PHYSIOLOGIA PLANTARUM 87: 467–474. 1993
Printed in Denmark – all rights reserved

ISSN 0031-9317

Growth characteristics of newly initiated cladodes of *Opuntia ficus-indica* as affected by shading, drought and elevated CO_2

Yiqi Luo and Park S. Nobel

Luo, Y. and Nobel, P. S. 1993. Growth characteristics of newly initiated cladodes of *Opuntia ficus-indica* as affected by shading, drought and elevated CO_2. – Physiol. Plant. 87: 467–474.

Biomass accumulation and area expansion of newly initiated cladodes of *Opuntia ficus-indica* were studied to help understand the high productivity of this Crassulacean acid metabolism species. In a glasshouse, both dry weight and area increased more and more rapidly for about 30 days and then increased linearly with time up to 63 days. The relative growth rate averaged 0.12 day^{-1}, comparable to values for productive C_3 and C_4 plants. New cladodes initiated on basal cladodes with 2-fold higher initial dry weight grew twice as fast. Drought reduced biomass accumulation and area expansion of new cladodes by 62 and 52%, respectively. A 70% reduction in irradiation decreased biomass accumulation of new cladodes by 17% and their thickness by 11%. In a growth chamber containing 720 μmol CO_2 (mol air)$^{-1}$, biomass of newly initiated cladodes was 7% higher, area was 8% less, specific mass was 16% higher and less carbohydrate was translocated from basal cladodes than for 360 μmol CO_2 mol^{-1}. The large capacity for storage of carbohydrate and water in basal cladodes of *O. ficus-indica* apparently buffered environmental stresses, thereby reducing their effects on growth of daughter cladodes.

Key words – Drought, elevated CO_2, growth rate, *Opuntia ficus-indica*, shading, specific cladode mass.

Y. Luo and P. S. Nobel (corresponding author), Dept of Biology and Laboratory of Biomedical and Environmental Sciences, Univ. of California, Los Angeles, CA 90024, USA.

Introduction

Plant growth determines canopy development and crop yield, as can be analyzed using absolute growth rates (dry weight increase per unit time), relative growth rates (dry weight increase per unit dry weight per unit time) and specific leaf mass (leaf dry weight per unit leaf area; Hunt 1982). Relative growth rates and the concept of plant life forms have also been used to understand productivity of species in their natural environments (Grime and Hunt 1975, Lambers et al. 1990). For example, tall fast-growing species with extensive lateral canopy spread predominate in productive undisturbed habitats, and short-lived species with high relative growth rates usually colonize disturbed habitats. Stress-tolerant plants characteristically have low relative growth rates and small stature (Grime and Hunt 1975).

Carbohydrate assimilated by leaves generally constitutes more than 90% of plant dry weight, so leaf growth responses to the environment have been extensively investigated (Dale and Milthorpe 1983, Baker et al. 1985). Water availability plays a key role; for example, leaf expansion is sensitive to water stress (Bradford and Hsiao 1982). Also, leaves developing under high irradiance tend to have small areas and high specific mass (Björkman 1981, Schnyder and Nelson 1989). Studies with *Abutilon theophrasti, Amaranthus retroflexus, Callisterphus chinensis* and *Glycine max* indicate that specific leaf mass increases with increasing external CO_2 concentration (Hughes et al. 1970, Bazzaz et al. 1989, Vu et al. 1989).

The main organs for light interception and CO_2 uptake by *Opuntia ficus-indica,* a highly productive and commercially cultivated Crassulacean acid metabolism (CAM) species, are its cladodes (flattened stem segments). Its maximal daily net CO_2 uptake rate on a projected area basis is 1 080 mmol m^{-2} day^{-1} (Nobel and Hartsock 1983), similar to values for highly productive C_3 and C_4 plants (Nobel 1991). Its water-use efficiency over a 24-h period can be 10 mmol CO_2 (mol H_2O)$^{-1}$

Received 12 June, 1992; revised 15 December, 1992

(Nobel 1988), about 10-fold higher than for C_3 plants and 5-fold higher than for C_4 plants (Nobel 1991). When water is not limiting, *O. ficus-indica* can have an annual aboveground dry-weight productivity of 47 Mg (tonnes) ha^{-1} $year^{-1}$, which is higher than for all other species except a few C_4 species such as *Pennisetum purpureum* and *Saccharum officinarum* (Nobel 1991). However, cladode biomass accumulation and area expansion by *O. ficus-indica* have not been systematically investigated. Moreover, information about cladode growth responses to various factors is essential for understanding the productivity and adaptability of this species to highly variable environments in arid and semi-arid regions.

The present study was initiated to quantify biomass accumulation, area expansion and specific mass of newly initiated cladodes as affected by basal cladode initial dry weight, light level, water availability and external CO_2 concentration. Basal cladodes of two different initial dry weights were treated with two levels of light and two levels of water in a glasshouse, and the effect of CO_2 concentration on cladode growth was studied in growth chambers. Nondestructive methods were used to determine the time course of cladode biomass accumulation and area expansion, which were described by a combination sigmoidal-linear function.

Abbreviation – SCM, specific cladode mass.

Materials and methods

Plant material

Cladodes of *Opuntia ficus-indica* (L.) Miller about 35 cm long, 20 cm wide and 2 cm thick were obtained from a commercial plantation. They were planted with approximately one-third of their surface area below the soil surface in 5-l pots containing a loamy sand. The plants were maintained in a glasshouse at the University of California, Los Angeles, for 6 or 18 months with average daily maximum/minimum air temperatures of 27/16°C, daily maximum/minimum relative humidities of 60/30%, and about 80% of ambient solar radiation. The plants were watered twice weekly with 0.1-strength Hoagland's solution no. 1 supplemented with micronutrients (Hoagland and Arnon 1950). The dry weight of the basal (planted) cladodes averaged 83 ± 5 g (mean ± SE) and 143 ± 9 g for plants maintained in the glasshouse for 6 and 18 months, respectively, before use in the experiments.

Glasshouse experiments

Biomass accumulation and area expansion for a single daughter cladode growing on the basal cladode were investigated for two levels for each of three variables (initial dry weight, light level and water availability). After the first daughter cladode was initiated, subsequent daughter cladodes were periodically removed. One week after the daughter cladodes were initiated, the plants were well watered as usual or droughted (no watering) and the total daily photosynthetic photon flux density (PPFD) on a horizontal plane averaged 40 mol photons (from 400 to 700 nm) m^{-2} day^{-1} (measured with LI-190S quantum sensors; LI-COR, Lincoln, NE, USA) or reduced by 70% with neutral-density shade cloth; the total daily PPFD in the planes of the daughter cladodes averaged about 20 mol m^{-2} day^{-1} for the control and 6 mol m^{-2} day^{-1} for the shaded condition. The soil water potential in the root zone (measured with PCT-55-05 soil thermocouple psychrometers; Wescor, Logan, UT, USA) was above -0.3 MPa for the well-watered plants and decreased below -1.5 MPa for the droughted plants at 10 days after the cessation of watering.

Growth-chamber experiment

To study the effect of external CO_2 concentration on cladode growth, plants with the low initial dry weight were placed in growth chambers with CO_2 concentrations of 360 or 720 μmol (mol air)$^{-1}$. The plants were well watered, and the day/night air temperatures were 25/15°C. The photoperiod was 12 h with a PPFD of 300 μmol m^{-2} s^{-1}, leading to a total daily PPFD similar to the shaded treatment in the glasshouse.

Measurements of cladode biomass and area

Dry weight and surface area of cladodes were determined weekly for 2 months. For the glasshouse experiment, the area (cm^2) of both sides of a cladode (cladodes are thick and hence opaque, so the two sides act independently for PPFD absorption) was calculated from 1.54 × length in cm × width in cm ($r^2 = 0.99$), a relationship derived from the areas of 26 cladodes of different sizes measured with a leaf area meter (Delta-T Devices, Cambridge, UK). Dry weight (g) of a cladode was determined from 0.0477 × length in cm × width in cm × thickness in cm ($r^2 = 0.93$), a relationship derived from 35 cladodes of different sizes dried in a forced-air oven at 80°C until no further weight change occurred. For the growth-chamber experiment, the relationship between cladode surface area and the product of length and width was the same as for the glasshouse experiments, whereas dry weight of such cladodes was determined from 0.0413 × length × width × thickness ($r^2 = 0.96$), a relationship derived from 20 cladodes of different sizes.

Cladode growth analyses

Biomass accumulation and area expansion of the new daughter cladodes were described by a combination sigmoidal-linear function:

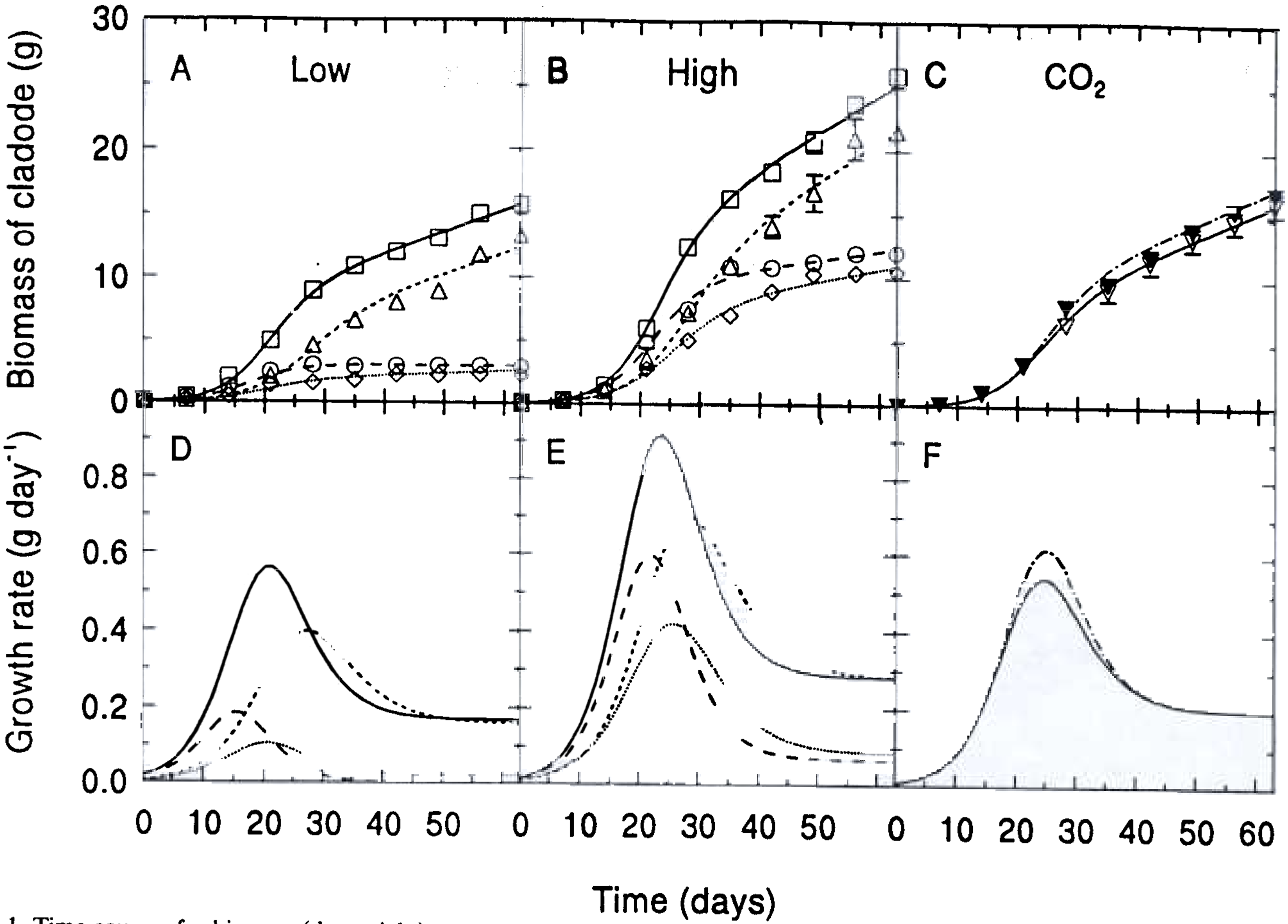

Fig. 1. Time courses for biomass (dry weight) accumulation (A–C) and absolute growth rate (D–F) for new daughter cladodes of *Opuntia ficus-indica*: (A, D) low or (B, E) high initial dry weight of basal cladode, showing influence of water availability and light level; and (C, F) influence of ambient CO_2 concentration with low initial dry weight. Symbols represent mean ± SE (n = 4), except when the error bar is smaller than the symbol: □, control under wet unshaded conditions; ○, droughted; △, shaded; ◇, droughted and shaded; ▽, 360 μmol CO_2 mol^{-1}; and ▼, 720 μmol mol^{-1}. Lines in A–C represent fitted curves (Eq. 1) and in D–F represent the corresponding time courses for growth rates (Eq. 2); ——, control; – – –, drought; -----, shading; ·····, drought plus shading; —·—·—, 720 μmol mol^{-1} CO_2.

$$Y = \frac{K + a\,t}{1 + e^{b-c}} \tag{1}$$

where Y is the cladode dry weight (g) or total surface area for both sides (cm^2); K, a, b and c are empirical parameters; and t is the time (day). Optimal values of parameters were determined by a nonlinear least-squares method (Press et al. 1989).

Cladode absolute growth rate (G), representing the absolute biomass accumulation rate (g day^{-1}) or the absolute area expansion rate (cm^2 day^{-1}), was calculated as follows:

$$G = \frac{dY}{dt} = \frac{a}{1 + e^{b-ct}} + \frac{c\,(K + a\,t)\,e^{b-}}{(1 + e^{b-ct})^2} \tag{2}$$

The maximal absolute growth rate and the time of its occurrence were calculated numerically with the Golden-section search method (Press et al. 1989). The time at which cladode growth changed from sigmoidal to linear($t_{s\to l}$, day) was estimated as

$$t_{s\to l} = \frac{b + 4.595}{} \tag{3}$$

After $t_{s\to l}$, the term e^{b-ct} in Equation 2 approached zero, so the absolute growth rate approached the constant a. The relative growth rate (R, day^{-1}) in both the sigmoidal and the linear phases was

$$R = \frac{\ln y_2 - \ln y_1}{t_2 - t_1} \tag{4}$$

where y_1 and y_2 are the cladode dry weight or surface area at times t_1 and t_2, respectively.

Specific cladode mass (SCM, g cm^{-2}) was calculated by dividing the cladode dry weight by the cladode surface area. Four randomly chosen plants were used for each treatment in all experiments.

Tab. 1. Parameter values for biomass accumulation by new daughter cladodes, as affected by basal cladode initial dry weight (DW), water availability, light level and ambient CO_2 concentration. Biomass accumulation was described by Equation 1; r^2 is the coefficient of determination. G_{max} is the maximal absolute biomass accumulation rate, which occurred at time $t_{G,max}$; $t_{s\to l}$ is the time at which biomass growth changed from sigmoidal to linear; and R_s and R_l are the relative growth rates in the sigmoidal and linear phases, respectively.

Experiment	Treatment			Parameter values									
				K (g)	a (g day^{-1})	b –	c (day^{-1})	r^2 –	G_{max} (g day^{-1})	$t_{G,max}$ (days)	$t_{s\to l}$ (days)	R_s (day^{-1})	R_l (day^{-1})
Glasshouse	DW	Water	Light										
	low	wet	high	5.16	0.17	4.22	0.22	0.998	0.56	21	40	0.131	0.013
	low	dry	high	2.99	0.00	3.86	0.25	0.995	0.19	15	34	0.116	0.000
	low	wet	low	2.37	0.16	4.62	0.19	0.984	0.40	28	50	0.106	0.029
	low	dry	low	1.49	0.01	3.28	0.19	0.980	0.08	18	42	0.090	0.001
	high	wet	high	7.46	0.28	4.86	0.22	0.998	0.92	23	41	0.141	0.016
	high	dry	high	8.14	0.07	5.03	0.23	0.993	0.60	22	41	0.128	0.005
	high	wet	low	3.85	0.28	4.88	0.19	0.993	0.70	29	50	0.119	0.018
	high	dry	low	5.60	0.08	4.76	0.19	0.994	0.41	26	48	0.109	0.002
Growth chamber	CO_2 concentration (μmol mol^{-1})												
	360			3.50	0.20	4.73	0.21	0.999	0.54	25	45	0.130	0.016
	720			4.70	0.20	5.10	0.22	0.997	0.63	25	44	0.131	0.016

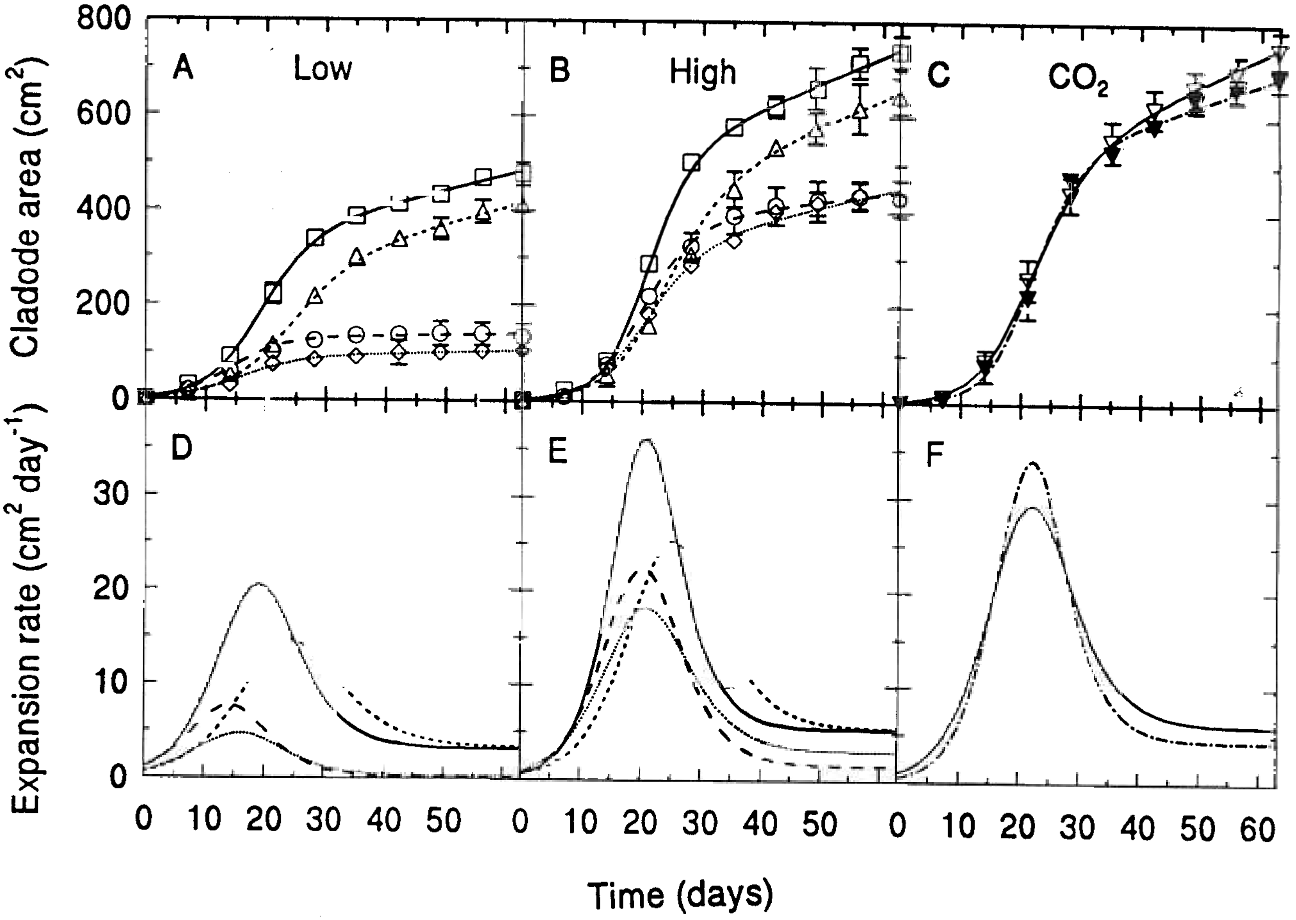

Fig. 2. Time courses for area expansion of new daughter cladodes, as affected by basal cladode initial dry weight, water availability, light level and ambient CO_2 concentration. Data are presented as for Fig. 1.

Tab. 2. Parameter values for area expansion by new daughter cladodes, as affected by basal cladode initial dry weight (DW), water availability, light level, and ambient CO_2 concentration. Data are presented as for Tab. 1.

Experiment	Treatment			Parameter values									
				K (cm^2)	a ($cm^2 day^{-1}$)	b –	c (day^{-1})	r^2 –	G_{max} ($cm^2 day^{-1}$)	$t_{G.max}$ (days)	$t_{s \to l}$ (days)	R_s (day^{-1})	R_l (day^{-1})
Glasshouse	DW	Water	Light										
	low	wet	high	282	3.21	4.02	0.22	0.999	20.5	19	39	0.143	0.007
	low	dry	high	127	0.21	3.19	0.23	0.997	7.5	14	34	0.140	0.000
	low	wet	low	204	3.37	4.12	0.18	0.999	14.8	24	47	0.120	0.009
	low	dry	low	85	0.32	3.09	0.20	0.985	4.6	16	39	0.110	0.002
	high	wet	high	403	5.39	5.26	0.26	0.999	36.6	21	37	0.182	0.009
	high	dry	high	343	1.58	4.56	0.23	0.998	22.4	20	40	0.143	0.002
	high	wet	low	314	5.40	4.82	0.20	0.999	25.3	25	47	0.130	0.008
	high	dry	low	262	3.00	4.10	0.20	0.996	18.1	21	42	0.143	0.003
Growth chamber	CO_2 concentration ($\mu mol\ mol^{-1}$)												
	360			375	5.90	4.42	0.21	1.000	29.9	22	42	0.153	0.009
	720			416	4.34	5.36	0.25	0.998	34.2	22	40	0.152	0.008

Results

Biomass accumulation of daughter cladodes

Biomass (dry weight) of new daughter cladodes initiated from basal cladodes of *Opuntia ficus-indica* with low initial dry weight in the glasshouse increased more and more rapidly for about 30 days and then linearly with time up to 63 days (Fig. 1A,D, Tab. 1).Under wet unshaded conditions (the control), the maximal absolute growth rate for biomass was 0.56 g day^{-1} at 21 days; the absolute growth rate in the linear phase was 0.17 g day^{-1}. The relative growth rate was 0.13 day^{-1} in the sigmoidal phase and 0.013 day^{-1} in the linear phase (Tab. 1). When plants were droughted, new cladodes stopped growing at 34 days and biomass accumulation was reduced by 81% at 63 days compared with the control (Fig. 1A); the maximal absolute growth rate was 0.19 g day^{-1} (Fig. 1D, Tab. 1). When plants were shaded, biomass accumulation of new cladodes was slow for the first 20 days and reached a maximal rate of 0.40 g day^{-1} at 28 days, after which the rate was similar to that of the control (Fig. 1A,D, Tab. 1). When plants were both droughted and shaded, biomass accumulation of new cladodes was reduced by 87% at 63 days compared with the control (Fig. 1A).

Biomass accumulation for new cladodes initiated on basal cladodes with high initial dry weight followed a pattern similar to that of plants with low initial dry weight (Fig. 1A vs 1B). However, under wet unshaded conditions, the maximal absolute growth rate during the sigmoidal phase was 0.92 g day^{-1} and the constant growth rate during the linear phase was 0.28 g day^{-1} (Fig. 1E, Tab. 1), both about 65% higher than for new cladodes growing on basal cladodes with low initial dry weight. When plants were droughted, shaded, or both, biomass accumulation at 63 days was reduced by 50, 14 or 58%, respectively, compared with the control (Fig. 1A vs 1B).

Biomass of new cladodes under both 360 and 720 $\mu mol\ CO_2\ mol^{-1}$ in the growth chamber increased slowly for the first 15 days, more rapidly for the following 20 days, and then linearly with time at about 0.20 g day^{-1} (Fig. 1C,F). The relative growth rates were 0.13 day^{-1} in the sigmoidal phase and 0.016 day^{-1} in the linear phase for the two CO_2 treatments (Tab. 1). Biomass of new cladodes under 720 $\mu mol\ CO_2\ mol^{-1}$ was 17.3 g at 63 days, 7% higher than for 360 $\mu mol\ mol^{-1}$ (Fig. 1C).

Area expansion of daughter cladodes

Surface area of new daughter cladodes initiated from basal cladodes of *O. ficus-indica* with low initial dry weight increased slowly for the first 10 days, more rapidly for the following 20 days, and then linearly with time (Fig. 2A). Under wet unshaded conditions, the maximal absolute expansion rate was 20.5 $cm^2\ day^{-1}$ at 19 days; the constant rate after 40 days during the linear phase was 3.2 $cm^2\ day^{-1}$ (Fig. 2D). The relative growth rate for area was 0.14 day^{-1} in the sigmoidal phase and 0.007 day^{-1} in the linear phase (Tab. 2). When the plants were droughted, the area of new cladodes was reduced by 71% at 63 days compared with the control (Fig. 2A). When plants were shaded, new cladode expansion was slow for the first 15 days, at a maximal absolute rate of 14.8 $cm^2\ day^{-1}$ at 24 days, and then at a rate slightly higher than that of the control (Fig. 2D, Tab. 2). When plants were both droughted and shaded, the area of new cladodes at 63 days was 78% less than that of the control (Fig. 2A).

Area expansion of new cladodes initiated from basal cladodes with high initial dry weight followed a pattern similar to that of plants with low initial dry weight (Fig.

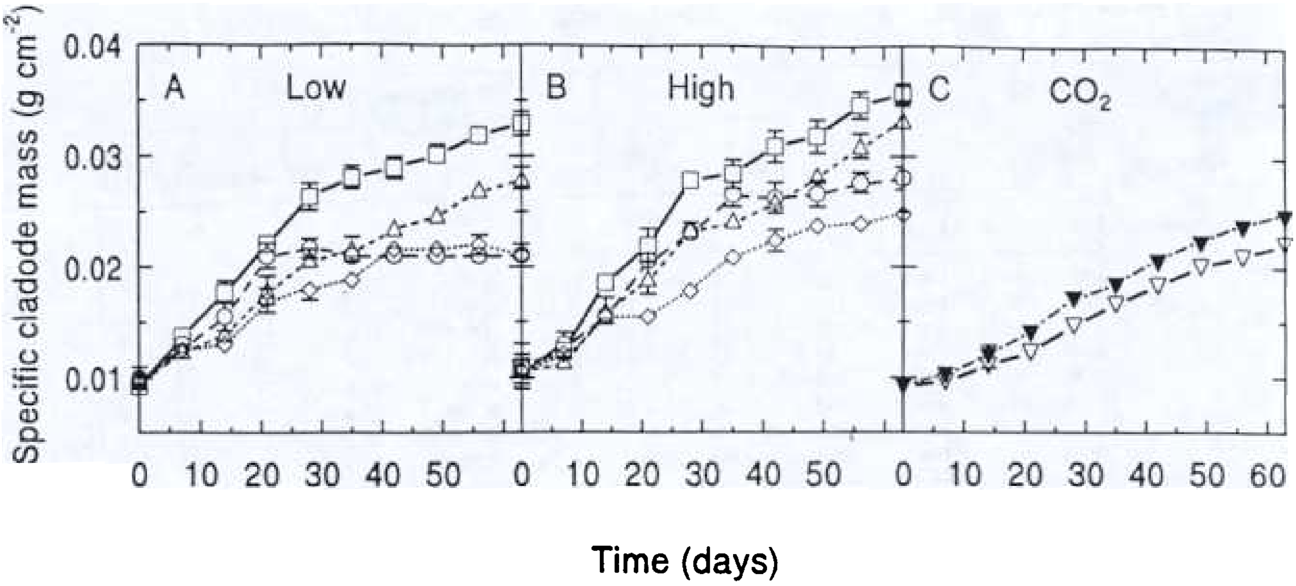

Fig. 3. Time courses for specific cladode mass of new daughter cladodes. Data are presented as for Fig.

2A vs 2B). Under wet unshaded conditions, the maximal absolute expansion rate during the sigmoidal phase was 36.6 cm^2 day^{-1} and the constant absolute rate during the linear phase was 5.4 cm^2 day^{-1} (Fig. 2E, Tab. 2), which were 79 and 31%, respectively, higher than new cladodes on basal cladodes with low initial dry weight. Droughting, shading or both reduced new cladode area at 63 days by 40, 12 and 39%, respectively (Fig. 2B, Tab. 2).

In the growth chamber with 360 µmol CO$_2$ mol^{-1}, newly initiated cladodes expanded slowly for the first 15 days, more rapidly for the following 20 days with a maximal absolute expansion rate of 29.9 cm^2 day^{-1} at 22 days, and then linearly with time at about 5.9 cm^2 day^{-1} (Fig. 2C,F, Tab. 2). The area of new cladodes was 747 cm^2 at 63 days (Fig. 2C). In the chamber with 720 µmol CO$_2$ mol^{-1}, growth was slower in the linear phase and new cladode area was 689 cm^2 at 63 days, 8% less than with 360 µmol mol^{-1}.

Specific cladode mass

Specific cladode mass (SCM) of new cladodes on basal cladodes with low initial dry weight began at about 0.010 g cm^{-2}, increasing to 0.033 g cm^{-2} at 63 days under wet unshaded conditions (Fig. 3A). When plants were droughted, SCM increased to 0.021 g cm^{-2} at 21 days and then remained fairly constant. Shading reduced SCM of new cladodes by 15% at 63 days. When plants were both droughted and shaded, SCM increased to 0.021 g cm^{-2} at 42 days and then became constant (Fig. 3A).

SCM of new cladodes on basal cladodes with high initial dry weight also began at about 0.010 g cm^{-2}, increasing to 0.036 g cm^{-2} at 63 days under wet unshaded conditions (Fig. 3B). When plants were droughted, SCM increased to 0.026 g cm^{-2} at 35 days and then became constant. When plants were shaded, SCM was reduced about 10% at 63 days. When plants were both droughted and shaded, SCM increased to 0.025 g cm^{-2} at 63 days (Fig. 3B).

In the growth chamber with 360 µmol CO$_2$ mol^{-1}, SCM initially was 0.009 g cm^{-2}, increasing to 0.022 g cm^{-2} at 63 days (Fig. 3C). When plants were exposed to 720 µmol CO$_2$ mol^{-1}, SCM increased to 0.025 g cm^{-2} at 63 days, which was significantly higher ($P < 0.01$) than the SCM for 360 µmol mol^{-1}.

Biomass changes of basal cladodes

In the glasshouse experiment under wet unshaded conditions, the biomass of basal cladodes of plants with either low or high initial dry weight increased during 30 days by 2.3 or 4.6 g, respectively, whereas no change in biomass occurred when plants were droughted, shaded or both. In the growth-chamber experiment, the biomass of basal cladodes decreased by 21.7 g during 63 days at 360 µmol CO$_2$ mol^{-1} and by 18.6 g at 720 µmol mol^{-1}.

Discussion

The relative growth rates of daughter cladodes of *Opuntia ficus-indica* during the sigmoidal growth period ranged from 0.09 day^{-1} to 0.14 day^{-1} under different conditions of basal cladode initial dry weight, water availability, light level and external CO$_2$ concentration, and were comparable to the relative growth rates for C$_3$ and C$_4$ plants. For example, the relative growth rates of 143 British herbaceous and woody species range from 0.03 to 0.32 day^{-1}, with an average of 0.16 day^{-1} (Grime and Hunt 1975). Relative growth rates are about 0.15 day^{-1} for leaves of *Vitis vinifera* (Silk 1983) and increase from 0.08 to 0.16 day^{-1} as irradiance is raised for leaves of *Festuca arundinacea* (Schnyder and Nelson 1989). At 700 µmol CO$_2$ mol^{-1}, the maximal relative growth rates are 0.24 day^{-1} for the C_3 species *Abutilon theophrasti* and 0.37 day^{-1} for the C_4 species *Amaranthus retroflexus* (Bazzaz et al. 1989).

The proposition that fast-growing species are associated with productive habitats and slow-growing plants are from unproductive habitats (Grime and Hunt 1975) does not apply to *O. ficus-indica,* which presumably is native to semi-arid environments yet has a high growth rate (Nobel 1988). It can have a high daily net CO_2 uptake (Nobel and Hartsock 1983), a low root/shoot ratio (Nobel 1988), and reduced specialized supporting structure compared with trunks of trees or stems of annual crops. The high water-use efficiency of *O. ficus-indica* can lead to appreciable biomass production in water-limited environments (Nobel 1988, 1991). Moreover, reserves of nonstructural carbohydrate as high as 20% of its dry weight (Nerd and Nobel 1991) can support the rapid growth of new daughter cladodes.

Growth of new cladodes of *O. ficus-indica* was sigmoidal for about 30 days followed by a linear phase. Determinate plants or organs usually follow sigmoidal growth patterns, with growth ceasing when a maximum is reached, e.g. rice-grain filling (Zhu et al. 1988) and internode elongation of tree shoots (Brown and Sommer 1992). Plants or organs with indeterminate growth have more complicated patterns. Shoots of some pines and deciduous trees elongate linearly during growing seasons of 5 months duration (Brown and Sommer 1992). Indeterminate growth of cladodes at fairly high growth rates favors aboveground biomass accumulation and high productivity when water and nutrients are adequately supplied. Moreover, the growth pattern for cladodes of *O. ficus-indica* may indicate that young cladodes import carbohydrates from the basal cladodes in the sigmoidal phase and export carbohydrates during the linear phase. Based on the net CO_2 uptake of 0.48 mol CO_2 m^{-2} day^{-1} for *O. ficus-indica* under conditions similar to those of the control (M. Cui and P.S. Nobel, unpublished observations) and the measured surface area of the daughter cladodes, their predicted daily increase in dry weight became greater than the measured growth rate at about 28 days. At this stage, the daughter cladodes of the control apparently switch from being sinks for carbohydrate to being sources.

At 63 days the biomass and the area of new cladodes initiated from basal cladodes with low initial dry weight averaged half of those from basal cladodes with high initial dry weight, indicating different mobilization of carbohydrate reserves from basal cladodes to newly initiated daughter cladodes. Indeed, cladode excess dry weight, which is the dry weight per cladode above the minimum value for a particular surface area (Garcia de Cortázar and Nobel 1992), was 42 and 93 g for basal cladodes with low and high initial dry weight, respectively. Fruit growth for *O. ficus-indica* also greatly varies with cladode excess dry weight (Garcia de Cortázar and Nobel 1992).

Biomass and area for the newly initiated cladodes of droughted plants at 63 days averaged 38 and 48%, respectively, of those for the control. Although drought profoundly influenced cladode growth, the succulence of *O. ficus-indica* mitigated such effects compared with C_3 and C_4 plants. Leaf enlargement of *Zea mays, Helianthus annuus* and *Glycine max* can be halted when the leaf water potential decreases to only −0.4 MPa (Bradford and Hsiao 1982). Leaf water potential at noon on a sunny day can decrease below −1.0 MPa for many C_3 and C_4 plants, even when the soil water potential is high (Jones 1983). In contrast, cladodes of *O. ficus-indica* store a large amount of water, preventing large diel changes in tissue water potential. Also, turgor pressure in the chlorenchyma of well-watered plants of *O. ficus-indica* is less than 0.15 MPa (Goldstein et al. 1991), much lower than the critical turgor pressure of 0.38 MPa for leaf elongation of *Zea mays* (Hsiao et al. 1985). After 3 months of drought, turgor pressure in the chlorenchyma still reaches 0.12 MPa at dawn (Goldstein et al. 1991). Moreover, stomata of *O. ficus-indica* can fully open 2 weeks into drought and stomatal opening is still one-third of maximal after 2 months of drought (Acevedo et al. 1983, Nobel 1988). Such water relationships greatly enhance cladode growth during drought.

Shading plants by 70% delayed biomass growth of the daughter cladodes. For instance, maximal biomass accumulation and area expansion occurred 6 and 5 days later, respectively, than for unshaded plants. However, biomass and area of daughter cladodes at 63 days were reduced only 17 and 13%, respectively, suggesting that more carbohydrate was imported from the basal cladode under shaded conditions. Indeed, based on the relationships between total daily PPFD and net CO_2 uptake over 24-h periods for *O. ficus-indica* (Nobel and Hartsock 1983, Nobel 1988), reducing the total daily PPFD on the cladodes from 20 to 6 mol m^{-2} day^{-1} should decrease net CO_2 uptake by 91%. Moreover, compartmental analysis of $^{14}CO_2$ tracer experiments with *O. ficus-indica* predicts that nearly 3-fold more carbohydrate from the basal cladode is incorporated into the structural material of a daughter cladode over 42 days when plants are 70% shaded (Luo and Nobel 1992).

Specific cladode mass for shaded plants was 10 to 15% less than for unshaded plants. Similar responses to low light levels occur for other succulent species (Tissue and Nobel 1990), although the relative leaf mass can vary more than 2-fold with light level for nonsucculent plants (Björkman 1981, Sims and Pearcy 1992). When *O. ficus-indica* was both droughted and shaded, drought was the dominant limiter of cladode growth, especially during the later stages.

Doubling the CO_2 concentration from the current ambient value increased the biomass accumulation by new cladodes at 63 days by 7% but with an 11% lower area for the new cladodes. Furthermore, the biomass of the basal cladodes decreased 3.1 g less with 720 µmol CO_2 mol^{-1} than 360 µmol mol^{-1}, indicating that less carbohydrate was translocated to the daughter cladode for the elevated CO_2 condition. The combination of more biomass and less area caused the specific cladode mass to be 16% higher for the doubled CO_2 concentration. Doubling the CO_2 concentration increases specific leaf mass of *Callisterphus chinensis* by 28% (Hughes et al. 1970), *Abutilon theophrasti* by 60%, *Amaranthus retroflexus* by 40% (Bazzaz et al. 1989) and *Glycine max* by about 30% (Vu et al. 1989).

Newly initiated daughter cladodes grew at a high growth rate, favoring aboveground biomass accumulation and leading to the high productivity of this species. Growth of new cladodes was markedly influenced by the initial dry weight of basal cladodes, implying enhancement of new cladode growth by carbon supplied from the basal cladodes. Growth responses to environmental changes of water availability, light level and CO_2 concentration were accompanied by adjustments in carbon partitioning and specific cladode mass that would help maximize biomass accumulation under stress conditions.

Acknowledgement – The authors thank Drs Muyi Cui and Patsy Miller for help with the growth-chamber experiments. This research was sponsored by the Environmental Sciences Division of the Office of Health and Environmental Research, U.S. Department of Energy, contract DE-FC03-87-ER60615 and grant DE-FG03-91ER61252.

References

Acevedo, E., Badilla, I. & Nobel, P. S. 1983. Water relations, diurnal acidity changes, and productivity of a cultivated cactus, *Opuntia ficus-indica*. – Plant Physiol. 72: 775–780.

Baker, N. R., Davies, W. J. & Ong, C. K. 1985. Control of leaf growth. – Cambridge University Press, Cambridge. pp. 155–200. ISBN 0-521-30480-6.

Bazzaz, F. A., Garbutt, K., Reekie, E. G. & Williams, W. E. 1989. Using growth analysis to interpret competition between a C_3 and a C_4 annual under ambient and elevated CO_2. – Oecologia 79: 223–235.

Björkman, O. 1981. Responses to different quantum flux densities. – *In* Physiological Plant Ecology. Encyclopedia of Plant Physiology, New Series, Vol. 12A (O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler, eds), pp. 57–107. Springer-Verlag, Berlin. ISBN 3-540-10763-0.

Bradford, K. J. & Hsiao, T. C. 1982. Physiological responses to moderate water stress. – *In* Physiological Plant Ecology. Encyclopedia of Plant Physiology, New Series, Vol. 12B (O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler, eds), pp. 263–324. Springer-Verlag, Berlin. ISBN 3-540-10906-4.

Brown, C. L. & Sommer, H. E. 1992. Shoot growth and histogenesis of trees possessing diverse patterns of shoot development. – Am. J. Bot. 79: 335–346.

Dale, J. E. & Milthorpe, F. L. 1983. The growth and functioning of leaves. – Cambridge University Press, Cambridge. pp. 179–206. IBSN 0-521-23761-0.

Garcia de Cortázar, V. & Nobel, P. S. 1992. Biomass and fruit production for the prickly pear cactus, *Opuntia ficus-indica*. – J. Am. Soc. Hortic. Sci. 117: 558–562.

Goldstein, G., Ortega, J. K. E., Nerd, A. & Nobel, P. S. 1991. Diel patterns of water potential components for the Crassulacean acid metabolism plant *Opuntia ficus-indica* when well-watered or droughted. – Plant Physiol. 95: 274–280.

Grime, J. P. & Hunt, R. 1975. Relative growth-rate: its range and adaptive significance in a local flora. – J. Ecol. 69: 393–422.

Hoagland, D. R. & Arnon, D. I. 1950. The water-culture method for growing plants without soil. – Calif. Agric. Exp. Stn. Circ. 347: 1–32.

Hsiao, T. C., Silk, W. K. & Jing, J. 1985. Leaf growth and water deficits: biophysical effects. – *In* Control of Leaf Growth (N. R. Baker, W. J. Davies and C. K. Ong, eds), pp. 239–266. Cambridge University Press, Cambridge. ISBN 0-521-30480-6.

Hughes, A. P., Cockshull, K. E. & Heath, O. V. S. 1970. Leaf area and absolute leaf water content. – Ann. Bot. 34: 259–266.

Hunt, R. 1982. Plant Growth Curves. The Functional Approach to Plant Growth Analysis. – Edward Arnold, London. pp. 16–33. ISBN 0-8391-1757-4.

Jones, H. G. 1983. Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology. – Cambridge University Press, Cambridge. pp. 116–123. ISBN 0-521-27016-2.

Lambers, H., Cambridge, M. L., Konings, H. & Pons, T. L. 1990. Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants. – SPB Academic Publishing, The Hague. pp. 257–267. ISBN 90-5103-033-9.

Luo, Y. & Nobel, P.S. 1992. Carbohydrate partitioning and compartmental analysis for a highly productive CAM plant, *Opuntia ficus-indica*. – Ann. Bot. (In press).

Nerd, A. & Nobel, P. S. 1991. Effects of drought on water relations and nonstructural carbohydrates in cladodes of *Opuntia ficus-indica*. – Physiol. Plant. 81: 495–500.

Nobel, P. S. 1988. Environmental Biology of Agaves and Cacti. – Cambridge University Press, Cambridge. pp. 62–65. ISBN 0-521-34322-4.

– 1991. Achievable productivities of certain CAM plants: basis for high values compared with C_3 and C_4 plants. Tansley review no. 32. – New Phytol. 119: 183–205.

– & Hartsock, T.L. 1983. Relationships between photosynthetically active radiation, nocturnal acid accumulation, and CO_2 uptake for a Crassulacean acid metabolism plant, *Opuntia ficus-indica*. – Plant Physiol. 71: 71–75.

Press, W. H., Flannery, B. P., Teukolsky, S. A. & Vetterling, W. T. 1989. Numerical Recipes in PASCAL. – Cambridge University Press, Cambridge. pp. 309–374. ISBN 0-521-37516-9.

Schnyder, H. & Nelson, C. J. 1989. Growth rates and assimilate partitioning in the elongation zone of tall fescue leaf blades at high and low irradiance. – Plant Physiol. 90: 1201–1206.

Silk, W. K. 1983. Kinematic analysis of leaf expansion. – *In* The Growth and Functioning of Leaves (J. E. Dale and F. L. Milthorpe, eds), pp. 89–108. Cambridge University Press, Cambridge. ISBN 0-521-23761-0.

Sims, D. A. & Pearcy, R. W. 1992. Response of leaf anatomy and photosynthetic capacity in *Alocasia macrorrhiza* (Araceae) to a transfer from low to high light. – Am. J. Bot. 79: 449–455.

Tissue, D. T. & Nobel, P. S. 1990. Carbon translocation between parents and ramets of a desert perennial. – Ann. Bot. 66: 551–557.

Vu, J. C. V., Allen, Jr., L. H. & Bowes, G. 1989. Leaf ultrastructure, carbohydrates and protein of soybeans grown under CO_2 enrichment. – Environ. Exp. Bot. 29: 141–147.

Zhu, Q., Cao, X. & Luo, Y. 1988. Growth analysis on the process of grain filling in rice. – Acta Agron. Sin. 14: 182–193.

Edited by A. Stemler