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Functional Ecology, Volume 6, Issue 1 (1992), 79-85.

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Growth respiration, maintenance respiration and structural-carbon costs for roots of three desert succulents

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Summary

Water and nutrient uptake are provided at a cost of the carbon incorporated structurally into roots as well as that used for respiratory activities supporting root growth and maintenance. Gas-exchange and dry weight measurements on growing attached roots of *Agave deserti* indicated a respiratory CO₂ requirement of 6.8 ± 0.6 mol CO₂ per kg dry weight for newly elongating nodal roots emanating from the stem and 7.2 ± 0.9 for lateral roots occurring as fine branches on the nodal roots. Similar gas-exchange measurements indicated a growth respiration of 9.4 ± 1.4 mol CO₂ kg⁻¹ for new roots of *Ferocactus acanthodes* and 8.7 ± 0.7 for *Opuntia ficus-indica*. Root growth respiration was also estimated using the heat of combustion of dried root material, which was assumed to contain 47% carbon in the non-ash fraction. For roots 1–20 weeks of age, growth respiration based on the heat of combustion averaged 9.4, 8.4 and 7.7 mol CO₂ kg⁻¹ for *A. deserti*, *F. acanthodes*, and *O. ficus-indica*, respectively, averaging 0.7 mol CO₂ kg⁻¹ higher for 1-week-old roots. The direct measurements of CO₂ evolution and the indirect estimate of growth respiration both indicate that the roots of desert succulents have low respiratory costs for growth compared with other species. The carbon incorporated into the dry weight of the roots averaged 38 mol kg⁻¹ for the three species. Thus, the carbon costs for new roots of these desert succulents represented mainly carbon incorporated structurally into the roots, not growth respiration, and such total carbon costs can become similar to carbon expended by maintenance respiration after about 3 months under wet conditions at 20°C. For *A. deserti* under conditions appropriate to the Sonoran Desert, the water acquired from the soil per unit carbon expended was over twice as high for the drought-deciduous lateral roots and for nodal roots in their second year compared with first-year nodal roots.

Key-words: *Agave deserti*, carbon dioxide efflux, *Ferocactus acanthodes*, growth, maintenance, *Opuntia ficus-indica*, respiration, root

Functional Ecology (1992) **6**, 79–85

Introduction

Respiration of whole plants and of plant organs has conventionally been divided into two components, one attributable to the growth of new tissue and the other for the maintenance of growing and mature tissues (McCree 1970; Thornley 1970; Hesketh, Baker & Duncan 1971). Such separation does not imply separate substrate pools or entirely separate biochemical pathways and has been found to be compatible with more complex theoretical treatments (Thornley 1977; Barnes & Hole 1978; Loehle 1983). A convenient expression describing the respiratory CO₂ efflux (Q_{CO_2} ; mol CO₂ day⁻¹) for the two-component model is (Amthor 1989):

$$Q_{CO_2} = R_m W + G_r \frac{\Delta W}{\Delta t} \quad \text{eqn 1}$$

where R_m is the maintenance respiration rate (mol CO₂ kg⁻¹ day⁻¹), W is the dry weight (kg) that can change by ΔW in time Δt (day), and G_r is the respiratory cost of growth (mol CO₂ kg⁻¹). In the present study, this approach has been used to analyse the CO₂ efflux from growing roots of three desert succulents, *Agave deserti* Engelm. (Agavaceae), *Ferocactus acanthodes* (Lem.) Britton and Rose (Cactaceae), and *Opuntia ficus-indica* (L.) Miller (Cactaceae). R_m , which decreases with root age, has already been determined for roots of these three

species through the use of small chambers placed on attached non-growing roots (Palta & Nobel 1989a,b).

Root systems of agaves and cacti have rapid growth responses to precipitation or artificial watering. Branch roots induced by rain can occur in a few hours on roots of *O. decumbens* and in 24 h on *O. ficus-indica*, *Trichocereus bridgesii*, *Trichocereus pachanoi*, and *Trichocereus spachianus* (Kausch 1965). Similarly, a 5-mm-long root can develop 6 h after watering *A. deserti* and new roots are visible in 8 h after watering *F. acanthodes*, some roots becoming 6 mm long after 24 h (Nobel & Sanderson 1984; Nobel 1988). Two categories of roots can be recognized for *A. deserti*, nodal roots emanating from the base of the stem, often called 'established roots', and those induced by increases in soil water as lateral roots on the nodal roots, often called 'rain roots' (Nobel 1988). Lateral rain-induced roots for the monocotyledon *A. deserti* are ephemeral, being shed during the droughts that commonly occur in its native habitats in the Sonoran Desert (Gentry 1982). Watering also induces fine branch roots on cacti, although such roots tend not to be drought deciduous for these dicotyledons. Watering also leads to the elongation of existing roots for both agaves and cacti (Cannon 1911, 1916; Nobel 1988). Such growth of new roots (both nodal and lateral) induced by precipitation can occur steadily for about 30 days in wet soil for *A. deserti* in the north-western Sonoran Desert (Franco & Nobel 1990), with a similar period of steady growth observed for *F. acanthodes* and an even longer period for *O. ficus-indica* in the laboratory in wet soil (P. S. Nobel, unpublished data).

The total carbon cost for constructing plant material can be estimated from the heat of combustion together with the nitrogen and ash contents of the sample (Williams *et al.* 1987). Such an approach takes into account the energetics of the biochemical pathways used to synthesize the various cellular components by focusing on the energies of specific chemical bonds (Penning de Vries, Brusting & van Laar 1974; McDermitt & Loomis 1981). Thus, construction costs can be related to the amount of glucose consumed for the various synthetic pathways, which corresponds to the carbon used in growth respiration plus the carbon that is incorporated structurally into the cellular components. In the present study, this method of determining growth respiration for new roots of the three desert succulents was compared with the growth respiration calculated from the CO₂ efflux from growing roots corrected for maintenance respiration (equation 1). Moreover, the carbon present in the non-ash fraction of the roots can be compared with the carbon expended by root respiration. Such information is crucial for understanding the energetics of root functioning, such as in benefit:cost models (Bloom, Chapin & Mooney 1985) seeking to evaluate the

water acquisition per unit of carbon expended by roots.

Materials and methods

A. deserti and *F. acanthodes* were collected from the University of California Philip L. Boyd Deep Canyon Desert Research Center at Agave Hill (33°38'N, 116°24'W, 850 m elevation) near Palm Desert, California. Cladodes of *O. ficus-indica* were obtained from a private farm (at 34°7'N, 117°30'W, 395 m) near San Bernardino, California. Plants of all three species were grown in 4-litre plastic pots containing a 1:1 sand:soil mixture, using sandy loam soil from Agave Hill (Nobel 1976). Shoot height averaged 25 cm for *A. deserti* and 20 cm for *F. acanthodes*; one-third of the approximately 30-cm-long cladodes of *O. ficus-indica* was placed below the soil surface. The plants were maintained in a glasshouse with 80% of ambient solar radiation, daily maximum/minimum temperatures averaging 27°C/16°C, and weekly watering with 0.1-strength Hoagland's solution no. 1 supplemented with micronutrients (Hoagland & Arnon 1950). To minimize variations in soil temperature during measurement of CO₂ efflux from roots, plants were placed in environmental growth chambers with day/night air temperatures of 21°C/21°C, leading to a steady temperature of 20°C in the root zone (a 12-h photoperiod with a photosynthetic photon flux density of 700 µmol m⁻² s⁻¹ was provided).

CO₂ efflux from individual attached roots was determined using a relatively new technique (Palta & Nobel 1989a,b). After sterilizing the root surface by dipping in an NaOCl solution (0.5% by weight) for 1 min and rinsing with distilled water, a single attached root 6–10 cm in length was placed on wet soil about 8 mm deep in a cylindrical acrylic chamber 12 cm in length with an inside diameter of 2 cm; the root was covered with an equally thick layer of wet soil, and its proximal end protruded through a split rubber stopper placed at the open end of the chamber. The soil, which had been obtained from Agave Hill and sterilized at 130°C for 2 h in an autoclave, was rewetted every 24 h. Temperature was monitored with three 0.25-mm in diameter copper-constantan thermocouples appressed to the root surface. After insertion of the root, the chamber was placed in the soil at the root's original location and orientation, and the chamber was then covered with soil. Air containing 350 µmol CO₂ mol⁻¹ was humidified by bubbling through water and then passed into the chamber at 25 ml min⁻¹ (measured with a LFC mass flow meter; Technology Inc., Dayton, Ohio, USA); 0.1-strength Hoagland's solution was added to the root chamber approximately every other day to maintain the soil in a wet condition. The CO₂ content of the entering and the exiting air was routinely monitored daily (from 09.00

to 18.00h) with an Li-6200 portable photosynthesis system (Li-Cor, Lincoln, Nebraska, USA); consistent results were obtained for occasional measurements at night.

Over the course of this study, 39 roots (22 for *A. deserti*, 10 for *F. acanthodes* and seven for *O. ficus-indica*) were placed in chambers, generally using three root chambers per plant, and growth of new roots or extension of nodal roots was observed 14 times. After a relatively quiescent period of up to 8 days, a substantial increase in the rate of CO₂ efflux was observed when a new root was induced. The CO₂ efflux was then monitored daily for an additional 7–12 days so that the growth respiratory cost (G_r) could be calculated using equation 1. Following this growth period, the new roots were excised and their dry weight (ΔW) was determined after drying in a forced-draft oven at 70°C until no further weight change occurred (generally 24h). The initial rate of CO₂ efflux over the first few days was assumed to represent maintenance respiration of the root placed in the chamber, and the average dry weight of the new roots over the subsequent growth period was assumed to equal $\Delta W/2$. Hence, the average increment in daily CO₂ efflux ($\overline{\Delta Q_{CO_2}}$) caused by the respiration of new roots was represented as follows:

$$\overline{\Delta Q_{CO_2}} = R_m \frac{\Delta W}{2} + G_r \frac{\Delta W}{\Delta t} \quad \text{eqn 2}$$

Based on previous measurements at 20°C on non-growing roots of various ages, R_m for 5-day-old roots is 0.52 and 0.72 mol CO₂ kg⁻¹ day⁻¹ for established nodal roots and lateral rain roots, respectively, of *A. deserti* (Palta & Nobel 1989a), and 0.68 and 0.86 mol CO₂ kg⁻¹ day⁻¹ for new lateral roots of *F. acanthodes* and *O. ficus-indica*, respectively (Palta & Nobel 1989b).

The total construction cost for plant material, C (kg glucose equivalents per kg dry weight), can be represented as follows:

$$C = 0.0783 H_c - 0.0783 H_c A + 0.0730 A + 3.01 N - 0.0730 \quad \text{eqn 3}$$

where H_c is the heat of combustion of the non-ash fraction (MJ kg⁻¹), A is the fraction of ash in the dry weight, and N is the fraction of nitrogen in the dry weight (Williams *et al.* 1987). This formulation assumes that the incorporated nitrogen is in the form of nitrate and that the growth efficiency was 89%, a typical value for plant material (Penning de Vries *et al.* 1974; Williams *et al.* 1987). H_c was determined with a Phillipson oxygen microbomb calorimeter (Gentry Instruments, Aiken, South Carolina, USA). Nitrogen in organic compounds was determined with a micro-Kjeldahl technique (Alm, Yčas & Hesketh 1989). The carbon content of the non-ash fraction was assumed to be 47%, as is typical for plants

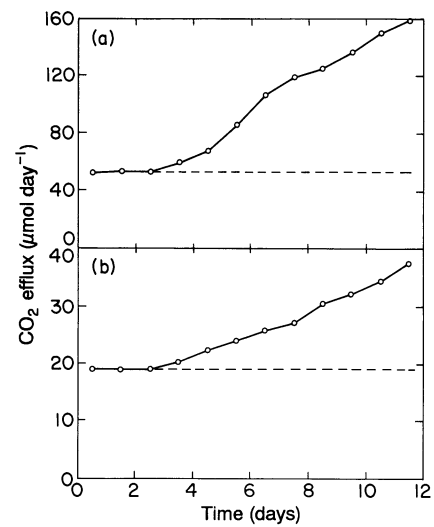


Fig. 1. Time course for net CO₂ efflux (Q_{CO_2}) from the growth of new roots on *Agave deserti*: (a) elongation of an established nodal root and (b) a lateral root, initiated as a branch on a nodal root. The mass of the new roots at the end of the observation period was 54.3 mg for the nodal root and 9.6 mg for the lateral root. The dashed horizontal lines indicate the maintenance respiration of the nodal root initially placed in the chamber.

(Rankama & Sahama 1950; Allen 1989). Growth respiration was calculated as the difference between C (equation 3) and the carbon incorporated structurally into the roots, assuming six CO₂ molecules evolved per glucose (molecular weight of 180.15). The age of new roots was based on root colour and diameter (Palta & Nobel 1989a,b).

Results

Although the daily CO₂ efflux rates for nodal roots of *A. deserti* placed in root chambers were typically fairly constant for up to 8 days, the CO₂ efflux sometimes increased considerably after a few days in the chambers (Fig. 1), signalling the initiation of new root growth. The elongation of established nodal roots (Fig. 1a) led to a larger increase in Q_{CO_2} than the initiation of fine lateral roots (Fig. 1b) that occurred as branches on the nodal roots. After subtracting the baseline maintenance respiration of the nodal roots placed in the chambers, the average daily increase in Q_{CO_2} ($\overline{\Delta Q_{CO_2}}$) was determined over the growth period (Δt). Using the mass of new roots at the end of this period (ΔW), the respiratory cost of growth (G_r) was then calculated using equation 2 (Table 1). For the elongation of five nodal roots of *A. deserti*, ΔW averaged 38 ± 5 mg in dry weight and G_r averaged 6.8 ± 0.6 mol CO₂ kg⁻¹ (data presented as mean \pm SE). For the initiation of three lateral roots of *A. deserti*, ΔW averaged 10 ± 2 mg and G_r averaged 7.2 ± 0.9 mol CO₂ kg⁻¹ (Table 1).

Induction and growth of new roots also caused considerable increases in the rate of CO₂ efflux for *F.*

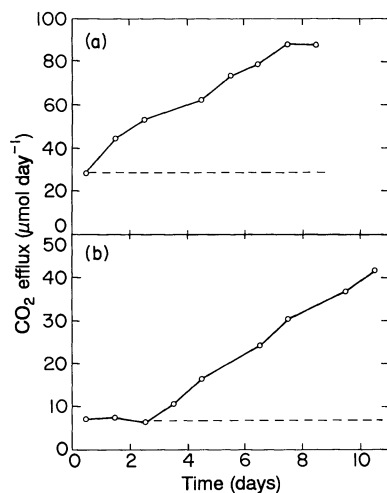


Fig. 2. Time course for net CO_2 efflux (Q_{CO_2}) from the growth of new roots on (a) *Ferocactus acanthodes* and (b) *Opuntia ficus-indica*. The mass of the new roots was 23.7 mg for *F. acanthodes* and 12.2 mg for *O. ficus-indica*.

acanthodes (Fig. 2a) and *O. ficus-indica* (Fig. 2b). In all cases the new roots occurred as branches on the roots placed in the chambers, such induction typically occurring within hours for *F. acanthodes* and after a few days for *O. ficus-indica*. For new branch roots on *F. acanthodes*, ΔW averaged 22.5 ± 3.7 mg in dry weight and G_r averaged 9.4 ± 1.4 mol CO_2 kg^{-1} (data presented as mean \pm SE for $n=3$; Table 1). For three new branch roots on *O. ficus-indica*, ΔW averaged 11.2 ± 3.3 mg and G_r averaged 8.7 ± 0.7 mol CO_2 kg^{-1} (Table 1).

The heat of combustion (H_c) decreased an average of 3% as root age increased from 1 to 20 weeks for the three species (Fig. 3a). The average H_c was 19.4 MJ kg^{-1} for *A. deserti*, 19.1 for *F. acanthodes*, and 18.7 for *O. ficus-indica*. The fractional ash content decreased an average of 39% with root age from 1 to 20 weeks (Fig. 3b). The average ash content was 3.5% for *A. deserti*, 6.2% for *F. acanthodes*, and

2.3% for *O. ficus-indica*. The fractional nitrogen content decreased an average of 24% with root age from 1 to 20 weeks (Fig. 3c). The average N content was 0.67% for *A. deserti*, 0.80% for *F. acanthodes*, and 0.78% for *O. ficus-indica*.

The respiratory cost of growth (G_r) decreased an average of 16% as root age increased from 1 to 20 weeks for the three species (Fig. 4). The mean G_r was

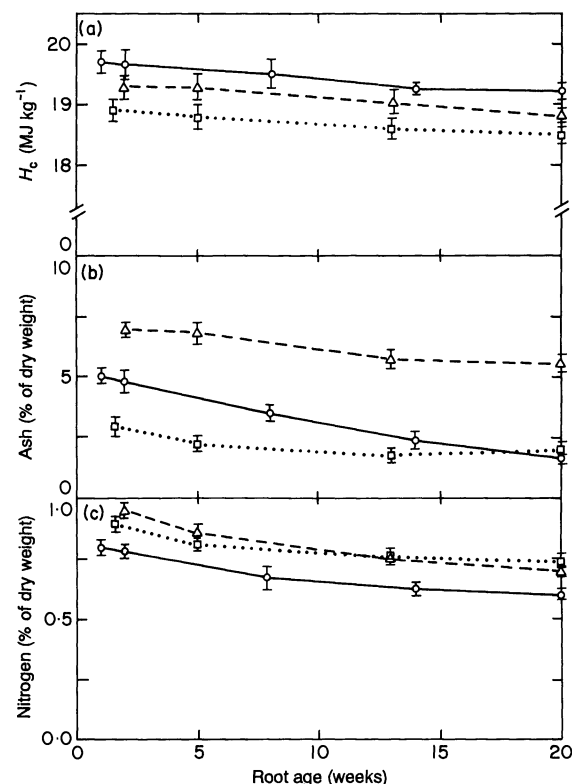


Fig. 3. Variation with root age in (a) heat of combustion (H_c) in the non-ash fraction of the dry weight, (b) the ash fraction and (c) the nitrogen fraction for roots of *Agave deserti* (\circ — \circ), *Ferocactus acanthodes* (\triangle — \triangle) and *Opuntia ficus-indica* (\square — \square). Data are presented as means \pm SE for three to four measurements in each case.

Table 1. New root growth, the accompanying average daily increase in CO_2 efflux, and the growth respiratory cost

Species	$\overline{\Delta Q_{\text{CO}_2}}$ ($\mu\text{mol CO}_2 \text{ day}^{-1}$)	Δt (days)	ΔW (mg)	G_r (mol $\text{CO}_2 \text{ kg}^{-1}$)
<i>Agave deserti</i>				
Established nodal root	60.4	9	54.3	7.7
	32.2	9	30.4	6.9
	23.3	12	25.6	7.8
	49.6	9	46.6	7.2
	26.7	9	34.4	4.6
Lateral rain root	9.3	9	9.6	5.5
	10.5	8	7.2	8.8
	19.4	7	13.9	7.3
<i>Ferocactus acanthodes</i>				
	39.8	8	23.7	10.7
	48.0	8	28.2	10.9
	18.1	8	15.7	6.5
<i>Opuntia ficus-indica</i>				
	19.7	8	12.2	9.5
	7.6	7	5.1	7.4
	25.8	8	16.3	9.2

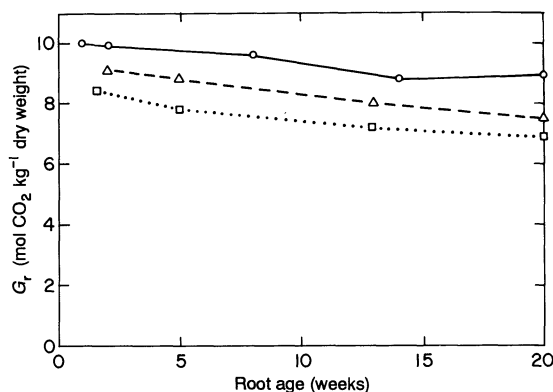


Fig. 4. Variation with root age in the respiratory cost for growth (G_r) for roots of *Agave deserti* (○—○), *Ferocactus acanthodes* (△---△) and *Opuntia ficus-indica* (□····□). Values are calculated from data in Fig. 3, assuming that the non-ash fraction was 47% carbon.

9.4 mol CO₂ kg⁻¹ for *A. deserti*, 8.4 for *F. acanthodes*, and 7.7 for *O. ficus-indica*. For roots 1 week of age, G_r was 10.0 mol CO₂ kg⁻¹ for *A. deserti*, 9.2 for *F. acanthodes*, and 8.5 for *O. ficus-indica* (Fig. 4; measured for *A. deserti* and obtained by extrapolation for the two cacti).

Discussion

Both direct measurement of CO₂ efflux from growing roots and a consideration of the heat of combustion for roots indicated similar average values for the respiratory cost of growth, G_r (equations 1 and 2). In particular, G_r determined from the CO₂ efflux of growing roots corrected for maintenance respiration (Palta & Nobel 1989a,b) averaged 8.4 mol CO₂ kg⁻¹ for new roots of *A. deserti*, *F. acanthodes* and *O. ficus-indica*. Using the heat of combustion together with the fractions of ash and nitrogen in the dry weight (Williams *et al.* 1987), G_r for roots 1 week of age averaged 9.2 mol CO₂ kg⁻¹ for these three species. With the exception of a G_r of 4.5 mol CO₂ kg⁻¹ for *Helianthus annuus* (Mariko 1988), which is inconsistent with another measurement of 15.0 mol CO₂ kg⁻¹ for this species (Szaniawski & Kielkiewicz 1982), the values of the growth respiratory cost of roots were lower for the three desert succulents than for agronomic and other non-agronomic species (Amthor 1989). Specifically, G_r for roots of agronomic species at 20°C is 27.2 mol CO₂ kg⁻¹ for *Cicer arietinum* (Kallarackal & Milburn 1985), 23.2–28.4 for *Lolium multiflorum* (Hansen & Jensen 1977; Hansen 1978), 17.9 for *Pisum sativum* (Mahon 1977), and 12.7 for *Triticum aestivum* (Lambers *et al.* 1982). Also, root G_r was much higher for 12 non-agronomic, non-desert species of *Hylochaeris*, *Plantago*, *Senecio* and *Urtica*, averaging 24 mol CO₂ kg⁻¹ (Lambers 1979).

The respiratory costs of root growth were very similar for the two measurement techniques for *F.*

acanthodes (9.4 vs 9.2 mol CO₂ kg⁻¹) and *O. ficus-indica* (8.7 vs 8.5). However, for *A. deserti*, direct measurement of CO₂ efflux led to lower values of G_r (essentially the same values of 6.8 mol CO₂ kg⁻¹ for nodal roots and 7.2 for lateral roots) than did using the heat of combustion (10.0 mol CO₂ kg⁻¹). The latter method incorporates assumptions on the form of nitrate, the growth efficiency and the carbon content (Rankama & Sahama 1950; Penning de Vries *et al.* 1974; Williams *et al.* 1987; Allen 1989), whose validity may vary among the species. Different daily amounts of growth also affect the model underlying the calculation of G_r (equation 2), such as the assumption that the average daily dry weight of the new roots equals $\Delta W/2$.

For all three species, the heat of combustion of the non-ash fraction and the nitrogen content of the roots on a dry weight basis decreased as root age increased from 1 to 20 weeks. Because the construction costs are 17 MJ kg⁻¹ for carbohydrates and 24 MJ kg⁻¹ for proteins (Allen 1989), the decrease in H_c with root age most likely represented, at least in part, the decrease per unit mass in the relatively more energy-rich proteins. Such changes probably accounted for the slight decline with root age in the growth respiratory cost (G_r) as measured by the caloric value of the tissue, because the export of proteins and/or amino acids, or their dilution during cell maturation or by secondary growth, would reduce the apparent construction cost of the plant material. Dilution of lipids, which have a high construction cost of 39 MJ kg⁻¹ (Allen 1989), could also lower G_r with age. In any case, G_r extrapolated to 1 week more closely approximated the growth respiration of new roots.

For all three species of desert succulents, the carbon structurally incorporated into the roots far exceeded that used for growth respiration. Assuming that 47% of the non-ash fraction was carbon (Rankama & Sahama 1950; Allen 1989), 1 kg of dry weight contained about 38 mol structural carbon but on average required only 7–10 mol carbon for respiratory activity supporting its construction. Such costs can also be compared with the maintenance respiration (R_m), which decreases an average of 35% from 5 days to 1 month of age, 29% from 1 month to 3 months, and 36% from 3 months to 1 year for roots of the three succulents under wet conditions; under dry conditions (soil water potential in the root zone < -0.5 MPa), root R_m for these species averages 13% of the values under wet conditions (Palta & Nobel 1989a,b). The maintenance respiration for the initial 3 months under wet conditions at 20°C amounts to 40 mol C kg⁻¹ dry weight for lateral rain roots and 28 for established nodal roots of *A. deserti*, 32 mol C kg⁻¹ for new roots of *F. acanthodes* and 49 for *O. ficus-indica*. The additional maintenance requirements for 1 year amount to 47 mol C kg⁻¹ for *A. deserti*, 46 for *F. acanthodes*, and 69 for *O. ficus-indica* under wet conditions and 6, 6 and 10 mol

C kg⁻¹, respectively, under dry conditions (because of periodic droughts, lateral rain-induced roots of *A. deserti* are generally shed within 3 months in the field and hence are not considered for this longer time period). Thus, maintenance respiration (Palta & Nobel 1989a,b) for the first 3 months under wet conditions is similar to the total construction cost (growth respiration plus carbon incorporated structurally) for the roots of these three desert succulents, becoming about 2.1-fold greater for roots of *A. deserti* and *F. acanthodes* and 2.5-fold greater for *O. ficus-indica* for 1 year under wet conditions.

Based on the carbon costs for root construction and maintenance together with the water uptake properties, root functioning can be analysed using a benefit:cost approach (Bloom *et al.* 1985). The volumetric water uptake rate, J_V (m³ s⁻¹), by roots can be quantified using the root hydraulic conductivity coefficient, L_P (m s⁻¹ MPa⁻¹):

$$J_V = L_P A \Delta\Psi \quad \text{eqn 4}$$

where A (m²) is the lateral surface area of the root and $\Delta\Psi$ (MPa) is the water potential drop from the soil to the root xylem (Passioura 1988; Nobel 1991). For both lateral roots and nodal roots of *A. deserti*, L_P decreases approximately linearly with root age from 2.60×10^{-7} m s⁻¹ MPa⁻¹ at 2 weeks to 0.89×10^{-7} at 3 months, followed by a more gradual decrease to 0.62×10^{-7} m s⁻¹ MPa⁻¹ at 1 year (Nobel, Schulte & North 1990). The rainfall pattern in the native habitat of *A. deserti* tends to be biannual, rainfall generally occurring in late summer and during the winter (Nobel 1988). The mean annual rainfall of 240 mm leads to about 120 days per year when the soil water potential in the root zone of *A. deserti* is above -0.5 MPa, allowing water uptake to occur (Nobel 1976, 1988).

A benefit:cost comparison can be made between the ephemeral rain-induced lateral roots and the permanent nodal roots, which has previously been attempted for *A. deserti* but using incorrect values for growth respiration (Hunt, Zakir & Nobel 1987). Assuming that the nodal roots of *A. deserti* are initiated during the first rainy period of 2-months duration and then maintained for a second rainy period of the same duration 6 months later, water uptake for nodal roots for a $\Delta\Psi$ of 0.3 MPa at 20°C for 120 days is 1.97×10^5 mol kg⁻¹ (Nobel *et al.* 1990) and maintenance respiration is 32 mol CO₂ kg⁻¹ (Palta & Nobel 1989a). These nodal roots have an initial total construction cost of 48 mol C kg⁻¹ and a maintenance respiration cost of 5 mol C kg⁻¹ for the 8 dry months of the year. During a similar second year, such nodal roots would take up 0.83×10^5 mol H₂O kg⁻¹ and expend 16 mol CO₂ kg⁻¹. For lateral rain roots of *A. deserti* over each 2-month wet period, water uptake is 4.45×10^5 mol H₂O kg⁻¹ (Nobel *et al.* 1990) and maintenance respiration is 33 mol CO₂ kg⁻¹ (Palta & Nobel 1989a). These lateral roots have

an initial total construction cost of 48 mol C kg⁻¹ and a small annual maintenance respiration cost, because they are shed during drought. Thus, the water acquired per carbon expended is 2300 mol H₂O mol⁻¹ C during the first year and 5200 during the second year for the nodal roots of *A. deserti* compared with 5400 mol H₂O mol⁻¹ C for the lateral roots. The lateral roots, which have a mean diameter of 0.8 mm compared with 2.7 mm for the nodal roots of *A. deserti* (Palta & Nobel 1989a) and thus have over three-fold the surface area per unit dry weight, exhibited a much higher benefit:cost ratio than did the nodal roots during the first year. However, the benefit:cost ratio for the nodal roots during their second year was similar to that of the drought-deciduous lateral roots.

The present studies on growth respiration and previous studies on maintenance respiration (Palta & Nobel 1989a,b) provide the basis for certain generalizations concerning the respiratory activity of the roots of desert succulents. For instance, the respiratory cost of root growth for *A. deserti*, *F. acanthodes* and *O. ficus-indica* is low compared with agronomic as well as non-agronomic species. In addition, maintenance respiration is also low for these three desert succulents, being less than 1 mol CO₂ kg⁻¹ day⁻¹ even for the youngest roots (Palta & Nobel 1989a,b) compared with 1–3 mol CO₂ kg⁻¹ day⁻¹ typical of maintenance respiration for agronomic plants (Hansen & Jensen 1977; Mahon 1977; Hansen 1978; Szaniawski & Kielkiewicz 1982; Kallarackal & Milburn 1985). Moreover, R_m for 12 species of non-agronomic, non-desert species averages 4.8 mol CO₂ kg⁻¹ day⁻¹ (Lambers 1979). Roots of desert succulents, which may be influenced more by the soil water potential than by any other environmental variable, are apparently produced and maintained at a much lower carbon cost than are roots of other species. Instead of having as their primary functions active transport and control of specific element ratios (Van der Werf, Hirose & Lambers 1989; Johnson 1990), the overriding importance of water uptake for root systems of plants in arid and semi-arid regions may lead to roots that are inherently cheaper to produce in terms of carbon expended, a matter to be clarified by future research. Besides being interesting ecologically, breeding efforts might be warranted to introduce the root growth properties of certain desert succulents into species presently of commercial importance, as root growth can utilize an appreciable fraction of crop carbon gain (Amthor 1989).

Acknowledgements

This research was supported by the National Science Foundation (grant DCB-90-02333) and the Ecological Research Division of the Office of Health and Environmental Research, Department of Energy (contract DE-FCO3-87-ER60615).

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Received 11 February 1991; revised 29 April 1991; accepted 9 May 1991