Seasonal, Light, and Temperature Influences on Organ Initiation for Unrooted Cladodes of the Prickly Pear Cactus *Opuntia ficus-indica*

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ADDITIONAL INDEX WORDS. carbohydrates, day/night temperatures, fruit, reproductive development, seasonality, shading, vegetative development

ABSTRACT. Detached, unrooted cladodes (stem segments) of the widely cultivated prickly pear cactus *Opuntia ficus-indica* (L.) Miller (Cactaceae), which remain alive for at least 12 months, provide a model system for investigating stem responses to environmental factors. Initiation of organs varied seasonally; on average 2.14 new organs were initiated per cladode over a 16-week period in a glasshouse for cladodes detached in winter, 0.76 when detached in late spring, and only 0.07 when detached in late summer. Shading by 45% halved new organ initiation and shading by 95% decreased it by 96%. The seasonal and light responses for new organ initiation are consistent with field observations on *O. ficus-indica*. For detached cladodes maintained in environmental chambers for 14 weeks, the new organs were 10 times more likely to be fruit than daughter cladodes at day/night temperatures of 15/5 °C, equally likely to be either organ at 25/15 °C, and 10 times more likely to be daughter cladodes than fruit at 35/25 °C. Decreasing the shading or the temperature favored stomatal opening, as shown by increases in the dry mass/fresh mass ratio of the detached cladodes. Such increased stomatal opening was accompanied by increased photosynthetic activity, as shown by greater starch content and higher concentrations of sucrose, glucose, and fructose. Why low day/night temperatures favored reproductive structures and high temperatures favored vegetative ones is not clear, but future research using unrooted cladodes may help elucidate the mechanisms involved.

Various species of cacti are cultivated in >20 countries, primarily for their fruit (Barbera, 1995; Mizrahi et al., 1997; Nobel, 1994). The flattened stem segments (cladodes) of platyopuntias, known as prickly pear cacti, are also used for forage and fodder as well as for human consumption as a vegetable (Felker, 1995; Flores-Valdéz, 1995; Russell and Felker, 1987). Because most cacti exhibit Crassulacean acid metabolism (CAM) and hence require less rainfall or irrigation than conventional crops and often flourish on soils with low nutrient availability (Nobel, 1988), their use may increase in the future. Yet, relatively little research has been done on commercially important cacti, so comprehensive information is not available on environmental influences on organ initiation, such as the production of new daughter cladodes or fruit. Such information can influence management decisions on where particular species should be planted for fruit production and when to harvest young cladodes for food or possible energy production (Felker, 1995; García de Cortázar and Varnero, 1995).

The two environmental variables that have received the most research attention for cactus growth are light and water (Nobel, 1988). Daughter cladodes of many platyopuntias, including the species considered in this study, *Opuntia ficus-indica*, are preferentially initiated on cladodes that are favorably oriented for sun-light interception (Nobel, 1982a); because such new cladodes tend to be oriented in the same plane as the cladodes on which they develop, light interception by the whole plant is maximized. In this regard, unrooted cladodes of *O. ficus-indica* shaded by 94% in the glasshouse initiate only ≈5% as many new organs as those without

shading (Nobel, 1996). Species such as *O. ficus-indica* and the barrel cactus *Ferocactus acanthodes* exhibit stem growth when soil water becomes available (Nobel, 1986, 1988). On the other hand, stem extension for the columnar cactus *Stenocereus queretaroensis* in Jalisco, Mexico, occurs in the fall after the summer rainy period when carbohydrates accumulate in the stem and new roots are formed (Nobel and Pimienta-Barrios, 1995).

The large size and tissue succulence of cladodes of *O. ficus-indica* offer an ideal model system for investigating environmental influences on organ initiation for stems independent of signals from the roots. Such detached, unrooted cladodes of *O. ficus-indica* can remain alive for >12 months, readily producing new roots when placed in moist soil (P.S. Nobel, personal observation). Injection of various solutes into rooted and unrooted cladodes has shown that the putative cryoprotectant glucose and the nonmetabolizable *N*-methyl-glucose can lower the temperature threshold for freezing damage to *O. ficus-indica*, underscoring the importance of tissue water content for low-temperature tolerance (Nobel et al., 1995). Weekly injection of various compounds into unrooted cladodes of *O. ficus-indica* for 6 weeks demonstrated that an average accumulated tissue concentration of 1 μM gibberellic acid (GA₃ and GA₄) virtually eliminates the production of new organs over a 16-week period but 50 μM indole-3-acetic acid or kinetin accelerates organ development by ≈3 weeks, as does injecting 90 mM sucrose, 45 mM KCl, or 45 mM KNO₃ (Nobel, 1996).

Although shading detached, unrooted cladodes by 94% nearly eliminates the production of new organs, responses to other light levels or the seasonal response of new organ initiation are not known. Such responses can help predict cladode production for an entire plant, which is valuable information when young cladodes are periodically harvested for vegetables (Russell and Felker, 1987) or cladodes of various ages are harvested for possible biogas or ethanol production (García de Cortázar and Varnero, 1995). Another environmentally related question is what temperatures favor cladode versus fruit initiation. Answers to such questions can

Received for publication 22 May 1997. Accepted for publication 25 Aug. 1997. Use of trade names does not imply endorsement of the products named nor criticism of similar ones not named. Starch contents were measured by Ning Wang and sugar concentrations by Eran Raveh. This research was financially supported by the UCLA Committee on Research and by Sol Leshin through the UCLA-Ben Gurion Program for Cooperation. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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Fig. 1. Kinetics of organ initiation on cladodes of *Opuntia ficus-indica* detached in winter (3 Jan. 1997) and maintained in an environmental chamber with day/night air temperatures of 25/15 °C (○) or in a glasshouse (Δ). In each case, data are the average accumulated number of new organs initiated on each of 10 cladodes.

have major implications for the future exploitation of *O. ficus-indica* and other cacti for fruit and stem production.

Materials and Methods

Mature cladodes from 10 to 17 months of age were harvested from ten 2-m-tall irrigated ≈7-year-old plants of *Opuntia ficus-indica* (L.) Miller (Cactaceae) growing at the Agricultural Research Station of the Univ. of California, Riverside, on three dates in 1996 and one in 1997. The plant material was originally obtained in 1984 at Chapingo, Mexico state, Mexico, and then grown at Texas A & M Univ., Kingsville; it has Texas A & M accession number 1279. The detached cladodes averaged 34 cm in length, 18 cm in width, 2.5 cm in thickness, 1190 g in fresh mass, and 85 g in dry mass (dry mass was estimated from the fresh mass/dry mass ratio of cores obtained with a cork borer 13 mm in diameter and dried in a forced-draft oven at 80 °C until no further mass change occurred, which usually was 72 h). The selected cladodes had a dry mass exceeding the minimum for their surface area by at least 33 g, the minimum excess dry mass previously identified as necessary for the production of new organs by *O. ficus-indica* (García de Cortázar and Nobel, 1992).

The detached cladodes were placed horizontally for 14 to 16 weeks on a bench in a glasshouse or in environmental chambers (Conviron E-15; Controlled Environment, Asheville, N.C.). The average daily maximum/minimum air temperatures in the glasshouse were 26/14 °C for January to May and 29/17 °C for June to December; the daily maximum/minimum relative humidities averaged 75/40%. The day/night air temperatures in the environmental chambers were 15/5 °C, 25/15 °C, and 35/25 °C, which for intact plants of *O. ficus-indica* leads to 87%, 99%, and 54% of the maximum net CO₂ uptake over 24-h periods (Nobel and Hartsock, 1984; Nobel, 1988). In the environmental chambers, the daily maximum/minimum relative humidities averaged 85/55% at 15/5 °C, 75/45% at 25/15 °C, and 65/40% at 35/25 °C. The 12-h photoperiods in the chambers provided ≈90% as much total daily photosynthetic photon flux [PPF; 400 to 700 nm; measured with a

line quantum sensor 1 m in length (LI-191SB; LI-COR, Lincoln, Nebr.)] as experienced in the glasshouse. Specifically, the average daily maximal PPF in a horizontal plane in the glasshouse was 1410 μmol·m⁻²·s⁻¹ and the constant value in the environmental chambers was 800 μmol·m⁻²·s⁻¹; the total daily PPF for the unshaded cladodes averaged 39 mol·m⁻²·d⁻¹ in the glasshouse (compared to 45 mol·m⁻²·d⁻¹ available outside the glasshouse) and 35 mol·m⁻²·d⁻¹ in the environmental chambers. Shading was provided using one to five layers of neutral density nylon shade cloth of various porosities positioned 80 cm above the cladodes. Initiation of daughter cladodes or flowers, all of which developed into fruit, was monitored weekly.

Fourteen weeks after detachment, three cores per cladode were removed near noon with a cork borer 6 mm in diameter and their starch content was determined. After weighing, the cores were frozen at -55 °C, pulverized, and then ground in 3.0 mL of 12 methanol : 5 chloroform : 3 water. The homogenate was transferred to a test tube together with three washes of the mortar with 2.0 mL of the methanol-chloroform-water mixture. After centrifuging for 3 min at 2000 g_n, the pellet was resuspended in 9 mL of the methanol-chloroform-water mixture, a step that was repeated twice with the methanol-chloroform-water mixture and twice with water. After adding 1.0 mL water to the final pellet, the suspension was heated to 100 °C for 2 h. Starch was then hydrolyzed with amyloglucosidase, and the hydrolysate was analyzed for glucose after treating with glucose oxidase (Sturgeon, 1990).

Also 14 weeks after detachment, five tissue samples per cladode were collected near noon for sugar analysis using the 6-mm-diameter cork borer. The samples were frozen at -55 °C and then squeezed in a tissue press at 25 °C. The exuded sap was heated to 100 °C for 3 min to denature enzymes, followed by passage through a C18 maxi-clean cartridge (Alltech, Deerfield, Ill.) to remove pigments and large molecules. After filtration through a nylon membrane with pores of 0.2 μm, the extract was separated by high-pressure liquid chromatography (HPLC) at 24 °C using an amino column (Microsorb; Rainin Instrument, Woburn, Mass.) with 7 acetonitrile : 3 water as the mobile phase. Sugars were detected by differential refractometry; integration of the curves for individual sugars was done using a 717 chromatography data system (Axxiom, Moorpark, Calif.).

Significant differences between treatments were tested by one-way ANOVA and Student's *t* test.

Results

New organs were readily initiated on unrooted cladodes of *Opuntia ficus-indica* detached in winter (Fig. 1). Although a similar number of daughter cladodes plus fruit were initiated over a 14-week period, initiation occurred sooner in an environmental chamber with day/night air temperatures of 25/15 °C than in the glasshouse with similar daily temperature extremes (26/14 °C). In

Table 1. Organ initiation on cladodes of *Opuntia ficus-indica* detached during various seasons. The numbers of daughter cladodes and fruit initiated over 16 weeks were determined for cladodes detached on the indicated dates and maintained in a glasshouse. Data are means ± SE (n = 30 cladodes).

Detachment date	New organs per cladode	
	Daughter cladodes	Fruit
Winter (4 Jan. 1996)	1.67 ± 0.14	0.47 ± 0.12
Late spring (20 May 1996)	0.63 ± 0.11	0.13 ± 0.06
Late summer (4 Sept. 1996)	0.07 ± 0.05	0.00 ± 0.00

Fig. 2. Organ initiation on cladodes of *O. ficus-indica* detached in winter (3 Jan. 1997) and maintained at various light levels in a glasshouse. The number of daughter cladodes plus fruit initiated over 14 weeks was determined for detached cladodes placed under neutral density screening leading to various degrees of shading. Data are means $\pm$ SE ($n = 10$ cladodes).

particular, an average of two new organs per detached cladode developed in 7 weeks in the environmental chamber compared with 11 weeks in the glasshouse (Fig. 1).

Initiation of new organs over a 16-week period varied with the date of cladode detachment (Table 1). Initiation was highest for cladodes detached in winter, 64% lower for those detached in late spring ($P < 0.05$), and 97% lower for those detached in late summer ($P < 0.01$). For cladodes detached in winter, 22% of the 2.14 new organs per detached cladode were fruit (Table 1). The number of new fruit was lower ($P < 0.05$) on cladodes detached in late spring and late summer, similar to the seasonal decrease in new cladodes.

Light level also influenced the initiation of new organs (Fig. 2). For cladodes detached in winter, essentially no new organs were initiated until the PPf exceeded 35% of that available outside the glasshouse, and the number of new organs per cladode was maximal at $\approx 75\%$ of the PPf available outside. The light level leading to half of the maximal initiation of new organs, 68% of which were daughter cladodes, was 55% of the PPf available outside (Fig. 2). At 14 weeks under 95% shading, the fresh mass of the new organs averaged only 0.3 g per detached cladode compared with 106 g for the unshaded condition.

Day/night air temperatures had a major influence on organ initiation over a 14-week period in environmental chambers with controlled temperatures (Table 2). For cladodes detached in winter, the number of newly initiated daughter cladodes increased 4-fold from day/night air temperatures of 15/5 to 25/15 $^{\circ}\text{C}$ ($P < 0.05$) and an additional 25% at 35/25 $^{\circ}\text{C}$, for which an average of 2.1 new cladodes occurred per detached cladode. On the other hand, fruit production was highest at the lowest temperatures of 15/5 $^{\circ}\text{C}$ at 4.7 per detached cladode, decreasing 77% at 25/15 $^{\circ}\text{C}$ ($P < 0.05$) and an additional 19% at 35/25 $^{\circ}\text{C}$ (Table 2). At 14 weeks the fresh mass of the new organs, which was ≈ 3 -fold higher per new cladode than per fruit, averaged 72 g per detached cladode at 15/5 $^{\circ}\text{C}$, 105 g at 25/15 $^{\circ}\text{C}$, and 99 g at 35/25 $^{\circ}\text{C}$.

Properties of the detached cladodes on which the new organs were initiated were also determined 14 weeks after detachment in

winter (Table 3). Shading by 95% led to the greatest water retention ($P < 0.01$), as the dry mass was then only 7% of the fresh mass, which had decreased $< 10\%$ from the initial value. The dry mass was highest ($P < 0.05$) at 18% of the fresh mass for cladodes maintained at 15/5 $^{\circ}\text{C}$, indicating the greatest water loss, consistent with their appearing the most shriveled. The dry mass was $\approx 13\%$ of the fresh mass for detached cladodes maintained at the two higher temperatures in the environmental chambers and when the detached cladodes were unshaded in the glasshouse (Table 3).

The starch content was much lower for shaded compared with unshaded detached cladodes in the glasshouse ($P < 0.01$; Table 3). Under 95% shade the sucrose concentration was 5-fold lower ($P < 0.01$), the glucose concentration was 7-fold lower ($P < 0.01$), and the fructose concentration was 2-fold lower ($P < 0.05$); the total concentration of monosaccharide equivalents of these sugars was 55 mM under the unshaded condition and 16 mM under the shaded condition (Table 3). The starch content was highest for detached cladodes maintained at 15/5 $^{\circ}\text{C}$, decreasing 31% at 25/15 $^{\circ}\text{C}$ ($P < 0.05$) and an additional 40% at 35/25 $^{\circ}\text{C}$ ($P < 0.05$; Table 3). The concentrations of sucrose, glucose, and fructose also decreased as the temperatures in the environmental chambers increased ($P < 0.05$); the total concentration of monosaccharide equivalents of these sugars was 45 mM at 15/5 $^{\circ}\text{C}$, 37 mM at 25/15 $^{\circ}\text{C}$, and 26 mM at 35/25 $^{\circ}\text{C}$ (Table 3).

Discussion

Initiation of new organs on cladodes of *Opuntia ficus-indica* maintained unrooted in a glasshouse was greatest when the cladodes were detached in winter, decreasing substantially for cladodes detached in late spring and becoming negligible for cladodes detached in late summer. Because initiation of new organs, most of which were daughter cladodes, required ≈ 2 months before the new organs were clearly visible, the highest production actually occurred in the early spring. Similarly, initiation of new cladodes for *O. ficus-indica* in the field also occurs in the early spring and becomes negligible in late summer (Acevedo et al., 1983). Such a time for cladode initiation can maximize seasonal PPf interception and hence annual growth of this cactus (Nobel, 1988).

Initiation of new organs, again most of which were daughter cladodes, increased dramatically (25-fold) with the light level incident on cladodes of *O. ficus-indica* detached in winter and maintained in a glasshouse, reaching a maximum during a 14-week period of 2.5 per cladode. This light response for detached, unrooted cladodes is consistent with field studies on *O. ficus-indica* showing that daughter cladodes are preferentially produced on cladodes with a favorable orientation for sunlight interception (Nobel, 1982a). Thus, cladodes are preferentially initiated on cladodes receiving higher PPf levels, leading to the preferred orientation for unshaded terminal cladodes of platyopuntias (Nobel,

Table 2. Organ initiation on cladodes of *O. ficus-indica* detached in winter (3 Jan. 1997) and maintained in environmental chambers at various day/night air temperatures. The numbers of daughter cladodes and fruit initiated over 14 weeks were determined. Data are means $\pm$ SE ($n = 10$ cladodes).

Day/night temp ($^{\circ}\text{C}$)	New organs per cladode	
	Daughter cladodes	Fruit
15/5	0.40 $\pm$ 0.16	4.70 $\pm$ 0.66
25/15	1.70 $\pm$ 0.26	1.10 $\pm$ 0.36
35/25	2.10 $\pm$ 0.23	0.20 $\pm$ 0.13

Table 3. Properties of cladodes of *O. ficus-indica* 14 weeks after detachment in winter (3 Jan. 1997). Treatments indicate shading in the glasshouse or day/night air temperatures in the environmental chambers. Data are means $\pm$ SE (n = 5 cladodes for dry mass and n = 7 cladodes for chemical analysis).

Treatment	Dry mass (% of fresh mass)	Starch content glucose equiv. fresh mass basis ($\mu\text{mol}\cdot\text{g}^{-1}$)	Sugar concn (mM)		
			sucrose	glucose	fructose
No shading	12.6 $\pm$ 0.4	46.7 $\pm$ 1.8	5.2 $\pm$ 0.4	24.4 $\pm$ 1.7	20.6 $\pm$ 1.6
95% shading	7.1 $\pm$ 0.2	0.34 $\pm$ 0.01	1.1 $\pm$ 0.1	3.4 $\pm$ 0.5	10.3 $\pm$ 1.1
15/5 °C	17.7 $\pm$ 0.5	35.5 $\pm$ 2.1	8.3 $\pm$ 1.1	17.6 $\pm$ 1.6	10.4 $\pm$ 0.8
25/15 °C	13.4 $\pm$ 0.3	24.6 $\pm$ 1.6	5.9 $\pm$ 0.6	16.1 $\pm$ 1.7	9.8 $\pm$ 1.4
35/25 °C	12.5 $\pm$ 0.3	10.4 $\pm$ 1.4	4.5 $\pm$ 0.4	10.9 $\pm$ 1.2	6.4 $\pm$ 0.6

1982b). By quantifying the response to light, the present results can facilitate modeling efforts directing management decisions as to which cladodes should be harvested so that productivity of the entire plant is not adversely affected (Felker, 1995; Garcia de Cortázar and Varnero, 1995).

Results on seasonality and light responses for daughter cladode initiation on detached, unrooted cladodes of *O. ficus-indica* were consistent with those in the field. Thus, detachment provides a living model system that could help elucidate the mechanisms leading to new organ initiation and responses to various environmental conditions. Shading greatly reduced transpiration, as the unrooted cladodes shaded by 95% for 14 weeks in the glasshouse had essentially the same dry mass/fresh mass ratio as when detached, whereas those kept unshaded had a nearly 2-fold increase in this ratio, indicating a substantial water loss. Such transpiration was apparently accompanied by net CO₂ uptake. In this regard, the level of starch plus soluble sugars in monosaccharide equivalents was 148 mM in the light [93 mM from starch; the starch calculation assumes that 1 g of tissue corresponds to 1 cm³, as is the case for *O. ficus-indica* (Nobel, 1988)] but only 17 mM when shaded by 95% for 14 weeks in the glasshouse. Indeed, the starch content was >100-fold higher in the unshaded cladodes. Thus shading reduced stomatal opening and photosynthetic activity in the detached cladodes, which was correlated with lack of development of new cladodes.

Daughter cladode initiation increased from 0.4 to $\approx$ 2 per detached cladode as the day/night growth temperatures in environmental chambers were increased from 15/5 to 25/15 °C or 35/25 °C, whereas the number of fruit per detached cladode decreased from 4.7 at the lowest temperatures to only 0.2 at the highest temperatures. Therefore, low temperatures favored reproductive development and moderate to high temperatures favored vegetative development on detached cladodes of this CAM species. In a related experiment, exposure of detached cladodes to constant temperatures of 10 °C for 3 weeks led to more flower production by *O. ficus-indica* than exposure to 35 °C (Guterman, 1995). One implication is that geographical regions with seasonally low temperatures are advantageous for fruit production by *O. ficus-indica*—this may prove important in the selection of new regions for the cultivation of this species. Actually, exposure to low temperatures, termed vernalization, is a prerequisite for flowering for many plants (Salisbury and Ross, 1992; Taiz and Zeiger, 1991). Such exposure to low temperatures serves to induce flowering usually at a later warmer period in vernalization-requiring plants, whereas flowering of *O. ficus-indica* was stimulated during the 14-week period of exposure to constant low temperatures.

Increasing the temperature from 15/5 °C to 25/15 °C was accompanied by a decrease in the dry mass/fresh mass ratio of the

detached cladodes, suggesting less transpiration at the moderate day/night temperatures, consistent with the decrease in nocturnal water vapor conductance for *O. ficus-indica* over this temperature range (Nobel and Hartsock, 1984). From 25/15 °C to the high day/night temperatures of 35/25 °C, the dry mass/fresh mass ratio decreased only slightly, as the continuing decrease in water vapor conductance with increasing temperature was apparently compensated for by an increase in the driving force for water loss at the higher temperatures. Increasing from low to high day/night temperatures decreased the starch content by 71% and decreased the sucrose, glucose, and fructose concentrations by an average of 41%. The decrease in stomatal opening was thus accompanied by a decrease in various metabolites associated with photosynthesis. The overall 20 °C temperature increase increased the initiation of new daughter cladodes by 5-fold but decreased fruit initiation by more than a factor of 20, leading to an overall 2-fold decrease in the number of new organs initiated. Thus new organ initiation was correlated with starch content and sugar concentrations, just as for changes in shading, but there was no consistent pattern for fruit versus daughter cladodes; i.e., temperature and shading apparently exerted a control over which organs were initiated other than via the carbohydrates examined.

Various consistencies as well as discrepancies occur in response to environmental factors among cladodes of *O. ficus-indica* in the field, rooted cladodes in environmental chambers, unrooted cladodes in chambers, and unrooted cladodes in the glasshouse. As already indicated, the seasonal variation in cladode initiation was similar in the field and for detached cladodes in the glasshouse, as was the qualitative response to light for the two conditions. The starch content in detached cladodes maintained at 25/15 °C was about twice that for rooted cladodes at the same day/night temperatures (Wang and Nobel, 1996), which may in part be due to a somewhat higher light level in the former case but also could represent carbohydrate mobilization for root growth in the latter case. At about the same maximum/minimum daily temperatures and total daily PPF, new organs were initiated 4 weeks earlier in an environmental chamber than in the glasshouse. Apparently the abrupt change in light level and temperature in the environmental chambers coupled with a constant daylength evoked different responses affecting organ initiation than did the more gradual and natural changes occurring in the glasshouse for similar average daily temperatures and light levels. The increases in flower initiation and fruit production at low temperatures need further investigation, such as vernalization studies using different exposure periods, daylengths, and a series of low temperatures for detached, unrooted cladodes in the laboratory. Such studies could prove valuable for management decisions on future cultivation locations for *O. ficus-indica* and other cacti whose fruit are commercially harvested.

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