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Carbohydrate Partitioning and Compartmental Analysis for a Highly Productive CAM Plant, *Opuntia ficus-indica*

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Carbon partitioning patterns of *Opuntia ficus-indica*, a widely cultivated crassulacean acid metabolism species, were analysed to estimate carbon fluxes. After labelling a cladode with $^{14}CO_2$, activities of ^{14}C in various organs were measured for 6 weeks; the observed ^{14}C time-courses for ^{14}C in the labelled cladode and for transfer into other organs were simulated with a compartment model. Within the first week, half of the newly synthesized carbohydrate in the labelled cladode was either converted into structural material in that cladode, lost by respiration of that cladode, or moved to other organs. In the non-labelled cladode and the roots, such newly synthesized carbohydrate initially increased, reached maxima, and then declined. The basal cladode and the daughter cladode used 65 and 96%, respectively, of their own assimilate. Roots imported 12 and 2% of carbohydrate from the basal cladode and the daughter cladode, respectively. When the whole plant was shaded, the daughter cladode incorporated nearly three-fold more carbohydrate from the basal cladode into structural material compared with the control. When plants were droughted, roots incorporated 23% more and the daughter cladode incorporated 68% less carbohydrate from the basal cladode into their structural material than for the control. The basal cladodes of the 18-month-old plants exported 60% more carbon than those of the 6-month-old plants. Carbon flux rates derived from compartmental analysis can be used as parameter values in plant production models.

Key words: Carbon partitioning, compartment model, drought, plant age, shading.

INTRODUCTION

Carbohydrate partitioning plays an important role in plant productivity and can vary with specific life forms. For example, annual plants invest most of their carbohydrate for leaf growth and seed formation, especially in frequently disturbed habitats, whereas perennial herbaceous plants adapted to alpine meadows or forest floors partition a large amount of carbon to roots and storage organs (Schultz, 1982; Tilman, 1988). Based on selective breeding during the past 60 years, the proportion of carbohydrate allocated to grain of cereals has risen from less than 40% to more than 50% of the above-ground biomass (Gifford *et al.*, 1984; Evans, 1990). Selection for carbon partitioning to grains has also been responsible for a five-fold increase in the productivity of *Zea mays* over this period (Russell, 1991).

Recently, *Opuntia ficus-indica*, the subject of the present study, has been shown to have an annual above ground dry weight productivity of 47 Mg ha^{-1} $year^{-1}$ (Garcia de Cortázar and Nobel, 1991; Nobel, García-Moya and Quero, 1992), exceeding that reported for all other species except the C_4 plants *Cyperus papyrus*, *Echinochloa polystachya*, *Pennisetum purpureum*, and *Saccharum officinarum* (Loomis and Gerakis, 1975; Beadle *et al.*, 1985; Jones, 1986; Nobel, 1991; Piedade, Junk and Long, 1991; Nobel *et al.*, 1992). The high productivity of *O. ficus-indica* may be partially attributable to its growth form and carbon partitioning patterns. In particular, it has a relatively small root/shoot ratio of 0·12 (Nobel, 1988) and generally does not have specialized structures for support, such as trunks of trees or stems of annual crops. Carbon partitioning between the two main vegetative organs of *O. ficus-indica*, roots and cladodes (flattened stem segments), however, has not been investigated. Indeed, carbon relations of *O. ficus-indica* may be just as important for its adaptability to arid and semi-arid regions as its water relations.

The amount of carbohydrate moved between plant organs is difficult to determine (Wardlaw, 1990). Root/shoot ratios provide only a static index of carbon partitioning between the two organs (Wilson, 1988) and do not reveal the underlying physiological processes, whereas investigations of phloem loading, transport, and unloading of carbohydrate usually do not indicate carbon partitioning at the whole plant level (Gifford and Evans, 1981; Wardlaw, 1990). Radioactive $^{14}CO_2$ has been used extensively to trace the movement of carbon from source to sink and clearly determines the direction of carbon movement (Cralle and Heichel, 1985; Dickson, Isebrands and Tomlinson, 1990; Tissue and Nobel, 1990; Kuhns and Gjerstad, 1991) but by itself does not quantify the amount of carbon translocated along individual pathways.

Compartmental analysis is a simulation approach for estimating carbon movement between organs based on data from radioactive carbon (^{14}C) tracers. Differential equations are employed to describe the time course of ^{14}C translocation and to estimate carbon fluxes. Compartment models have

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been applied to leaf storage and export processes for photoassimilated carbon (Moorby and Jarman, 1975; Geiger *et al.*, 1983) and the dynamics of carbon partitioning in whole plants of *Pseudotsuga menziesii* (Schroeder and Webb, 1978), *Festuca ovina*, *Nardus stricta* (Atkinson and Farrar, 1983), and *Glycine max* (Kouchi, Yoneyama and Akao, 1986; McCoy, Boersma and Ekasingh, 1989). Many of these studies deal with ^{14}C translocation over a period of hours during the daytime. Because *O. ficus-indica* is a crassulacean acid metabolism (CAM) plant, it takes up CO_2 primarily at night, assimilating carbon into photosynthetic products during the following daytime, with subsequent translocation of newly synthesized carbohydrate between organs. Thus, periods of days are necessary to understand the fate of initially fixed carbon in CAM plants.

In the present study, carbon partitioning from basal cladodes to daughter cladodes and to roots was investigated for *O. ficus-indica* for 6 weeks after labelling of basal or daughter cladodes with $^{14}CO_2$. Carbon flux rates between compartments and half-times for the retention of newly synthesized assimilate as nonstructural carbohydrate were estimated based on compartmental analysis. In addition, effects of soil water availability and light on carbon partitioning were studied for plants of two ages.

MATERIALS AND METHODS

Plant material

Cladodes of *Opuntia ficus-indica* (L.) Miller about 35 cm long and 20 cm wide were obtained from a commercial plantation. The cladodes were grown in 5-l pots containing a loamy sand with approximately one-third of the surface area of the planted (basal) cladode below the soil surface. 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 the ambient solar radiation. The plants were watered weekly with 0·1-strength Hoagland's solution No. 1 supplemented with micronutrients (Hoagland and Arnon, 1950). The thickness of the basal cladodes averaged $2{\cdot}45 \pm 0{\cdot}06$ cm (mean ± standard error) for the 6-month-old plants and $3{\cdot}75 \pm 0{\cdot}13$ cm for the 18-month-old plants.

Treatments

Two levels for each of three variables (age, light, and water) were investigated for their effects on carbon partitioning for *O. ficus-indica* with a basal and a daughter cladode. Plants were 6 months old and 18 months old. When the daughter cladodes were about 8 cm long, the plants were well-watered or droughted and the radiation was the ambient value or reduced by 70% with shade cloth immediately after labelling with $^{14}CO_2$ The soil water potential in the root zone (measured with PCT-55-05 soil thermocouple psychrometers; Wescor, Logan, UT, USA) was above −0·2 MPa for the well-watered plants and decreased below −1·5 MPa for droughted plants 7 d after the cessation of watering. In addition to the above treatments in which the basal cladodes were labelled with $^{14}CO_2$, daughter cladodes about 15 cm in length of 6-month-old plants were also labelled with $^{14}CO_2$. Four randomly chosen plants were used for each treatment.

^{14}C labelling and sample processing

$^{14}CO_2$, generated by adding 6 M HCl to $Ba^{14}CO_3$, was introduced with a cylindrical cuvette to a central region 9 cm in diameter of the basal cladodes or the daughter cladodes for 20 min at midnight. Immediately after labelling and at noon on subsequent days, tissue samples were removed with a cork borer 5 mm in diameter from the labelled region and surrounding locations on the labelled cladode (to determine total radioactivity in the labelled cladode) and from the centres of other cladodes; root samples were also harvested at these times. The samples were oven-dried at 80 °C for 1 d and then ground to a powder. Subsamples (5–7 mg) were solubilized for 1 d using 1 ml of Solvable (New England Nuclear, Boston, MA, USA), which increased the count rate by 22% (Tissue and Nobel, 1990), before addition of 10 ml of scintillation cocktail (Bio-Safe II; New England Nuclear). Chemiluminescence induced by the tissue solubilizer was virtually eliminated by adding 0·07 ml 6 N HCl 3 h before counting in a LS-1801 scintillation counter (Beckman Instruments, Irvine, CA, USA). Total ^{14}C activity of each organ was calculated from its ^{14}C activity per unit mass multiplied by dry mass and was converted to a relative activity by dividing by the total ^{14}C activity initially incorporated based on samples of each organ.

Compartment model

A compartment model was used to represent carbon pools and translocation pathways in plants with one basal cladode, one daughter cladode, and roots (Fig. 1). Each organ was divided into mobile, immobile, and respiration carbon compartments, leading to nine compartments for the whole plant. A mobile compartment represented soluble material available for transport between plant organs, and an immobile compartment represented carbon accumulation in structural material. Transfers between the mobile compartments were assumed to be bidirectional, whereas transfers from a mobile compartment to an immobile one or to the respiration compartment were unidirectional. The fractional transfer coefficient (a_{ij}, d^{-1}) was the amount of ^{14}C transferred from compartment i to compartment j during a 24-h period divided by the amount of ^{14}C in compartment i for that day.

The time course of relative ^{14}C activity in compartment i [$U_i(t)$] was described by a first-order differential equation:

$$\frac{dU_i(t)}{dt} = \Sigma a_{ji} U_j(t) - U_i(t) \Sigma a_i \qquad (1)$$

The first summation on the right-hand side of eqn (1) represents ^{14}C influxes into compartment i and the second summation represents ^{14}C effluxes from compartment i. When $^{14}CO_2$ was introduced into the mobile compartment

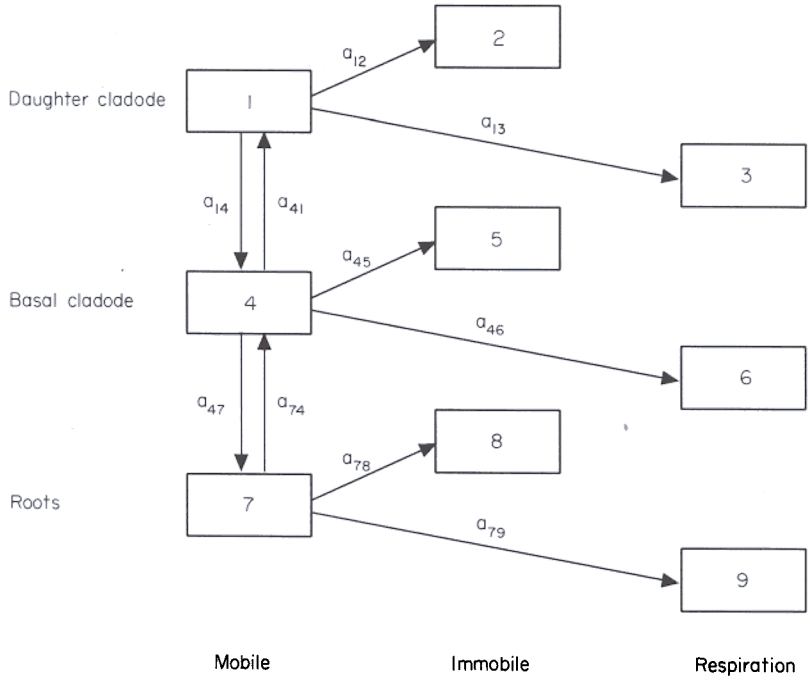


FIG. 1. Compartmental model of carbon translocation in plants with one basal cladode, one daughter cladode, and roots. Compartments 1, 4 and 7 represent mobile carbohydrate, compartments 2, 5 and 8 represent immobile material, and compartments 3, 6 and 9 represent respiratory loss for the daughter cladode, the basal cladode, and the roots, respectively; a_{ij} is a fractional transfer coefficient (d^{-1}) from compartment i to compartment j.

of the basal cladodes (compartment 4), the initial conditions were:

$$U_4(0) = 1; \quad U_i(0) = 0, \; i \neq 4 \tag{2}$$

When $^{14}CO_2$ was introduced to the mobile compartment of a daughter cladode (compartment 1), the initial conditions were:

$$U_1(0) = 1; \quad U_i(0) = 0, \; i \neq 1 \tag{3}$$

The system of differential equations was solved numerically by the Runge-Kutta method (Burden and Faires, 1989). Optimal values of a_{ij} were obtained with a nonlinear least-squares procedure (Press *et al.*, 1989).

The relative carbon pool sizes of the mobile compartments (P_i, d) was the total carbon in compartment i divided by the total carbon taken up by the labelled basal or daughter cladode per day. P_i was calculated for the steady state as follows (Kouchi *et al.*, 1986; McCoy *et al.*, 1989):

$$\Sigma a_{ji} P_j + S_i = P_i \Sigma a_{ij} \quad i = 1, 4, 7 \tag{4}$$

where the index S_i is 1 for a labelled cladode and 0 for the other organs. The relative carbon transfer rate (F_{ij}, dimensionless) was the carbon transferred from compartment i to compartment j per day divided by the carbon taken up by the basal or daughter cladode per day and was calculated by:

$$F_{ij} = a_{ij} P_i \tag{5}$$

Eventually, all the carbon incorporated was assumed to be converted to structural material or lost by respiration ($F_{12} + F_{13} + F_{45} + F_{46} + F_{78} + F_{79} = 1$; Fig. 1). The half-times for ^{14}C remaining in mobile compartment i (H_i, d), assuming no replenishment, were (Yoneyama and Takeba, 1984):

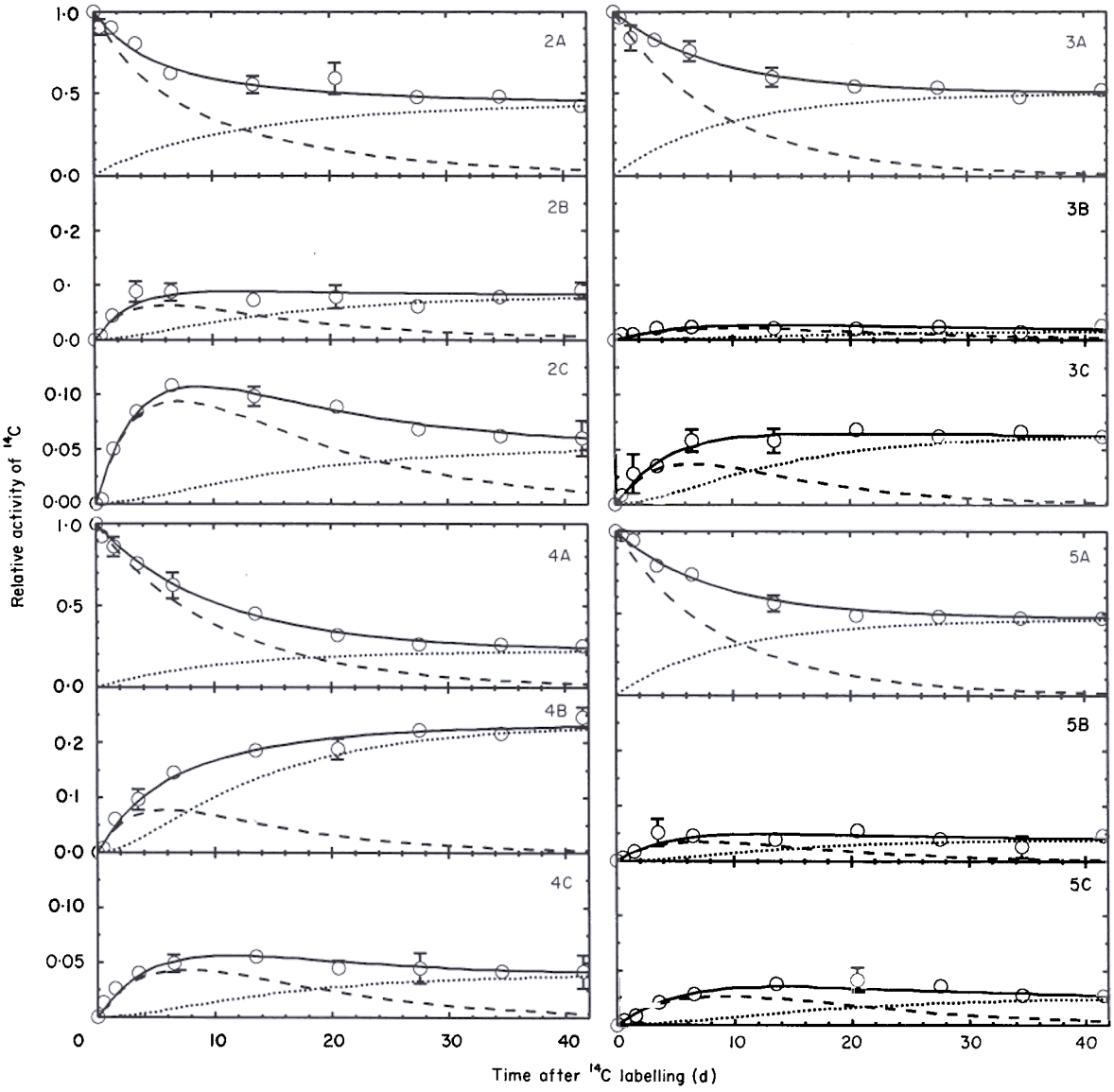
$$H_i = \frac{\ln 2}{\Sigma a_{ij}} \quad i = 1, 4, 7 \tag{6}$$

RESULTS

^{14}C kinetics for 6-month-old plants

After labelling the basal cladode, the relative activity of ^{14}C in the basal cladode of 6-month-old *Opuntia ficus-indica* under normal light and water conditions gradually declined and became 0·46 at 6 weeks (Fig. 2A). Mobile ^{14}C in the basal cladode also declined, about 50% remaining after 5 d and 10% after 28 d. Immobile ^{14}C in structural material continuously increased, nearly equalling the total relative activity at 6 weeks (Fig. 2A). Activity of ^{14}C in the daughter cladode initially was zero, increased, and then stabilized at 0·09 after about 10 d (Fig. 2B). Mobile ^{14}C in the daughter cladode also initially increased, reached a maximum of 0·06 in about 6 d, and then declined to 0·01 by 6 weeks. Relative ^{14}C activity in the roots reached a maximum at 9 d and then declined to 0·06 at 6 weeks (Fig. 2C). ^{14}C in the root mobile pool increased to 0·09 at 8 d and then decreased to 0·01 at 6 weeks.

When 6-month-old *O. ficus-indica* was droughted, its basal cladode exported less ^{14}C (Figs 3A *vs.* 2A). Relative ^{14}C activity stabilized at 0·02 after 7 d in the daughter cladode (Fig. 3B) and gradually increased to 0·06 in roots at 6 weeks (Fig. 3C). When the entire plant was shaded,

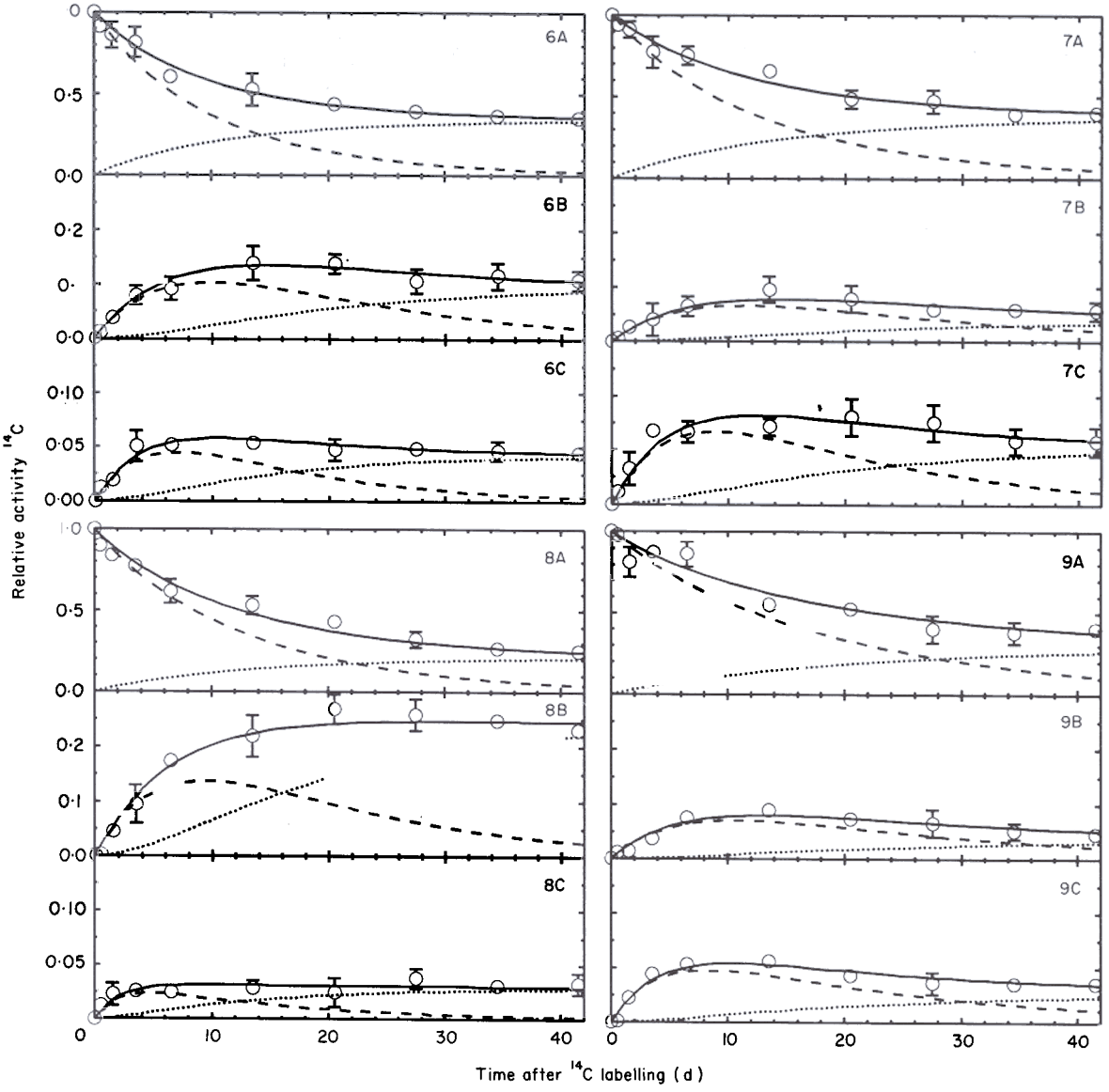


FIGS 2–5. Time courses of relative activities of ^{14}C for 6-month-old *Opuntia ficus-indica* following labelling of the basal cladode: A, basal cladode; B, daughter cladode; and C, roots. Plants were the control under normal water and light conditions (Fig. 2); droughted (Fig. 3); shaded (Fig. 4); or both droughted and shaded (Fig. 5). Data are presented as mean ± s.e. ($n = 4$), except when the error bars were smaller than the symbol. Solid lines represent simulated relative ^{14}C activity in the mobile plus immobile compartments of each organ. Dashed lines and dotted lines represent simulated relative ^{14}C activities in the mobile and the immobile compartments, respectively.

relative ^{14}C activity at 6 weeks declined to 0·24 in the basal cladode (Fig. 4A), gradually increased to 0·23 in the daughter cladode (Fig. 4B), and stabilized at 0·04 in the roots (Fig. 4C). When plants were both shaded and droughted, relative ^{14}C activity at 6 weeks was 0·47 in the basal cladode (Fig. 6A) and below 0·05 in both the daughter cladode and the roots (Fig. 5B, C).

^{14}C kinetics for 18-month-old plants

For 18-month-old *O. ficus-indica* under normal water and light conditions, relative ^{14}C activity steadily declined to 0·36 at 6 weeks in the basal cladode (Fig. 6A). In the daughter cladode, it gradually increased, reached a maximum at 14 d, and then declined to 0·11 at 6 weeks (Fig. 6B). Roots incorporated about 4% of the ^{14}C into their immobile pool (Fig. 6C). When plants were droughted, relative ^{14}C activity in the basal cladode declined to 0·41 at 6 weeks (Fig. 7A) and in the daughter cladode increased to a maximum at 14 d and then declined to 0·05 at 6 weeks (Fig. 7B). Roots incorporated about 6% of the ^{14}C from the basal cladode into their immobile pool (Fig. 7C). When the plants were shaded, relative ^{14}C activity gradually declined to 0·27 in the basal cladode (Fig. 8A) and gradually increased to 0·26 in the daughter cladode, most of the latter representing structural material (Fig. 8B). Roots imported only 3% of the ^{14}C from the basal cladode (Fig. 8C). The basal cladode of plants that were both shaded and droughted exported the least amount of ^{14}C to the daughter cladode (5%) and the roots (3%, Fig. 9).



FIGS 6–9. Time courses of relative activities of ^{14}C for 18-month-old *O. ficus-indica* following labelling of the basal cladode: A, basal cladode; B, daughter cladode; and C, roots. Plants were the control under normal water and light conditions (Fig. 6); droughted (Fig. 7); shaded (Fig. 8); or both droughted and shaded (Fig. 9). Data are presented as for Figs 2–5.

^{14}C kinetics with the daughter cladode labelled

When the daughter cladode of 6-month-old plants was labelled with $^{14}CO_2$, its relative activity declined to 0·52 at 6 weeks (Fig. 10A). Very little ^{14}C was translocated to the other organs. In particular, the relative activity at 6 weeks was only 0·02 for the basal cladode (Fig. 10B) and 0·01 for the roots (Fig. 10C).

Relative carbon fluxes between compartments

The largest transfer rate of carbohydrate for 6-month-old plants under normal water and light condition was immobilization into structural material of the basal cladode (F_{45} = 0·457, Table 1). Mobile carbohydrate was actively exchanged between the basal cladode and both the daughter cladode (F_{41} = 0·338 and F_{14} = 0·167) and the roots (F_{47} = 0·392 and F_{74} = 0·217). Respiratory loss of carbon was 0·207 from the basal cladode (F_{46}), 0·076 from the daughter cladode (F_{13}), and 0·115 from the roots (F_{79}). When the plants were droughted, much less carbon was transferred to the daughter cladode (F_{41} = 0·056) and incorporated into its structural material (F_{12} = 0·018). Upon shading, carbon translocated to the daughter cladode from the basal cladode (F_{41} = 0·387) was 14% higher than for the control, and incorporation of ^{14}C into structural material in the daughter cladode (F_{12} = 0·228) was nearly three-fold higher than for the control. When shaded, less carbon was converted into structural material in the basal cladode (F_{45} = 0·241). When plants were both droughted and shaded, a large amount of carbon was lost through respiration of the basal cladode (F_{46} = 0·412); translocation to the daughter cladode (F_{41} = 0·122) and to the roots (F_{47} = 0·075) was then small (Table 1).

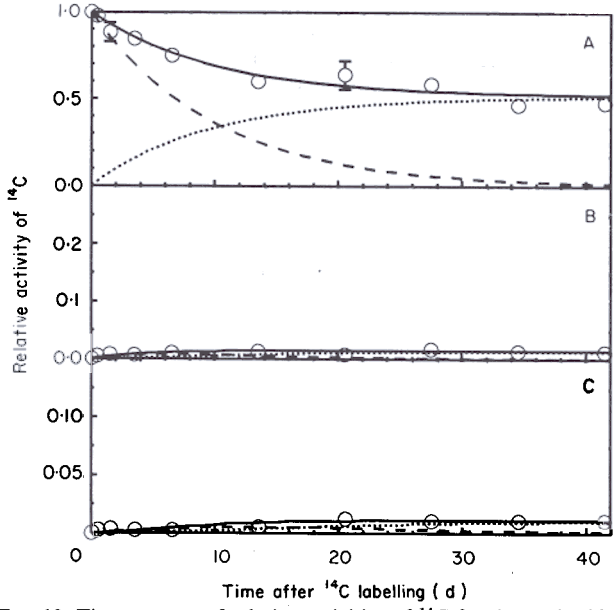


FIG. 10. Time courses of relative activities of ^{14}C for 6-month-old *O. ficus-indica* following labelling of the daughter cladode under normal water and light conditions: A, daughter cladode; B, basal cladode; and C, roots. Data are presented as for Figs 2–5.

TABLE 1. *Intercompartmental carbon fluxes for 6- and 18-month-old* Opuntia ficus-indica *under various conditions. Plants were the control under normal water and light conditions (unshaded, wet), droughted (unshaded, dry), shaded (shaded, wet), or shaded and droughted (shaded, dry).*

	Carbon fluxes [carbon transferred d^{-1} (carbon uptake $d^{-1})^{-1}$]							
	6-month-old plants				18-month-old plants			
	Unshaded		Shaded		Unshaded		Shaded	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
F_{12}	0·085	0·018	0·228	0·040	0·095	0·040	0·248	0·037
F_{13}	0·076	0·017	0·137	0·032	0·165	0·155	0·198	0·257
F_{14}	0·176	0·021	0·022	0·049	0·043	0·022	0·046	0·064
F_{41}	0·338	0·056	0·387	0·122	0·303	0·217	0·491	0·358
F_{45}	0·457	0·503	0·241	0·469	0·345	0·380	0·239	0·301
F_{46}	0·207	0·345	0·283	0·412	0·282	0·258	0·239	0·226
F_{47}	0·392	0·149	0·168	0·075	0·188	0·258	0·211	0·320
F_{74}	0·217	0·031	0·057	0·029	0·075	0·091	0·133	0·142
F_{78}	0·059	0·063	0·039	0·025	0·042	0·061	0·032	0·028
F_{79}	0·115	0·055	0·072	0·021	0·071	0·106	0·045	0·151

F_{ij} represents the flux from compartment i to compartment j. Compartments 1, 4, and 7 represent mobile carbohydrate, compartments 2, 5, and 8 represent immobile material, and compartments 3, 6, and 9 represent respiratory loss for the daughter cladode, the labelled basal cladode, and the roots, respectively.

Compared to 6-month-old plants, the 18-month-old plants under normal water and light conditions transferred less carbon from the mobile pool of the basal cladode to the immobile pool (F_{45} = 0·345, Table 1). The net transfer rate of carbohydrate from the basal cladode to the daughter cladode ($F_{41} - F_{14}$ = 0·260) was high. Respiratory loss was high in the basal cladode (F_{46} = 0·282) and in the daughter cladode (F_{13} = 0·165). When the plants were droughted, more carbon was translocated from the mobile pool of the basal cladode to its immobile compartment (F_{45} = 0·380) and to the roots (F_{47} = 0·258) than for the control. Under shaded conditions, carbon translocated to the daughter cladode from the basal cladode (F_{41} = 0·491) was 62% higher than for the control; less carbon was then converted into structural material in the basal cladode (F_{45} = 0·239). When the 18-month-old plants were both shaded and droughted, carbon transfer into immobile material was low in the daughter cladode (F_{12} = 0·037) and in the roots (F_{78} = 0·028) but relatively unchanged in the basal cladode (Table 1).

Nearly all carbohydrate synthesized in the daughter cladode of 6-month-old plants was incorporated into its structural material (F_{12} = 0·522) or lost through its respiration (F_{13} = 0·444). Of the 8% of carbon translocated to the basal cladode (F_{14} = 0·079), more than half was moved back to the daughter cladode (F_{41} = 0·045) and only a small amount was moved to the roots (F_{47} = 0·019). About 2% of the carbon from the daughter cladode remained in the basal cladode (F_{45} = 0·014) and in the roots (F_{78} = 0·010). A small amount of carbon was lost through respiration in the basal cladode (F_{46} = 0·002) and in the roots (F_{79} = 0·008) and a negligible amount of carbon was transferred back from the roots to the basal cladode (F_{74} = 0·001).

To check the steady-state assumption [eqn (4)], the carbon flux rates derived from the 6-week data were compared with those from the first week. Of the 72 parameters when the basal cladode was labelled under the various conditions for plants of both ages, 66 were within 10% of each other for the two time periods. Among six parameters that changed more than 10%, the greatest absolute change in carbon flux was 0·034 (F_{41} from the mobile compartment of the basal cladode to the mobile compartment of the daughter cladode of 6-month-old plants that were both shaded and droughted). Such a change for F_{41} was small compared with the accompanying major carbon fluxes F_{45} (0·469) and F_{46} (0·412; Table 1). Also, when the daughter cladode was labelled, the greatest absolute change in carbon flux for the 1-week compared with the 6-week data was only 0·028 (F_{14}).

Half-times for carbon retention

The half-time of newly synthesized assimilate remaining as nonstructural carbon in the basal cladode of 6-month-old plants under normal water and light conditions was 5·4 d (Table 2). When plants were either droughted, shaded, or both droughted and shaded, half-times of such mobile carbon were 13, 24 and 11% longer than for the control. For 18-month-old plants, half-times for retention of mobile carbon averaged 40% (2·4 d) longer than for the comparable 6-month-old plants, but the effects of shading and drought were similar. Retention half-times for mobile carbon in the daughter cladodes were 2·9 d for the control for 6-month-old plants and 6·6 d for 18-month old plants (Table 2). Droughting tended to increase the half-times, especially for the 6-month-old plants. When plants were shaded, half-times for retention of mobile carbon in the daughter cladode

TABLE 2. *Half-times for carbon retention in the mobile compartments for 6- and 18-month-old* O. ficus-indica *under various conditions. Plants were the controls under normal water and light conditions (unshaded, wet), droughted (unshaded, dry), shaded (shaded, wet), or shaded and droughted (shaded, dry).*

	Half-times (d)							
	6-month-old plants				18-month-old plants			
	Unshaded		Shaded		Unshaded		Shaded	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
H_1	2·85	7·37	2·59	4·17	6·60	7·07	5·37	4·75
H_4	5·41	6·13	6·73	6·03	6·48	8·45	8·25	10·83
H_7	2·69	3·33	3·92	6·13	3·47	3·81	1·59	3·14

H_i represents the half-time for compartment i. Compartments 1, 4, and 7 represent mobile carbon pools in the daughter cladode, the labelled basal cladode, and the roots, respectively.

were shorter than for the controls in all cases. Half-times for retention of mobile carbon in the roots were shorter than in the basal and the daughter cladodes, averaging 3·5 d, the longest times occurring when 6-month-old plants were shaded and droughted (Table 2). For mobile carbon synthesized in the daughter cladode, retention half-times were 4·8, 0·9, and 4·6 d in the daughter cladode, the basal cladode, and the roots, respectively.

DISCUSSION

Compartmental analysis for time-courses of relative ^{14}C activity after labelling cladodes with $^{14}CO_2$ revealed carbon partitioning patterns for *Opuntia ficus-indica*. Newly synthesized carbohydrate in the basal cladode was either converted into structural material in that cladode, lost by respiration of that cladode, or moved to the daughter cladode and the roots, where such carbohydrate initially increased, reached maxima, and then declined a few weeks later. For 6-month-old plants under the control conditions, 46, 8 and 6% of photo-assimilated carbohydrate were ultimately converted to structural material in the basal cladode, the daughter cladode, and the roots, respectively. Meanwhile, respiration in the basal cladode, the daughter cladode, and the roots consumed 21, 8 and 11%, respectively, of the carbohydrate initially incorporated in the basal cladode. The percentage of such carbohydrate used for structural material and respiration in the three organs varied with environmental conditions and plant age. When the daughter cladode was labelled, the newly synthesized carbohydrate was utilized mainly for its own structural material and respiration.

The half-times of newly synthesized assimilate remaining as nonstructural carbohydrate was 2 to 11 d for various organs of *O. ficus-indica* under different conditions. In contrast, labelled leaves of *Trifolium repens* export most ^{14}C within the first 24 h after labelling (Danckwerts and Gordon, 1989). Source leaves of *Medicago sativa* export up to 60% of incorporated ^{14}C to other organs within 24 h after labelling (Cralle and Heichel, 1985). Half-times of ^{14}C remaining in mobile carbon compartments in *G. max* range from only 0·17 to 1·23 h (Kouchi *et al.*, 1986; McCoy *et al.*, 1989). *Opuntia ficus-indica* has large reserve pools of total nonstructural carbohydrate in its cladodes, totalling up to 20% of the dry matter (Nerd and Nobel, 1991). When the newly synthesized assimilate was added to such carbon pools, ^{14}C levels in the labelled cladodes declined more slowly than in source leaves of the C_3 species. For *Agave deserti*, another CAM plant with large carbon reserves in its leaves (Tissue and Nobel, 1988), relative activity of ^{14}C also declined slowly (Tissue and Nobel, 1990).

The basal cladode and the daughter cladode of *O. ficus-indica* exported only 35 and 4%, respectively, of their photo-assimilate. In contrast, more than 90% of the assimilated ^{14}C in *T. repens* is exported from labelled leaves (Danckwerts and Gordon, 1989). The labelled leaves of *Pinus taeda* export up to 65% of the assimilated ^{14}C (Kuhns and Gjerstad, 1991). The cladodes of *O. ficus-indica* not only assimilate carbon, as do the leaves of non-succulent plants, but also store a considerable amount of carbohydrate and utilize carbohydrate for structural material and respiration related to growth for many years. Such a life form favours above-ground biomass accumulation, as much carbohydrate is invested in the photosynthetic apparatus. As a cladode becomes larger and thicker, its capacity as a storage organ for both water and carbon increases (Nobel, 1988). In this regard, the basal cladode of 18-month-old plants exported an average of 60% more assimilate to the daughter cladode and the roots than did that of 6-month-old plants, whose basal cladodes were 35% thinner.

When plants were shaded, the daughter cladode integrated nearly three-fold more carbohydrate from the basal cladode into its structural material than did the control. Similarly for the CAM plant *A. deserti*, the amount of carbon translocated from the parent to shaded ramets more than doubles compared with unshaded ramets (Tissue and Nobel, 1990), indicating mobilization of stored nonstructural carbohydrate for growth of its ramets (Denison and Nobel, 1988; Tissue and Nobel, 1988). Shading or defoliation of ramets of other species also usually results in an increase of carbon subsidy to ramets by the parental organs (Ashmun, Thomas and Pitelka, 1982; Alpert and Mooney, 1986).

When plants were droughted, roots incorporated 23% more and the daughter cladode incorporated 68% less carbohydrate from the basal cladode into their structural material than for the controls. Similar partitioning patterns are reported for water-stressed *Dactylis glomerata* (Brown and Blaser, 1970). Also, roots of droughted *M. sativa* contain more ^{14}C activity than the controls (Hall, Sheaffer and Heichel, 1988). Longer half-times of photo-assimilate remaining as nonstructural carbohydrate in the basal cladode and the daughter cladode when droughted than for the control is consistent with the increase in polysaccharides in the water storage parenchyma of *O. ficus-indica* during drought (Nerd and Nobel, 1991).

C_3 and C_4 plants generally partition more carbon to below-ground organs for water uptake under water stress and distribute more carbon to above-ground organs for light capture upon shading (Brouwer, 1983). When the

CAM plant *O. ficus-indica* was droughted, the functional balance between cladodes and roots was regulated in the same manner as for C_3 and C_4 plants. However, when the CAM plant *Agave lechuguilla* is overwatered, more carbon is partitioned to the root system, thereby compensating for the greater reliance on daytime CO_2 uptake and higher rates of transpiration under wet conditions (Nobel, Quero and Linares, 1989). Other CAM species including *A. deserti* and *A. americana* also switch to primarily daytime CO_2 uptake when supplied with abundant water (Hartsock and Nobel, 1976; Nobel, 1988). Moreover, young cladodes and flower buds of *O. ficus-indica* exhibit daytime stomatal opening, whereas mature cladodes and fruit have the nocturnal stomatal opening characteristic of CAM plants (Acevedo, Badilla and Nobel, 1983). Because of the variable daytime/nighttime behaviour of CO_2 uptake and stomatal opening, the functional balance between shoots and roots of CAM plants may be more complex than for non-CAM plants.

Physiological processes including photosynthesis and transpiration can be well simulated in crop production models, whereas carbon partitioning between organs during plant development and under different environmental conditions remains difficult to quantify (de Wit and Penning de Vries, 1983). Compartmental analysis of the time-courses of relative ^{14}C activities after labelling a cladode of *O. ficus-indica* with $^{14}CO_2$ quantitatively assessed the fate of newly synthesized carbohydrate, including carbon translocation rates among organs under different physiological conditions. Such carbon flux rates can be used as parameter values for carbon translocation between pools in multiple compartment models of plant productivity.

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