is limited to the winter–spring months (DiCasteri & Mooney, 1973). Even during this rainy season, there are frequent dry, clear periods, that

result in large week-to-week fluctuations in the total daily irradiance. Since total daily irradiance at this time of the year will be much lower than in the summer (even under clear skies), it is reasonable to expect that plants might have developed alternative methods for assessing environmental quality.

Previous investigations on the interactions of leaf development, photosynthesis, and irradiance have focused on the relationships between irradiance level and plant response under constant photoperiod (Singh, Ogren & Widholm, 1974; Chabot & Chabot, 1977; Chabot, Jurik & Chabot, 1979; Jurik, Chabot & Chabot, 1979; Longstreth, Hartsock & Nobel, 1981). These studies have clearly demonstrated that (i) photosynthetic capacity is proportional to the daily irradiance level and (ii) the total daily irradiance, and not peak irradiance, is of primary importance in affecting photosynthetic capacity and the morphological traits associated with the photosynthetic process.

In contrast, while many studies have focused on the role of photoperiod as a phenological cue for germination, flowering, dormancy and frost-hardiness (van den Driessche, 1970; Vince-Prue, 1975; Öquist *et al.*, 1980; Salisbury, 1981; Warrington & Kanemasu, 1983), the importance of natural photoperiods in triggering appropriate phenological changes in photosynthetic capacity has not previously been demonstrated for plants limited to the C<sub>3</sub> and C<sub>4</sub> pathways of photosynthesis. Mousseau (1981) has demonstrated a change in photosynthetic characteristics of *Chenopodium polyspermum* when exposed to 24/0 h versus 9/15 day/night photoperiods; the ecological significance of these observations are, however, difficult to interpret because of the unnatural photoperiods used in that study. There is a report that photoperiod is used by facultative crassulacean acid metabolism (CAM) plants as a cue in the switch from C<sub>3</sub> photosynthesis to CAM (Queiroz, 1983), but this has been only partially confirmed (Guralnick, Rorabaugh & Hanscom, 1984).

We have investigated the consequences of natural, seasonal changes in photoperiod on the photosynthetic performance of *Lotus scoparius* Nutt., a common C<sub>3</sub> drought-deciduous shrub of Mediterranean

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climates in California. Previous investigations of canopy dynamics with this species (Nilsen & Schlesinger, 1981; Nilsen & Muller, 1982) have shown that leaf abscission was more sensitive to water stress under long summer photoperiods than under shorter winter photoperiods. We anticipated that these canopy-dynamics changes might also infer differences in photosynthetic capacities, independent of water stress or other environmental limitations.

For gas-exchange measurements, mature plants were allowed to acclimate to growth chamber conditions of 10/14 h (day/night) photoperiod, 25/10 °C, and 30/80% relative humidity for a period of 4 weeks. They were then subdivided into two groups, one continuing to receive a 10/14 h (winter) photoperiod and the other receiving a 14/10 h (summer) photoperiod. Measurements were collected 3–4 weeks after the photoperiod treatment began; all tissues measured were produced during the treatment period. All plants were watered daily and received weekly fertilization with Hoagland's solution; fertilizer applications were sufficient to ensure that nutrient deficiencies would not occur. Since instantaneous irradiances (provided by a combination of four 400 watt high pressure sodium vapour, four 400 watt metal halide high intensity discharge lamps and eight 100 watt incandescent bulbs) were  $1.0 \text{ mol m}^{-2} \text{ s}^{-1}$  (400–700 nm) for both photoperiod treatments, the longer summer photoperiod resulted in substantially larger total daily irradiances. Total daily photon flux (400–700 nm) was  $36.0 \text{ mol m}^{-2} \text{ day}^{-1}$  under the winter photoperiod and  $50.4 \text{ mol m}^{-2} \text{ day}^{-1}$  under the summer photoperiod. Photosynthetic measurements using an open gas-exchange system (Ehleringer, 1983) were collected on new leaves developed under the experimental photoperiod.

In a second set of experiments to separate photoperiod from integrated daily photon levels, plants were grown under 10/14 h photoperiods and growth conditions as described above. They were then subdivided into two groups, one continuing to receive 10/14 h photoperiod and the other also receiving 10 h of light, but with the light distributed to simulate a 14 h photoperiod. In this treatment the plants were illuminated for 9 continuous hours followed by 3 h of dark, a tenth hour of full light, and a final 10 h of darkness. Leaf Kjeldahl nitrogen contents were measured on newly produced leaves after 3–4 weeks exposure to these treatments.

Maximum photosynthetic rates under ambient conditions (incident photon flux of  $2.0 \text{ mmol m}^{-2} \text{ s}^{-1}$ , leaf temperature of 28 °C,  $350 \text{ cm}^3 \text{ m}^{-3} \text{ CO}_2$ , 21%  $\text{O}_2$ , and a leaf to air water vapour gradient of  $18 \text{ mbar bar}^{-1}$ ) were significantly different between the two photoperiod treatments (Table 1). The highest photosynthetic rates occurred on leaves produced under the winter photoperiod, which is opposite to what would have been predicted if plants were responding to total irradiance as the environ-

mental indicator. Even though leaf water status in both treatments was the same (predawn water potentials ranging from  $-0.3$  to  $-0.5 \text{ MPa}$ ), the decreased photosynthetic rates in summer photoperiod treatment leaves were associated with a decreased leaf conductance to gaseous diffusion through the stomates. However, intercellular  $\text{CO}_2$  concentrations were similar between treatments, implying that the reduced  $\text{CO}_2$  diffusion rates associated with lower leaf conductances were not responsible for the observed differences in photosynthetic rate.

This was verified by measurements of the photosynthetic dependence on intercellular  $\text{CO}_2$  concentration (Fig. 1). These data clearly illustrate that winter photoperiod leaves had an increased capacity to fix  $\text{CO}_2$  at any intercellular  $\text{CO}_2$  concentration. The enhanced photosynthetic capacity of winter photoperiod plants was not associated with an increased leaf mass per unit area, but rather with increased leaf protein levels (Table 1). Additionally, the stomatal limitations to photosynthesis (Farquhar & Sharkey, 1982) caused by a reduction in  $\text{CO}_2$  diffusion through the stomates were 26 and 29% for winter and summer photoperiod leaves, respectively, again indicating that restrictions in leaf conductance were not the primary factors responsible for the observed differences in photosynthetic rate.

Both maximum photosynthetic rate under ambient conditions (Medina, 1970; Field, 1983) and the initial slope of the photosynthesis–intercellular  $\text{CO}_2$  dependence response curve (von Caemmerer & Farquhar, 1981; Ehleringer & Cook, 1984) are known to be correlated with leaf tissue Kjeldahl nitrogen levels. In our study, variations in leaf nitrogen content accounted for a significant fraction of the change in photosynthetic capacity ( $r^2=0.88$ ,  $P<0.01$ ). Since the leaf mass per unit area and the stomatal limitation on photosynthesis did not change

**Table 1.** Maximum photosynthetic rates under ambient conditions ( $A_{\text{max}}$ ) and the leaf conductance to water vapour diffusion ( $g$ ) and intercellular  $\text{CO}_2$  concentration ( $c_i$ ) measured at  $A_{\text{max}}$  for leaves of *Lotus scoparius* grown under winter (10/14 h) and summer (14/10 h) photoperiods

	Photoperiod treatment	
	10/14 h	14/10 h
$A_{\text{max}}$ ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	$27.7 \pm 3.9^*$	$12.5 \pm 3.0$
$g$ ( $\text{mol m}^{-2} \text{ s}^{-1}$ )	$0.383 \pm 0.048^*$	$0.181 \pm 0.022$
$c_i$ ( $\text{cm}^3 \text{ m}^{-3}$ )	$211 \pm 23$	$234 \pm 12$
$W$ ( $\text{g m}^{-2}$ )	$115.0 \pm 14.3$	$117.3 \pm 9.5$
Leaf nitrogen ( $\text{mg g}^{-1}$ )	$22.01 \pm 1.04^*$	$14.41 \pm 2.96$

Also presented are the leaf mass per unit area ( $W$ ) and leaf Kjeldahl nitrogen concentration for leaves developed under the two photoperiods.

\*Indicate that measurements on leaves under the different photoperiods were statistically significant at the  $P < 0.01$  level of significance (Student's  $t$ -test).

Data are means  $\pm 1 \text{ SD}$ .

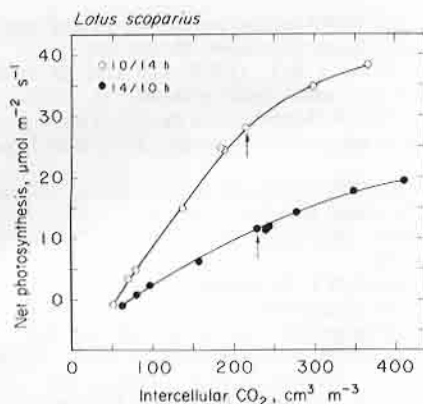


Figure 1. Net photosynthesis as a function of intercellular  $\text{CO}_2$  concentration for plants grown under different photoperiods. Arrows indicate intercellular  $\text{CO}_2$  concentrations experienced by plants under ambient conditions.

with photoperiod, it appears that almost all of the changes in photosynthetic rate arose from subcellular changes; the observed changes in leaf protein level support this notion.

The experiments described thus far do not distinguish between a reduction in photosynthetic capacity induced by short photoperiod versus an inhibitory reduction caused by exposure to high light. The latter possibility is unlikely, given that these plants grow in open habitats. However, to exclude this possibility, plants were grown under winter photoperiods and then exposed for a short period of light at a time coincident with the last hour of the summer photoperiod. Leaf Kjeldahl nitrogen values measured on plants exposed to the long nights (control) were  $28.9 \pm 5.0 \text{ mg g}^{-1}$  ( $\bar{x} \pm 1 \text{ SD}$ ) and to the interrupted nights were  $22.9 \pm 5.2 \text{ mg g}^{-1}$ . These data are significantly different at the  $P < 0.05$  level, indicating that it is the photoperiod which is of major importance and suggesting that phytochrome may be involved as the sensory system.

A reduction in leaf photosynthetic rate of over 50% in the absence of any water or mineral stresses, which is attributable solely to the longer photoperiods experienced in summer, does not in itself seem to be of adaptive value. The likely importance of the phenomenon becomes more clear, however, when considering performance of *L. scoparius* in its natural habitat. During long summer photoperiods, plants endure increasing levels of water stress under a predictable, severe drought lasting several months (Nilsen & Schlesinger, 1981; Nilsen & Muller, 1982). Under these conditions, leaf conductance would undoubtedly be low due to water stress (Hsiao, 1973; Mooney, 1980; Hanson, 1982), and this would severely limit photosynthetic rates even if leaf protein contents were high (von Caemmerer & Farquhar, 1981; Farquhar & Sharkey, 1982; Ehleringer & Cook, 1984). Thus, under field conditions, decreased protein content would not necessarily cause large decreases in carbon dioxide uptake during long days,

but would avoid other costs such as the higher maintenance respiration rates associated with higher leaf protein levels (Penning de Vries, 1975).

Photoperiodic control over photosynthetic activity may be an important feature in habitats with mild winters and seasonal droughts. We suggest it is likely that plants that are winter-active and summer-inactive, such as those in Mediterranean climates, may have photosynthetic rates that respond more to photoperiod than to total daily irradiance, and that this response is of adaptive value to the plant in its native habitat.

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