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CARBON RELATIONS OF FLOWERING IN A SEMELPAROUS CLONAL DESERT PERENNIAL¹

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Abstract. *Agave deserti* is a long-lived, semelparous perennial of the northwestern Sonoran Desert that flowers after ≈ 50 –55 yr. Measurements of CO₂ exchange over 24-h periods indicated that leaves of flowering rosettes had 24% more net CO₂ uptake than leaves of adjacent nonflowering rosettes during the first month of inflorescence production. Net CO₂ uptake for leaves of flowering rosettes was 32% less thereafter than for leaves of nonflowering rosettes, as senescing leaves of flowering rosettes exhibited dramatic reductions in nitrogen and chlorophyll contents. During the course of flowering, levels of total nonstructural carbohydrate (TNC) in the leaves of flowering rosettes dropped from 38 to 6% of the leaf dry mass, indicating substantial translocation of stored carbon to the inflorescence. TNC reserves of the rosette provided 70% of the carbon required to produce the 1.53 kg inflorescence, and CO₂ uptake by the leaves and the inflorescence provided the remaining 30%.

Rosettes must attain a minimum size (> 1000 g dry mass) to initiate flowering, unless they are connected to a large flowering rosette. Small rosettes did not produce inflorescences when their rhizome connection to a large rosette was severed ≈ 4 wk before inflorescences emerged, suggesting that a chemical signal is transmitted through the rhizome that induces the small rosette to flower precociously. Small flowering rosettes could not complete formation of the inflorescence unless partially supported by carbon supplied by the connected large rosette. The contribution of the large rosette declined from 74% for a 0–30 g dry mass connected rosette to 35% for a 200–600 g rosette. For both small and large flowering rosettes, the translocation of substantial carbohydrate reserves from the leaves is essential for production of the inflorescence.

Key words: *Agave deserti*; carbon balance; clonal; CO₂ exchange; flowering; herbivory; inflorescence CO₂ exchange; semelparous perennial; Sonoran Desert; total nonstructural carbohydrate (TNC).

INTRODUCTION

Most perennial plants flower more than once, but semelparous species, or Big Bang reproducers (Gadgil and Bossert 1970), experience a single, massive reproductive episode that is followed by fairly rapid plant death. Semelparous species exhibit postreproductive mortality in part because they allocate resources to their single reproductive event that otherwise would be used for maintenance and growth of vegetative structures. The evolution and maintenance of semelparity in perennials is promoted by increased fecundity with age that offsets the delay in reproductive maturity (Schaffer 1974, Bell 1980). Delayed reproduction is often accompanied by increased stored resources that can be used for greater flower and fruit production (Aker 1982a, b) and greater seed production (Janzen 1976).

Most species of agave are semelparous (Gentry 1982), including *Agave deserti*, a rosette perennial of the northwestern Sonoran Desert that exhibits crassulacean acid metabolism (CAM). It propagates primarily vegetatively by ramets, but reproduces sexually after

≈ 50 –55 yr (Nobel 1987). Within a population the number of rosettes that flower each year varies up to 50-fold, depending on soil water conditions 2 yr prior to flowering and the number of rosettes that flowered in the previous year (Nobel 1987). Most rosettes that flower are large, but $\approx 10\%$ of the flowering rosettes are small and are connected to large flowering rosettes.

The period from the initial emergence of the inflorescence of *A. deserti* until seed dispersal lasts ≈ 5 mo and involves the production of a single, 3–4 m tall, bracteate inflorescence from the shoot apex of the basal rosette of leaves, with lateral branches arising from the upper sixth of the main axis of the inflorescence (Nobel 1977). Evolution of such large inflorescences in Agavaceae has been attributed to pollinator preference for inflorescences with the greatest pollen and nectar rewards, which is associated with inflorescence size (Schaffer and Schaffer 1979). The production of the large inflorescence of *A. deserti* can require 18 kg water (Nobel 1977), completely exhausting the water stored in the succulent leaves, and presumably the demand for carbon is comparably great.

The present study examines the carbon relations of flowering in *Agave deserti*. Measurements of CO₂ exchange over 24-h periods were made on the leaves of

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flowering rosettes during inflorescence development to determine their contribution of current carbon to production of the inflorescence. Also, CO₂ exchange was measured for the inflorescence, whose contribution to its own carbon needs are frequently overlooked, but which can be significant (Bazzaz and Carlson 1979, Bazzaz et al. 1979, Williams et al. 1985). Carbohydrate reserves support intensive flowering periods in arctic and alpine plants (Fonda and Bliss 1966, Shaver and Billings 1976), crop plants (Sanz et al. 1987), grassland plants (Menke and Trlica 1981), and desert plants (Potter et al. 1986). Therefore, total nonstructural carbohydrate (TNC) levels were monitored to assess the contribution of stored carbon to production of the inflorescence. The role of rhizomatously connected large flowering rosettes in triggering and supporting the precocious flowering of small rosettes was also examined.

MATERIALS AND METHODS

Plant material and morphology

Agave deserti Engelm. (Agavaceae) was studied in the northwestern Sonoran Desert within the Philip L. Boyd Deep Canyon Desert Research Center (33°38' N, 116°24' W, 850 m elevation). After the initial emergence of inflorescences in March of 1987 and 1988, the height of the inflorescence and the number of lateral flower branches were periodically measured. To express the distribution of flowering rosettes according to size, the number of leaves and mean leaf length were used to estimate nondestructively the rosette dry mass ($r^2 = 0.95$; Nobel 1984). The fraction of all rosettes that flowered, and the fate of their inflorescences (e.g., consumption, abortion, or maturation), was determined in 1987 and 1988 over a 5000-m² region.

Severing experiment

Thirty large rosettes and their connected small rosettes, all of which occurred in clonal groups that had exhibited precocious flowering of small rosettes within the past 2 yr, were monitored in 1988. In late February 4 wk before inflorescences were visible, small rosettes were severed from 15 of the connected large rosettes by cutting the connecting rhizome. For the remaining unsevered large rosettes, 12 connected small rosettes produced inflorescences. Four of these small rosettes were placed into each of three size classes: 0–30, 60–200, and 200–600 g dry mass. On 30 March, 6 d after the inflorescence of the small rosettes became visible, two of the small rosettes in each size class were severed from connected flowering large rosettes. Growth of all inflorescences, measured as height changes, was monitored every 2 wk until growth ceased in June.

CO₂ exchange

In 1988, three flowering and three nonflowering large rosettes (≈4000 g dry mass) were used for CO₂ exchange measurements, and each flowering rosette was

matched with an adjacent nonflowering rosette within the same clonal group. CO₂ exchange was measured using a LICOR 6200 portable photosynthesis system with a cuvette designed to fit the contours of the succulent leaves and the stalk of the inflorescence. Measurements were taken over a 24-h period on the abaxial side of two leaves per rosette and at midheight on the inflorescence stalk of flowering rosettes beginning in March and continuing every 2–3 wk until late June when net CO₂ exchange was nearly zero. Interception of photosynthetically active radiation by leaves and inflorescences was monitored with a LICOR LI-190S quantum sensor. Soil water potential was determined with Wescor PCT 55-15 soil thermocouple psychrometers inserted near the base of each rosette at a soil depth of 0.10 m, the mean rooting depth for *A. deserti* (Nobel 1976).

Chlorophyll and nitrogen contents of leaves of the three flowering and the three nonflowering rosettes were measured every 3–4 wk beginning in March and ending in August. Chlorophyll content was determined on leaf disks (13 mm in diameter) removed with a cork borer and triply extracted with 80% (vol/vol) acetone (Arnon 1949). Total nitrogen was determined following micro-Kjeldahl digestion (Bremner and Mulvaney 1982).

Total nonstructural carbohydrate

In 1987 total nonstructural carbohydrate (TNC) was measured approximately monthly for five flowering rosettes and five adjacent nonflowering rosettes of similar size (≈4800 g dry mass). Tissue samples of unfolded leaves were collected from the onset of flowering in March until September 1987, when seed had been produced. In 1988 tissue samples of unfolded leaves were collected every 2 mo from 12 flowering rosettes and 24 nonflowering rosettes to quantify the influence of rosette size on TNC level. The TNC level of unfolded leaves, which account for ≈60% of total rosette dry mass, closely approximates the TNC level of the entire rosette (Tissue and Nobel 1988) and therefore leaf TNC level was used to represent rosette TNC level. Rosettes varied in size from 445 to 7730 g dry mass and were divided into six size classes: 0–1000, 1000–2000, 2000–3000, 3000–4000, 4000–5000, and >5000 g. Leaf tissue samples were dried in an oven at 80°C until no further mass change occurred (≈4 d) and then ground into a fine powder. TNC level was determined for leaves by the anthrone method (Spiro 1966) after extraction and hydrolysis of starch using amylase (Smith 1981).

Carbon balance

The amount of carbon necessary to produce an inflorescence was determined for the three flowering rosettes from CO₂ exchange measurements on the leaves and inflorescences as well as from changes in TNC levels during inflorescence development. Total carbon

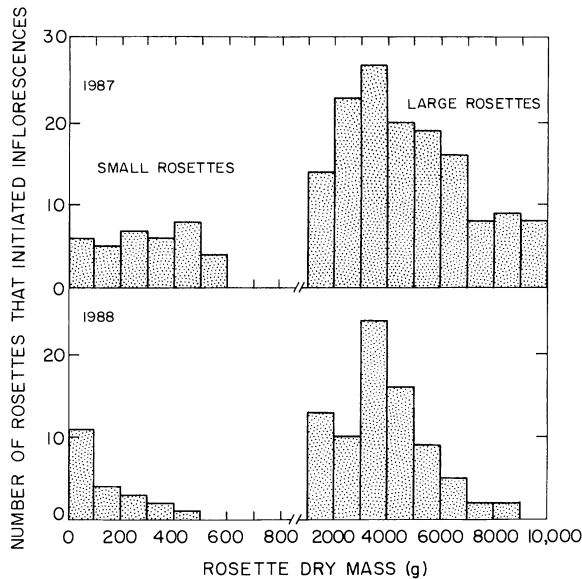


FIG. 1. Frequency distribution of dry mass for rosettes of *Agave deserti* whose inflorescences emerged in 1987 and 1988. Size class intervals are 100 g dry mass for small rosettes and 1000 g for large rosettes.

gain from CO₂ exchange by the leaves and the inflorescence was calculated as the average carbon gain in grams per day, based on two 24-h determinations of CO₂ exchange during a measurement period, multiplied by a conversion factor of 2.63 g dry mass per gram carbon (McCree 1986) and by the number of days in that measurement period. Carbon gain from TNC depletion was calculated as the change in TNC content (grams) during a measurement period multiplied by a production value (grams dry mass produced per gram TNC consumed; Penning de Vries et al. 1974) for the inflorescence and the number of days in that measurement period. The production value of the inflores-

cence, which accounts for respiratory costs associated with the production of the inflorescence, was based on percent protein, determined by multiplying the percent N by 5.75 (Novoa and Loomis 1981), and percent lipid, determined using a chloroform-methanol extraction (Bligh and Dyer 1959).

Statistical analyses used a one-way analysis of variance (ANOVA), with balanced and unbalanced designs as necessary, and was performed with SAS statistical programs (SAS 1985). Significant differences were accepted at the .05 level of probability, and a posteriori testing for significant differences between individual means used the Student-Newman-Keuls multiple comparison test (Keuls 1952).

RESULTS

Morphology and herbivory

Rosettes with inflorescences occurred in two distinct size classes. More than 80% of the rosettes (235 out of 292 for the 2-yr period) had a dry mass >1000 g, with an average of 4010 g, whereas the remaining rosettes had a dry mass <600 g, with an average of 300 g (Fig. 1). Among the small rosettes that flowered, >95% were attached to large rosettes that also flowered; the remaining small rosettes that flowered were attached to nonflowering large rosettes.

The percentage of rosettes in the 5000-m² plot that produced inflorescences declined from 3.55% in 1987 to 0.62% in 1988; 13% of flowering rosettes were <600 g in 1987 and 23% were <600 g in 1988. Small rosettes that flowered in 1987 had significantly higher dry masses and produced taller inflorescences than did flowering small rosettes in 1988 (Table 1). Flowering large rosettes also had more leaves and taller inflorescences in 1987 compared with 1988. When large rosettes and their connected small rosettes both flowered, large rosettes had a greater dry mass and produced taller in-

TABLE 1. Leaf and inflorescence characteristics of *Agave deserti* for large rosettes and connected small rosettes. Data are means \pm 1 SE. For a given rosette size (large or small) and within each of the five rosette morphological characteristics, means with the same superscript letter are not significantly different ($P > .05$, Student-Newman-Keuls test). N = number of rosettes examined.

Condition of rosettes	Rosette morphology	Year			
		1987		1988	
		Large rosette	Small rosette	Large rosette	Small rosette
Large rosette flowered, small rosette did not flower		($N = 38$)	($N = 10$)	($N = 54$)	($N = 14$)
	Leaves per rosette	49 \pm 2 ^a	5.3 \pm 0.6 ^d	40 \pm 1 ^b	5.7 \pm 0.5 ^d
	Mean leaf length (cm)	30 \pm 1 ^a	25 \pm 2 ^d	32 \pm 1 ^a	25 \pm 1 ^d
	Rosette dry mass (g)	4310 \pm 285 ^a	291 \pm 57 ^d	3800 \pm 231 ^b	307 \pm 42 ^d
	Height of inflorescence (m)	3.47 \pm 0.12 ^a	...	3.11 \pm 0.10 ^b	...
	Number of lateral branches	17 \pm 1 ^a	...	15 \pm 1 ^b	...
Large rosette flowered, small rosette flowered		($N = 22$)	($N = 48$)	($N = 19$)	($N = 22$)
	Leaves per rosette	49 \pm 3 ^a	9.4 \pm 0.4 ^e	44 \pm 3 ^b	6.5 \pm 0.4 ^d
	Mean leaf length (cm)	34 \pm 1 ^a	20 \pm 1 ^e	33 \pm 1 ^a	17 \pm 1 ^f
	Rosette dry mass (g)	5270 \pm 310 ^c	354 \pm 33 ^d	4620 \pm 300 ^a	143 \pm 29 ^f
	Height of inflorescence (m)	3.92 \pm 0.12 ^c	1.18 \pm 0.04 ^e	3.52 \pm 0.16 ^a	0.79 \pm 0.04 ^f
	Number of lateral branches	14 \pm 1 ^b	5.6 \pm 0.3 ^e	15 \pm 1 ^b	4.9 \pm 0.4 ^e

TABLE 2. Percent of inflorescences of large rosettes and small rosettes in different conditions in 1987 and 1988. *N* = number of rosettes examined.

Inflorescence condition	1987		1988	
	Large rosette (<i>n</i> = 122)	Small rosette (<i>n</i> = 50)	Large rosette (<i>n</i> = 81)	Small rosette (<i>n</i> = 22)
	Percent of rosettes in each condition			
Matured	84	24	88	9
Aborted	0	12	1	14
Consumed	16	64	11	77

inflorescences than did large rosettes without flowering small rosettes (Table 1).

Herbivory by desert mammals, usually within 2–3 wk of inflorescence emergence, reduced the number of inflorescences that attained a mature, seed-bearing stage. For 1987 and 1988, only desert bighorn sheep (*Ovis canadensis*) were observed to consume the inflorescences of large rosettes, consuming an average of 14% of them (Table 2). The diurnal antelope ground squirrel (*Ammospermophilus leucurus*) was the only herbivore observed consuming the inflorescences of small rosettes, and they consumed an average of 71% of these inflorescences over the 2-yr period.

Severing experiment

Small rosettes that were severed from large rosettes in February 1988 before any inflorescences emerged did not produce inflorescences, even though 73% of the previously connected large rosettes flowered. When the rhizome connection between a flowering small rosette and a flowering large rosette was severed 6 d after the inflorescence of the small rosette emerged, growth of the inflorescence of the small rosette was reduced. For very small rosettes (<30 g dry mass), inflorescence growth ceased 8 d after severing and the height was reduced 63% compared with intact small rosettes (Fig. 2A). Small rosettes of 60–200 g dry mass exhibited continued growth of the inflorescence until 29 d after severing; height was reduced 64% compared with intact small rosettes (Fig. 2B). The largest of the small rosettes (200–600 g dry mass) exhibited growth of the inflorescence for 49 d, irrespective of severing, but the final height of the inflorescence was 36% lower for severed small rosettes compared with intact small rosettes (Fig. 2C). Although severing the rhizome connection reduced the growth of the inflorescence of small rosettes, there was no concomitant change in the height of the inflorescence of large rosettes (Fig. 2D).

CO₂ exchange

During the early stages of inflorescence development for the two measurement dates in March, total net CO₂ uptake over 24-h periods for leaves of flowering rosettes was 24% greater than that for leaves of nonflow-

ering rosettes (Fig. 3A, B). However, during inflorescence elongation in April and early May, leaves of flowering rosettes exhibited 32% less total net CO₂ uptake than did their nonflowering counterparts (Fig. 3C, D). Decreasing soil water availability ($\psi_{\text{soil}} < -1.5$ MPa) from mid-May until seed maturation in August likely reduced net CO₂ exchange for all rosettes; in late May and June, exchange rates were <10% of the maximum values measured in March (Fig. 3E, F). Total daily net CO₂ exchange by the inflorescence was always negative (i.e., release), but such fluxes became less negative as the inflorescence matured (Fig. 3). Two days after a 48-mm rainfall on 21 August 1988, leaves of nonflowering rosettes had nearly maximal nighttime stomatal conductance, indicating recovery from the drought, whereas leaves of flowering rosettes had maximal conductances over 100-fold less.

The decline in net CO₂ exchange capacity of leaves of flowering rosettes was accompanied by reductions in leaf nitrogen and chlorophyll contents in 1988. The leaf nitrogen content expressed as a percentage of leaf dry mass declined from $0.57 \pm 0.09\%$ (mean \pm SD, *n*

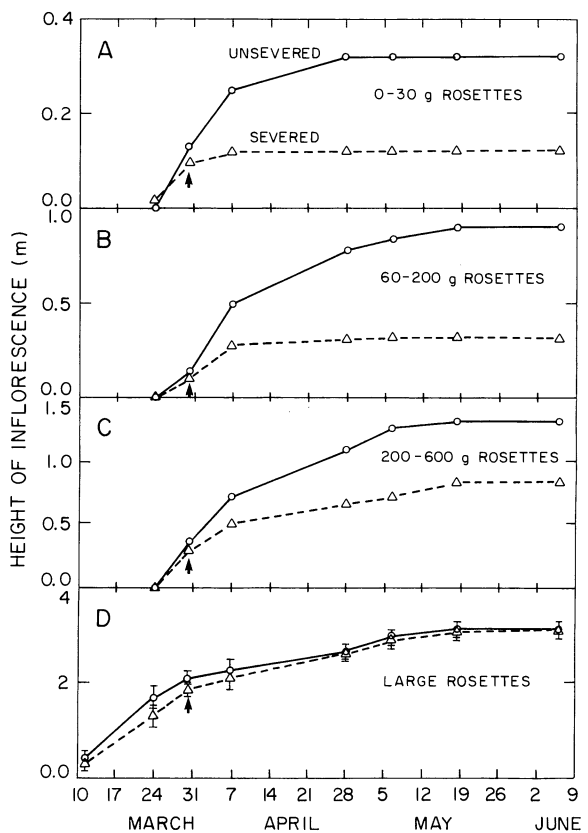


FIG. 2. Growth of inflorescences for severed (Δ — Δ) and unsevered (\circ — \circ) rosettes of different sizes. The connection between flowering large rosettes and flowering small rosettes was severed (indicated by arrows) on 30 March 1988. Data are based on two small rosettes or six large rosettes (standard error bars are shown) in each size class for each treatment.

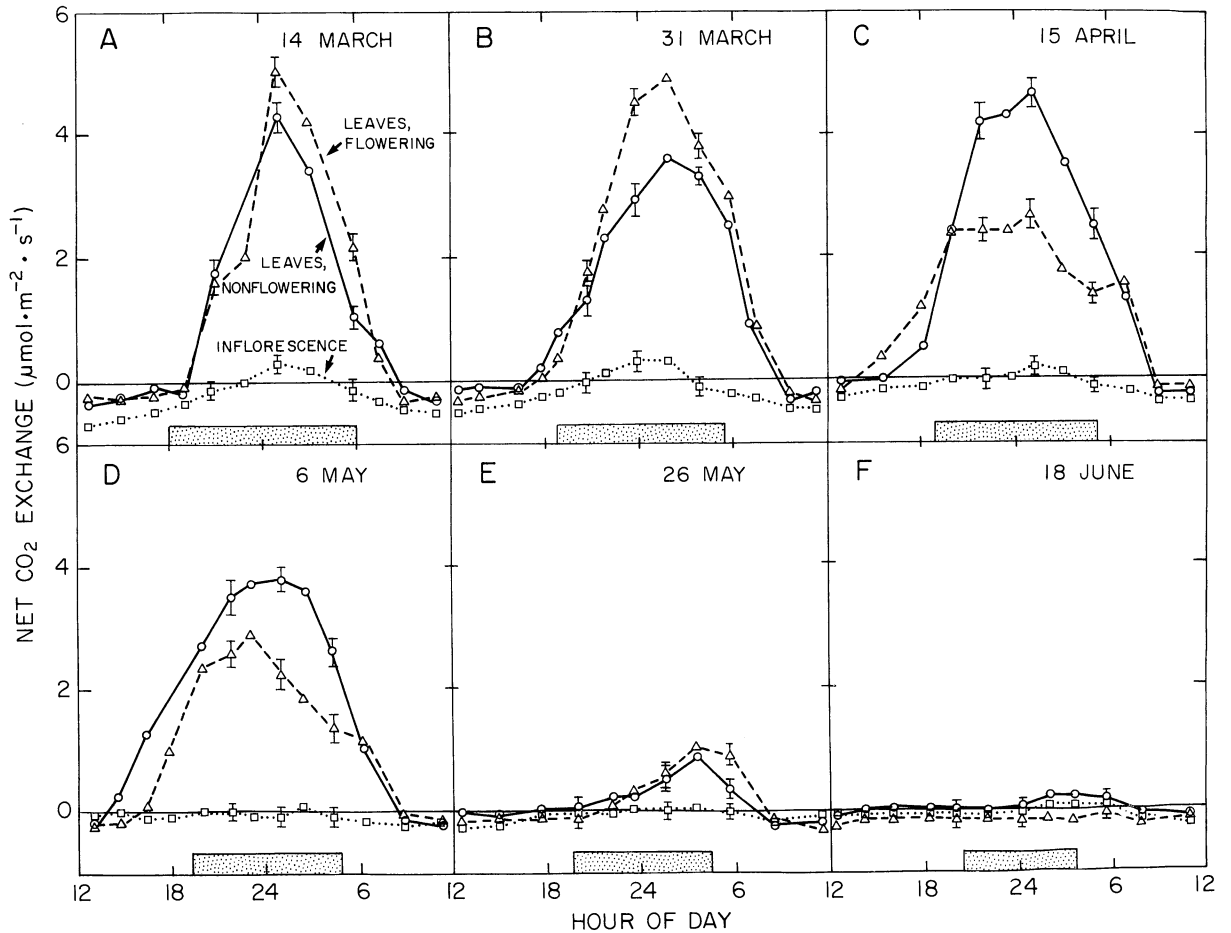


FIG. 3. Daily net CO₂ exchange over 24-h periods for the leaves of flowering (Δ - Δ) and nonflowering (\circ - \circ) large rosettes and midheight on the inflorescence (\square - \square) of flowering large rosettes for six dates in 1988. Data for leaves are expressed as the mean for two leaves per rosette and three rosettes per condition; data for inflorescences are means for three inflorescences. Representative standard error bars are shown. Stippled horizontal bars indicate night.

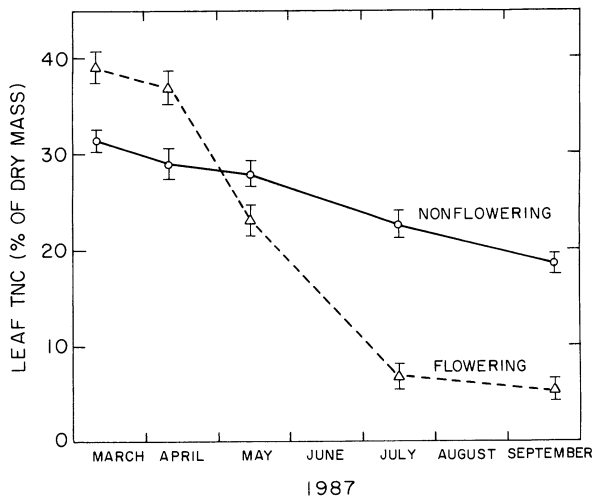


FIG. 4. Changes in total nonstructural carbohydrate (TNC) in leaves of flowering (Δ - Δ) and nonflowering (\circ - \circ) rosettes during inflorescence development in 1987. Data are expressed as means \pm SE for five rosettes under each condition.

= 3 rosettes) on 7 March to $0.25 \pm 0.02\%$ on 6 May and $0.21 \pm 0.04\%$ on 18 June; dead leaves on 12 September had $0.14 \pm 0.01\%$ N. Leaves of nonflowering rosettes had a nitrogen content of $0.59 \pm 0.06\%$ ($n = 12$) on these four dates. Leaves of flowering rosettes progressively became chlorotic, older leaves first, as the inflorescence grew and matured. The leaf chlorophyll content was $920 \pm 15 \text{ mg/m}^2$ ($n = 3$) on 7 March, $730 \pm 11 \text{ mg/m}^2$ on 15 April, and $465 \pm 12 \text{ mg/m}^2$ on 18 May in leaves of flowering rosettes; by 17 August, these leaves were brown and had chlorophyll contents of $45 \pm 3 \text{ mg/m}^2$. Leaves of nonflowering rosettes had a chlorophyll content of $910 \pm 20 \text{ mg/m}^2$ ($n = 12$) on these four dates.

Total nonstructural carbohydrates

When the inflorescence emerged in early March 1987, leaves of flowering rosettes had TNC levels of nearly 40% compared with 31% for nonflowering rosettes of similar size (Fig. 4). By mid-May, when the stalk of

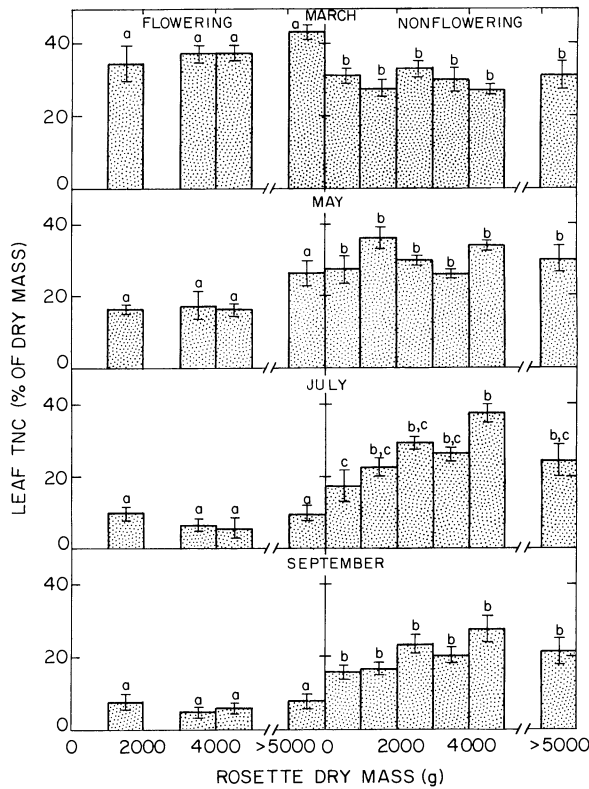


FIG. 5. Total nonstructural carbohydrate (TNC) in leaves of flowering ($n = 12$) and nonflowering ($n = 24$) rosettes of different sizes during inflorescence development in 1988. Means with the same letter within a treatment are not significantly different ($P > .05$, Student-Newman-Keuls test). Data are presented as means \pm SE.

the inflorescence had nearly attained its maximum height and flowers had begun to open, TNC levels in the leaves of the flowering rosettes decreased to 23%. TNC levels declined to 7% in mid-July during fruit maturation. TNC levels in leaves of nonflowering rosettes also decreased, but not as precipitously, and reached a low of 18% in September (Fig. 4). Leaf TNC levels for flowering rosettes decreased from 38% in March 1988 to 6% in September 1988, while TNC levels in nonflowering rosettes decreased from 30 to 20% (Fig. 5), similar to the decrease in 1987. Within the same treatment, no significant differences occurred among rosettes of different sizes for the four measurement periods, except that in July nonflowering rosettes < 1000 g in dry mass had significantly lower TNC levels than did larger rosettes (Fig. 5).

Carbon balance

The TNC reserves of flowering rosettes provided 70% of the carbon required to produce the inflorescence, and CO_2 uptake by the leaves and the inflorescence provided the remaining 30% (Table 3). The nitrogen content averaged $1.02 \pm 0.04\%$ ($\bar{X} \pm \text{SD}$ for $n = 3$

rosettes) of inflorescence dry mass, indicating a protein content of 5.87%, and the lipid content of the inflorescence averaged $1.89 \pm 0.09\%$ ($n = 3$). These percentages indicated a production value of 0.77 g dry mass of inflorescence produced per gram TNC consumed. The measured dry mass of the inflorescence averaged 1533 ± 230 g ($n = 3$), of which the main stalk and lateral branches contributed 84%, the fruit pods 5%, and the seeds 11%. The estimated contribution of carbon toward production of the inflorescence (Table 3) was thus within 6% of the measured dry mass of the inflorescence.

DISCUSSION

Before flowering will occur, isolated rosettes of *Agave deserti* must attain a minimum size, above which the probability of flowering increases with size, as noted for other plants (Gross 1981, Threadgill et al. 1981, Hirose and Kachi 1982, Pitelka et al. 1985). Rosettes of *A. deserti* that flowered had significantly higher leaf TNC levels than rosettes that did not flower, suggesting that a critical carbohydrate level must be attained for flowering to occur (Sadik and Ozbun 1968, Bodson 1977, Friend et al. 1984, Sanz et al. 1987). A high critical level of leaf carbohydrate required to initiate flowering, nearly 40% for rosettes of *A. deserti*, has the selective advantage of ensuring sufficient carbohydrate reserves to support the energy demands of producing an inflorescence. This is especially important for long-lived semelparous plants such as *A. deserti* and *Frasera speciosa* (Inouye 1986), whose elaborate and massive inflorescences represent their sole sexual reproductive output in 40–55 yr.

Nonflowering rosettes of *A. deserti* of different sizes had similar percent TNC levels in their leaves, although the total amount of TNC increased with rosette dry mass. The time required to increase the leaf TNC level prior to inflorescence emergence is not known, but the process probably begins 2 yr before emergence

TABLE 3. Estimated sources of carbon for production of the inflorescence in 1988. Carbon gain from CO_2 exchange was determined from 24-h measurements of CO_2 exchange, and carbon gain from TNC was determined from changes in leaf TNC content during production of the inflorescence.

Measurement period	Source of carbon for inflorescence			
	CO ₂ exchange		TNC from rosette (g dry mass)	Total (g dry mass)
	Leaf (g dry mass)	Inflorescence (g dry mass)		
14 Mar–31 Mar	128	–1.5	72	198
31 Mar–15 Apr	111	–1.3	176	286
15 Apr–6 May	127	–1.2	228	354
6 May–26 May	65	–1.1	158	222
26 May–18 Jun	2	–1.2	198	199
18 Jun–11 Aug	0	0.0	185	185
14 Mar–11 Aug	433	–6.3	1017	1444

when the vegetative shoot apex becomes a reproductive apex (Nobel 1987). The subsequent buildup of carbohydrates may result from reduced vegetative growth (Gent 1986) and increased storage of carbon to support growth of the inflorescence. The decline in TNC level in nonflowering rosettes of *A. deserti* during the dry summer, especially within small rosettes having low TNC content, reflects carbohydrate utilization for plant maintenance and growth when drought severely reduces net CO₂ exchange (Tissue and Nobel 1988). Similar seasonal declines in TNC level due to drought have been noted for *Opuntia lindheimeri* (Potter et al. 1986) and *O. bigelovii* (Sutton et al. 1981).

The occurrence of large nonflowering rosettes suggests that other factors, in addition to stored carbohydrate reserves, are necessary to support flowering. The percentage of rosettes of *A. deserti* that flower annually is positively correlated with the number of wet days ($\psi_{\text{soil}} > -0.5$ MPa) 2 yr prior to flowering and negatively correlated with the percentage of rosettes in the population that flowered in the previous year (Nobel 1987). Conversion of the vegetative shoot apex into a reproductive shoot apex 2 yr prior to emergence of the inflorescence thus appears to be cued by soil moisture, as might be expected in a desert environment. High rates of flowering induced by favorable soil water conditions leave a small pool of rosettes with sufficient carbohydrate reserves to flower the next year. Nearly the maximum percentage of rosettes in the Agave Hill population of *A. deserti* that can flower in a year (3.80%; Nobel 1987) flowered in 1987, leading to \approx sixfold fewer rosettes flowering in 1988.

The large rosettes that flowered in 1987 produced taller inflorescences with more flowers and fruits than did the rosettes that flowered in 1988. Plant size and fruit production generally were positively correlated, as has been shown for *Yucca whipplei* (Udovic 1981, Aker 1982a, b) and *Agave schottii* (Schaffer and Schaffer 1979). Because seedling establishment of *A. deserti* is rare and dependent on soil water conditions (Jordan and Nobel 1979), greater seed production in 1987 compared with 1988 will not necessarily result in greater seedling establishment. From 1961 to 1984, only 2 yr (1967 and 1982) supported seedling survival beyond the 1st yr of establishment (Jordan and Nobel 1979, Nobel 1985). Besides low rates of inflorescence production and harsh environmental conditions for seedling establishment, herbivory and abortion reduce the percentage of inflorescences that reach a mature seed-bearing stage.

Small rosettes contributed carbohydrate to the production of their own inflorescences. Assuming that the entire TNC reserve of the small rosette was used to produce the inflorescence and the CO₂ exchange rate of the small rosette was equivalent to that of its connected flowering large rosette, small rosettes of up to 30 g dry mass provided 26% of the carbon necessary to produce their inflorescence, with the remaining car-

bon supplied by the large rosette. The contribution of carbon by small rosettes increased with size, reaching 65% for 200–600 g rosettes, reflecting the gradual independence of small rosettes from their connected large rosettes (Raphael and Nobel 1986). Indeed, small nonflowering rosettes of *A. deserti* depend on their connected large rosette for carbohydrate (Tissue and Nobel 1988) and water (Raphael and Nobel 1986) until they reach \approx 300 g dry mass.

The precocious flowering of small rosettes appears to be a consequence of the rhizome connection between small rosettes and large rosettes of *A. deserti*, as the rhizome apparently functions as a conduit for a growth substance or a set of chemical conditions that triggers the flowering process. When the rhizome connection between large rosettes and their connected small rosettes was severed \approx 4 wk before inflorescences emerged on any rosette, most of the large rosettes eventually flowered, but in the same period none of the previously connected small rosettes flowered. This suggests that the signal to emerge for the inflorescence of the connected small rosette is transmitted at approximately the same time as the inflorescence of the large rosette emerges. These data do not indicate the time required for floral initiation of the small rosette; however, a 2-yr period is required for large rosettes of *A. deserti* (Nobel 1987) and a 2–3 yr period is needed for *Frasera speciosa*, another long-lived semelparous plant (Inouye 1986).

During the early stages following inflorescence emergence, higher rates of net CO₂ uptake for leaves of flowering rosettes of *A. deserti* compared with nonflowering rosettes can partially offset the additional energy requirements associated with flowering. In this regard, higher net CO₂ uptake at night for the CAM plant *Kalanchoe blossfeldiana* is associated with a higher fraction of the plants flowering (Spear and Thimann 1954). Studies on illuminated *Solidago canadensis* ramets connected to shaded sibling ramets (Hartnett and Bazzaz 1983) and on partially defoliated trees and range grasses (Detling et al. 1979, Heichel and Turner 1983) demonstrate that leaf net CO₂ uptake increases in response to an additional energy demand. The decline in net CO₂ uptake for leaves of flowering rosettes of *A. deserti*, beginning in April and continuing throughout the flowering period, was accompanied by lower chlorophyll and nitrogen contents in the leaves. Similar decreases in leaf photosynthesis during inflorescence development occur in soybean (Wittenbach et al. 1980), in part reflecting decreased chlorophyll content and translocation of nitrogen from leaves to nitrogen-rich seeds (Koch and Schrader 1984).

Net CO₂ exchange for inflorescences of *A. deserti* was always negative over a 24-h period but occasionally reached positive values for a few hours at night. CO₂ exchange for the reproductive structures of other plants is also usually negative but can still largely offset respiration and provide 2–65% of the reproductive struc-

ture's carbon requirement (Tieszen and Imbamba 1978, Bazzaz et al. 1979, Werk and Ehleringer 1983, Williams et al. 1985). The decreased loss of CO₂ as the inflorescence matured and respiration costs diminished suggests that CO₂ exchange by the inflorescence of *A. deserti* largely offsets its own respiration costs. In any case, the carbon loss from CO₂ exchange of the inflorescence was only 0.4% of the total carbon required to produce the inflorescence.

In summary, the CO₂ uptake capability of *A. deserti* is not sufficient to meet the carbon needs of the rapidly growing inflorescence, so a massive translocation of carbohydrates to the inflorescence is required. In particular, the substantial carbohydrate reserves of *A. deserti* provided 70% of the carbon required to produce the 1.53 kg inflorescence, and CO₂ uptake by the leaves and inflorescence provided the remaining 30%. The movement of carbohydrates in such large quantities contrasts with iteroparous plants that annually allocate no > 15% of their carbohydrate to reproduction (Larcher 1975, Abrahamson 1979). Evidently, the evolutionary advantage of semelparity in *A. deserti* offsets the cost of delaying reproduction such that sufficient carbohydrates can be stored to support the production of a single massive inflorescence.

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