THE ROLE OF PHOTOPERIOD IN DETERMINING SEASONAL PATTERNS OF VEGETATIVE ACTIVITY IN THE CHAPARRAL

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ABSTRACT. Due to the variability in yearly precipitation, it has generally been assumed that photoperiod, used as a cue to trigger phenological events, would not be adaptive in a mediterranean-type climate. The importance of opportunistic responses to water availability has been stressed, and field data have generally been interpreted with the assumption that immediate environmental conditions, especially soil and plant water status, exert the primary control over plant responses. Several studies now indicate, however, that some chaparral plants utilize photoperiod to control a wide range of phenological responses including seasonal dormancy, leaf dimorphism, leaf abscission, and photosynthetic capacity. This suggests that the highly predictable annual cycle of winter rain and summer drought coupled with considerable short-term uncertainty may have led to the evolution of multiple cue control systems. Photoperiod cues may control major changes in seasonal growth patterns, while the vigor and exact timing of growth in any particular season are still sensitive to environmental parameters such as water status. This hypothesis still recognizes the seasonal patterns of temperature and water availability as the most important constraints on chaparral plant phenology. It nonetheless challenges the practice of inferring unique functional relationships between environmental parameters such as soil water status taken from field data that have been collected over more than one season, and plant characteristics such as shoot and leaf demographic patterns or photosynthetic rates.

INTRODUCTION

Photoperiod cues have been widely studied in respect to the phenological control of plant growth. The use of photoperiod as a cue involves an assessment of seasonal progression based on changes in daylength. Measurement of daylength in plants is thought to involve the phytochrome pigment system, and it is largely independent of light intensity variations due to partial shading or cloudiness (Vince-Prue 1975). The use of such cues can permit the timing of critical, seasonal responses to be independent of the vagaries of immediate environmental conditions. This can allow plant responses to be synchronized with other, predictable, environmental events, and it also allows plant responses to effectively anticipate future environmental conditions. Events where photoperiod has often been shown to be important include germination, flowering, dormancy, frost-hardiness, and leaf abscission (van den Driessche 1970, Vince-Prue 1975, Öquist et al. 1980, Salisbury 1981, Warrington and Kanemasu 1983). Several studies, primarily on crop plants, have demonstrated that photoperiod can also affect leaf conductance and photosynthetic capacity (Meidner 1970, Chang 1981, Mousseau 1981, Ma and Hunt 1983). Ouedraogo and Hubac (1982) found that cotton grown under short days had lower stomatal conductance and that this was correlated with increased survival during prolonged drought. Whether photosynthesis was enhanced by long or short photoperiods in most of these studies, however, varies with crop species, cultivar, maturity, and even leaf position on individual plants. The ecological implications of these photoperiod responses have remained obscure.

Although it is assumed in most studies that immediate environmental conditions, chiefly temperature and soil water potential, are sufficient to explain the vegetative phenology of chaparral species, a few authors have argued for the importance of indirect cues. If resistance to severe drought stress requires a prior growth response or shift in biochemistry, it may be important for a plant to anticipate the drought via photoperiod (Ofir and Kerem 1982, Queiroz 1983). In a mediterranean-type climate such as that of the chaparral in southern California, a long and predictable summer drought alternates with a distinct winter rainy season. Most of the winter rain comes in a few intense storms, and moderate levels of drought stress can develop between the major winter storms (Hanes 1977). The exact dynamics of winter rain and dry spells are highly variable from year to year. Based on a series of experiments with *Lotus scoparius*, a suffrutescent chaparral perennial, Nilsen and Muller (1982) concluded that photoperiod cues can allow chaparral plants to anticipate the future probability of rain and thus modify the response to water stress during winter as opposed to summer seasons.

Very few studies have examined the use of photoperiod cues in the chaparral, and none has yet dealt with the dominant woody shrubs. A careful search of the literature, however, yields a handful of studies reporting the use of photoperiod cues in modifying plant responses to drought in regions with mediterranean-type climates. These indicate that in several diverse life forms vegetative functions at the physiological and organ demographic levels respond in important ways to photoperiod.

INDUCTION OF CAM PHOTOSYNTHESIS

Experimental work with a few facultative CAM plants from regions with highly seasonal precipitation has shown that photoperiods corresponding to the season of expected drought can facilitate the switch from C_3 to CAM photosynthesis (Gregory et al. 1954, Queiroz 1979, 1983). The induction of CAM by photoperiod cues in *Kalenchoe blossfeldiana* v. Poelln., involves both changes in the diurnal timing of stomatal opening and the synthesis of a distinct isoform of phosphoenolpyruvate carboxylase, the enzyme responsible for nighttime fixation of carbon dioxide (Brulfert et al. 1982). In contrast, Guralnick et al. (1984) found only weak evidence of a photoperiod induction of CAM in fully mature leaves of *Portulacaria afra* (L.) Jacq. Deleens and Queiroz (1984) report that photoperiod caused variation in the relative CAM activity, as indicated by changing carbon isotope ratios, in an obligate CAM plant. Whereas the use of photoperiod to modulate the relative amounts of carbon assimilation, or to initiate a switch between daytime and nighttime assimilation, has been clearly demonstrated for a few species, the frequency and ecological importance of this syndrome is not yet established. Other facultative CAM plants appear to use more immediate environmental conditions such as soil water potential and diurnal temperature fluctuations to determine the level of CAM expression (Guralnick et al. 1984).

DORMANCY AND CANOPY DYNAMICS

Poa bulbosa is a perennial grass that survives summer drought by means of bulbs formed at or just below the soil surface by several persistent leaf bases surrounding a dormant bud. Ofir and Kerem (1982) found that dormancy, assessed as greater than 50% leaf mortality, was induced by long days in a population near Jerusalem. High temperatures increased the rate of entry into dormancy while low growth temperatures retarded but did not prevent dormancy. The authors suggest that this response allows a drought-resistant state to be achieved before intense water stress develops with rapid drying of the surface soil in late spring.

Lotus scoparius Nutt., a drought-deciduous perennial of southern California's mediterranean climate region, sheds its leaves more rapidly in response to equivalent levels of water stress during summer as opposed to winter photoperiods (Nilsen and Muller 1981). The authors suggest that this prevents unnecessary leaf turnover during short winter droughts and thus reduces the costs of canopy construction and maintenance (Nilsen and Muller 1982). Nilsen and Muller (1981, 1982) investigated the physiological basis for these seasonal changes in leaf demography. Increased senescence of leaves under long days could not be attributed to impaired tissue water relations since leaf turgor maintenance actually improved under long-day treatments due to decreased leaf osmotic potential. Leaf protein contents, however, which were initially equivalent between photoperiod treatments, decreased more in long than in short photoperiod treatment plants when both sets of plants were subjected to low soil water potentials. When plant water stress was alleviated, protein content recovered only in short photoperiod treatment plants. This result is partially, but not entirely, consistent with the data of Comstock and Ehleringer (1986) working with the same species in which leaf Kjeldahl nitrogen contents were much higher in short than long photoperiod treatments even without subjecting plants to water stress. Gill and Mahall (1986) suggest that an important role for photoperiod cues in determining leaf abscission is also consistent with the leaf demography patterns measured in a natural population of *Salvia mellifera*.

PHOTOSYNTHETIC RATES

In ecological studies of plant photosynthetic activity, it has generally been assumed that environmental factors directly affecting photosynthetic rates during growth are the most important factors determining subsequent photosynthetic capacity. Rarely do experimenters look for indirect cues determining photosynthetic performance. While this view has proven to be productive, evidence now exists that it is not always correct, and the potential roles of indirect cues in determining the photosynthetic activity of a wide range of plants should be considered.

Comstock and Ehleringer (1986) reported that *Lotus scoparius* Nutt. grown in environmental chambers had a much higher photosynthetic rate under winter (10:14 h light : dark) than summer (14:10 h) photoperiods (Table 1). A similar result has

Table 1. Photosynthetic and morphological measurements taken on plants of *Lotus scoparius* grown under winter and summer photoperiods. Amax refers to light saturated net photosynthesis measured under ambient conditions of 28°C leaf temperature, 22 pa kpa^{-1} leaf to air water vapor concentration gradient, 1.8 mmol (400–700 nm) m^{-2} s^{-1} photon flux, and ambient CO_2 = 350 μl liter^{-1}. Nitrogen contents are leaf Kjeldahl nitrogen. The initial slope of the photosynthetic response to intercellular CO_2 concentration (c_i) was measured over the range c_i = 50–80 μl liter^{-1}. Relative stomatal limitation is calculated as the percent reduction in net photosynthesis observed when c_i drops from 350 μl liter^{-1} (equal to ambient CO_2 during Amax measurement) to the actual c_i observed during measurement of Amax. Significance values were determined using Student's t-test on the difference between the mean values between photoperiod treatments. n = 4 plants for each treatment. Data are presented as mean ± SD. ** = $p < 0.01$, *** = $p < 0.001$.

	Photoperiod (light : dark)		
	10:14	14:10	
Amax, μmol m^{-2} s^{-1}	27.7 ± 3.9	12.5 ± 3	**
Leaf conductance at Amax, mol m^{-2} s^{-1}	0.383 ± 0.048	0.181 ± 0.022	**
c_i at Amax, μl liter^{-1}	220 ± 24	229 ± 14	NS
Initial slope of CO_2 response, mol m^{-2} s^{-1}	0.173 ± 0.028	0.072 ± 0.019	***
Relative stomatal limitation	33.8 ± 5.1	31.5 ± 3.7	NS
Leaf nitrogen content, mg g^{-1}	22.0 ± 1.0	14.4 ± 3.0	**
Leaf nitrogen content, g m^{-2}	2.45 ± 0.24	1.60 ± 0.31	**
Unit leaf weight, g m^{-2}	115 ± 14	117 ± 10	NS

now been found for a second chaparral perennial, *Artemisia douglasiana* Bess. (Table 2) (details of growth conditions and experimental procedure for *A. douglasiana* were equivalent to those used for *L. scoparius* in Comstock and Ehleringer 1986). Photosynthetic rates were 2.22 and 1.52 times higher in the winter compared to the summer photoperiod-grown plants for *L. scoparius* and *A. douglasiana*, respectively. These differences in net photosynthetic rate were apparent even when plants were compared at equivalent intercellular CO_2 concentrations (c_i) (Fig. 1) and were thus not due to differing stomatal behavior. Leaf Kjeldahl nitrogen content, which has been shown to be closely correlated with total protein content and RuBP carboxylase activity (von Caemmerer and Farquhar 1981), was much higher on an area basis in the short photoperiod grown leaves. Since short photoperiod treatment leaves were either of equal thickness (*Lotus*) or thinner (*Artemisia*) than long photoperiod grown leaves, the main factor determining differences in photosynthetic capacity appears to be protein content at the subcellular level.

Other effects of photoperiod were observed which differed between species. In *L. scoparius*, c_i was not significantly different between treatments, but in *A. douglasiana* it was significantly lower in the winter photoperiod treatment under an ambient CO_2 con-

Table 2. Photosynthetic and morphological measurements taken on plants of *Artemisia douglasiana* grown under winter and summer photoperiods. Amax refers to light saturated net photosynthesis measured under ambient conditions of 28°C leaf temperature, 22 pa kpa^{-1} leaf to air water vapor concentration gradient, 1.8 mmol (400–700 nm) m^{-2} s^{-1} photon flux, and ambient CO_2 = 350 μl liter^{-1}. Nitrogen contents are leaf Kjeldahl nitrogen. See Table 1 for definition of initial slope of CO_2 response and relative stomatal limitation. Significance values were determined using Student's t-test on the difference between the mean values between photoperiod treatments. n = 3 plants for each treatment. Data are presented as mean ± SD. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	Photoperiod (light : dark)		
	10:14	14:10	
Amax, μmol m^{-2} s^{-1}	16.3 ± 2.6	10.7 ± 3.6	*
Leaf conductance at Amax, mol m^{-2} s^{-1}	0.188 ± 0.044	0.149 ± 0.043	NS
c_i at Amax, μl liter^{-1}	199 ± 8	231 ± 4	**
Initial slope of CO_2 response, mol m^{-2} s^{-1}	0.100 ± 0.017	0.054 ± 0.001	*
Relative stomatal limitation	29 ± 1	17 ± 5	*
Leaf nitrogen content, mg g^{-1}	23.4 ± 0.3	13.9 ± 0.4	***
Leaf nitrogen content, g m^{-2}	1.4 ± 0.11	1.0 ± 0.03	**
Unit leaf weight, g m^{-2}	55.8 ± 1.1	67.1 ± 1.8	***
Shoot height at 4 weeks, m	0.126 ± 0.024	0.187 ± 0.008	*
Internode length, mm	4.6 ± 0.8	10.4 ± 0.4	*
Number of leaves/shoot	28.7 ± 2.1	18.7 ± 5.5	*

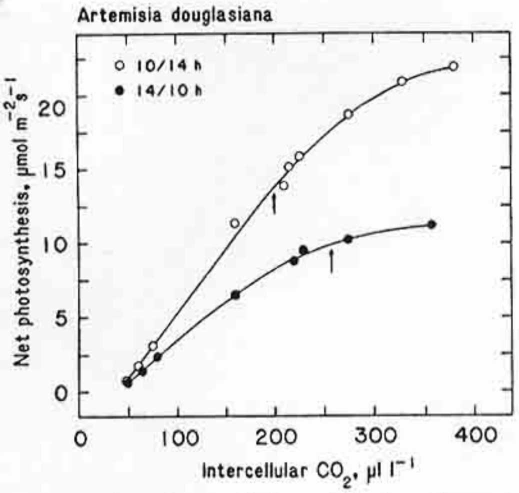

Figure 1. Net photosynthesis as a function of intercellular CO_2 concentration for plants of *Artemisia douglasiana* grown under different photoperiods. Arrows indicate mean intercellular CO_2 measured in plants under ambient CO_2 concentrations of 350 μl liter^{-1}. Intercellular CO_2 (c_i) was varied experimentally by varying ambient CO_2 around the leaf.

centration of 350 μl liter^{-1}. Unit leaf weight also remained constant between treatments in *L. scoparius*, but leaves were thinner under the winter photoperiod in *A. douglasiana*. *Artemisia douglasiana* also showed several photoperiod effects on shoot morphology which were related to seasonal patterns of growth. *Artemisia douglasiana* is essentially an herbaceous perennial from a perennial rhizome. Annual shoots reach a height of 0.5–1.5 m and flower in summer and autumn. The plants under winter photoperiods had significantly more leaves, but much shorter internodes and consequently shorter shoots than plants under summer photoperiods. This indicates that the transition from a short, dense winter canopy to an erect, more diffuse summer canopy is under photoperiod control in *A. douglasiana*.

Lotus scoparius was also given a 9:4:1:10 h light : dark : light : dark treatment such that total irradiance was the same as the winter photoperiod, but the effective daylength was 14 h. Kjeldahl leaf nitrogen contents were 28.9 ± 5.0 mg g^{-1} (x ± 1 SD) and 22.9 ± 5.2 for the short day control and interrupted night treatments, respectively. These means are significantly different ($p < 0.05$), but the absolute magnitude of the response compared to that with a full 14-h light period was less. With a full 14-h light period nitrogen content was 34.5% lower than controls compared to 21.8% in the interrupted light period experiment. Further, a low intensity night interruption (0.05 mmol m^{-2} s^{-1} 400–700 nm, from 80 watt incandescent bulbs) failed to have any effect and an hour at full light period intensity (1.0 mmol m^{-2} s^{-1} 400–700 nm, from the combined irradiance of Na vapor, metal halide, and incandescent light sources) was required to induce a long-day response. This kind of behavior involving intermediate levels of response to interrupted night treatments and considerable dosage dependence has been observed in some other photoperiod studies (Vince-Prue 1984). These characteristics appear to indicate a distinct mechanistic type of photoperiod control system which is usually found in long-day plants.

Apical meristems (taken to be all leaf primordia less than 2 cm long and all associated tissues) of *A. douglasiana* were also measured for Kjeldahl nitrogen content. The measured values were 55.8 ± 4.2 and 43.33 ± 2.17 mg g^{-1} ($p < 0.02$) for winter and summer photoperiods, respectively. This supports the notion that the low leaf nitrogen content causing low photosynthetic rates is a consequence of a broader change in nitrogen metabolism in the whole plant. This is not conclusive, however, since much of the tissue of the meristem consisted of very immature leaves. Although these immature leaves and primordia were still tightly curled in a bud and were not yet photosynthetically competent, the different nitrogen contents of the meristems could have been primarily related to the future photosynthetic capacity of their respective leaves.

IMPLICATIONS OF PHOTOPERIOD TO CHAPARRAL STUDIES

The exact seasonal timing of the favorable growing periods varies considerably in a mediterranean-type climate due to erratic year-to-year variations in both annual totals and within-season patterns of rainfall. It has too often been assumed that the use of photoperiod cues would not be adaptive under these conditions, and that plant responses should therefore be purely opportunistic towards changes in the immediate environment (Mooney and Dunn 1970, Baker et al. 1982). An alternative hypothesis, however, is that the very predictable alternation between winter rainy season and summer drought occurs with a high level of environmental noise in the immediate conditions of light, temperature, and water status. Current environmental conditions which directly affect growth are thus poor indicators of seasonal progression. While flexibility in growth responses, especially as it relates to variable water status is important, photoperiod can provide a much more reliable cue for phenological events involving growth responses and tissue demographic patterns which must anticipate future conditions. A multiple cue control system is therefore predicted in which many broad phenological patterns will be controlled by photoperiod, but season-specific sensitivity to immediate conditions such as temperature and soil water status will also be important. Such season-specific sensitivity may often obscure the higher-level mechanisms controlling phenology. Conversely, data collected over a broad period of time may not be suitable for establishing direct relationships between plant performance and environmental parameters within a single season. Analyses, for example, inferring unique functional relationships between photosynthesis (Mooney et al. 1975) or leaf conductance (Miller and Poole 1979) and plant water status, utilizing data spanning one or more years of seasonally changing conditions, may have limited applicability unless the effect of seasonal cues such as photoperiod have been considered. More long-term and quantitative studies of phenology such as that of Gill and Mahall (1986) are needed, as well as specific tests of mechanistic responses.

The limited data available demonstrating photoperiod dependency in chaparral species raise far more questions than they answer. Initiation of dormancy, leaf demographic patterns, and photosynthetic rates have all been shown to depend partly on photoperiod cues, but the generality of such responses is not yet established. The ecological role of some responses such as reduced photosynthetic capacity during summer photoperiods needs further elucidation. Is it, in itself, a primary effect directly selected for as a means of controlling seasonal growth and nitrogen investments, or is this a secondary effect caused by changes in whole-plant nitrogen metabolism which may predispose the plants towards dormancy during summer photoperiods? In either case, the large potential impact on carbon balance makes the phenomenon an important one.

In the California chaparral, measurable precipitation during 14-h photoperiods is a rare event, and the potential photosynthetic ability of well-watered plants during midsummer is not of great ecological importance. The largest real impact on seasonal plant carbon gain under field conditions is likely to occur in late spring (May). A wet spring with large soil water reserves still present in the month of May, or with late spring rains, would not result in as much photosynthetic activity as might be predicted based solely on relationships between plant performance and plant water potential determined under short photoperiods. The relative importance of this effect will depend on whether there is a distinct critical photoperiod causing a switch between two discrete plant states (and what that critical photoperiod is), or whether intermediate photoperiods would result in intermediate plant responses.

If the photoperiod effects noted in drought-deciduous species serve primarily to control unnecessary leaf turnover by promoting or retarding leaf abscission under summer or winter conditions respectively, then evergreen species may not be expected to show a photoperiod response. However, leaf demographic data of Gill and Mahall (1986) for *Ceanothus megacarpus*, a sclerophyllous evergreen species, indicate that while the current year's cohort of leaves was highly resistant to water stress developed under summer drought conditions, the previous year's cohort of leaves showed a behavior similar to the drought-deciduous species *Salvia mellifera*. They were resistant to water stress during their second winter but were abscised rapidly during drought in June. This suggests the possibility of age-specific effects of photoperiod on canopy dynamics even in evergreen species. The leaf demographic data of Jow et al. (1980) for *Adenostoma fasciculatum* are also consistent with such an interpretation. The highly seasonal timing of long- and short-shoot growth, shown to be under photoperiod control in several mediterranean chamaephytes (Margaris 1975), is, again, likely to be controlled, at least partially, by photoperiod in chaparral sclerophylls. It is also possible that the physiological dormancy exhibited by leaves of evergreen species enduring the summer period will prove to be reinforced by photoperiod cues. Although drought is indisputably the ultimate cause of summer dormancy, many chaparral species may be using photoperiod cues as a proximate mechanism to initiate dormancy in addition to direct effects of water stress. The role of photoperiod should be re-examined for mediterranean plants, and it may be that this re-examination will lead to some meaningful refinements in our current understanding of their adaptive strategies.

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