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Allocation of resources to flowering and fruit production in *Hesperaloe funifera* (Agavaceae)

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Hesperaloe funifera has long, thin fibres that can be used to produce paper with exceptional physical properties. Agronomic investigations have shown that the crop can be harvested first after five years, and subsequently every three years thereafter. During the third or fourth year the plants produce a large inflorescence. The objective of this study was to determine the amounts of resources (carbohydrates and nitrogen) consumed during flowering, in order to gauge the potential for shortening the harvest cycle through control of flowering.

An average inflorescence in plants flowering for the first time had a mass of 1111 g, which required 1430 g of soluble carbohydrate and 16.9 g of nitrogen. Total carbohydrate stored in such a plant prior to flowering was estimated to be just 570 g, indicating that most of the carbohydrate used to support flowering had to come from current photosynthesis. Estimated N requirements for flowering in four-year-old stands are 165–220 kg N ha^{-1}. Removal or inhibition of developing flower stalks thus would appear to have the potential to redirect considerable amounts of carbohydrate to leaf production and greatly reduce nitrogen fertilizer requirements.

Keywords: Agavaceae; carbohydrates; flowering; fructan; fruit set; *Hesperaloe funifera*; nitrogen; total non-structural carbohydrates

Introduction

Hesperaloe funifera (Koch) Trel. is a member of the Agavaceae, a family which includes several 'hard fibre' crops and products such as sisal (*Agave sisalana* Perrine), henequen (*A. fourcroydes* Lem.), ixtle (*Agave lechuguilla* Torr. or *Yucca carnerosana* (Trel.) McKelvey), and Mauritius hemp (*Furcraea gigantea* Venth.). The leaf fibres of *H. funifera* consist of usually long, thin cells (McLaughlin & Schuck, 1991, 1992) that form exceptionally strong paper (Reeves *et al.*, 1994; McLaughlin, in press). Efforts are underway to develop this plant as a new fibre crop for arid and semi-arid lands (McLaughlin, 1995, 1996).

Hesperaloe funifera is an acaulescent rosette-forming plant. The plant initially consists of a single rosette which grows very slowly during its first year in cultivation (McLaughlin,

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1995, 1996). The apical meristem of this primary rosette changes from a vegetative to a reproductive condition in the third, (usually) fourth year, or fifth year in cultivation. After flowering, 3–6 lateral or secondary rosettes begin developing from the crown and the plant then grows at a much more rapid rate (McLaughlin, 1995).

The flower stalk of *Hesperaloe funifera* is 2–5 m tall. All inflorescences produce several floriferous primary branches; in addition some inflorescences produce shorter floriferous secondary branches, usually from the axils of the primary branches but occasionally from the axils of flowering nodes. Flowers are produced at nodes resembling short shoots along these lateral branches and along the distal portion of the flower stalk above the uppermost primary branch. Each node produces several flowers over an extended flowering season. Typically, several buds are present at each node but only one flower is open at any one time, and usually only a single fruit will mature per node, but not all nodes produce mature fruits. Plants begin flowering in May and most inflorescences continue producing some flowers until the first frost, usually in late October or early November in Arizona. The first capsules begin to mature in late June and early July. Weekly capsule production reaches a peak during the first two weeks of August and continues at a greatly reduced rate into early November.

Fields of *Hesperaloe funifera* can be harvested after five years in cultivation (McLaughlin, 1995). The field can essentially be 'mowed' like a lawn and will regrow to produce subsequent harvests every 3 years after the first harvest. Plants flower again during their regrowth, this time from the secondary rosettes. The economics of fibre production from *Hesperaloe* could be improved if this harvest cycle could be shortened, or if yields per harvest could be increased.

Numerous researchers have noted that plants in family Agavaceae must invest considerable resources to produce the large inflorescences that are characteristic of the species in this family. Specific resources needed for flowering include carbohydrates (CH_2O), water and nutrients. Resources consumed during inflorescence production, flowering, and fruit maturation can come from stored reserves (CH_2O, water, minerals) in the leaves, stems, crowns, or roots, or from current photosynthesis (CH_2O) and uptake (water, minerals). In *Agave americana* L. (MacCallum, 1908), *A. deserti* Engelm. (Nobel, 1977), *A. lechuguilla* (Freeman & Reid, 1985), and probably most species of *Agave*, leaves provide nearly all of the CH_2O and water needed to support flowering. During flowering of *A. deserti*, leaves lose dry matter and water, and chlorophyll is broken down (Nobel, 1977). That is, leaves of such species must be dismantled to provide the CH_2O, water, nitrogen, and other nutrients needed for flowering. In *Yucca baccata* Torr., considerable amounts of stored carbohydrate are mobilized to support flowering (Wallen & Ludwig, 1978; Ludwig *et al.*, 1980), but the leaves remain green, continuing to photosynthesize and transpire, usually for several years. *Hesperaloe funifera* is similar to *Y. baccata* in maintaining physiologically active leaves during and after flowering and fruit set.

Only over the short term do we need seed production in *Hesperaloe* to advance its commercialization. On a commercial farm managed only for leaf fibre production, the investment of CH_2O, water, and nutrients into flowering and seed production would come at a cost to leaf production. Removal of developing flower stalks could thus serve to reallocate resources to leaf production, either increasing the yield at five years or possibly shortening the harvest cycle. The objective of this study was to determine exactly how much CH_2O and N are invested in flowering and leaf production in *H. funifera*.

Materials and methods

Study sites

Studies were conducted at the University of Arizona's Bioresources Research Facility (BRF) at Tucson, Arizona, and at the Maricopa Agricultural Center (MAC) at

Maricopa, Arizona. The BRF is in southern Arizona (32°8′N, 110°58′W) at an elevation of 760 m; the MAC is in central Arizona (33°4′N, 111°58′W) at an elevation of 365 m. *Hesperaloe funifera* plants used in all studies came from irrigated, fertilized field plots.

Estimating flower number

During 1992 a sample of 32 *H. funifera* plants at BRF with emerging inflorescences were tagged and selected for intensive observations of flower production. Flower stalk heights and lengths of all primary and secondary branches were measured. With many species of Agavaceae it is possible to determine the number of flowers produced on an inflorescence simply by counting the persistent pedicels or pedicel scars of aborted flowers and fruits. Flowering pedicels on *H. funifera* are more fragile, however, and counting pedicels or scars on dried flower stalks after seeds have been dispersed did not prove to be a reliable method for determining the number of flowers produced. We therefore counted the number of nodes on each branch of each inflorescence and tagged a sample of three randomly selected nodes per branch for counting the number of flowers produced during the flowering season. For each plant the number of flowers was estimated by multiplying the mean number of flowers per node times the mean number of nodes per unit length of flowering branches times total flowering branch length. A regression equation was then developed for estimating number of flowers as a function of inflorescence height and branch length.

Estimating capsule production and fruit set

In 1997 a sample of 100 *H. funifera* plants with emerging inflorescences was selected for determining capsule production and fruit set. The plants had been harvested in 1992 and 1995 and were thus regrowing to produce their third crop. Individuals selected ranged from those with a single rosette and inflorescence to plants with numerous rosettes and up to 6 inflorescences. The 100 plants had a total of 228 inflorescences. Flower stalk height and branch lengths were recorded, and mature pods were harvested from the plants on a weekly basis from June to November. Number of flowers per inflorescence in this sample was estimated using the regression developed from the sample of 32 plants intensively investigated for flower production, described above. Fruit set was determined by totaling the number of capsules produced by each inflorescence and dividing by the estimated number of flowers produced.

Carbohydrate analyses

Thirty 3-year-old *H. funifera* plants from MAC were sampled. Ten plants that were just beginning to send up inflorescences were sampled on 27, March 1997, by first harvesting the leaves at 2–3 cm above ground level and then carefully excavating the crown and roots. ‘Crowns’ as used here actually include the crown *per se* and attached leaf bases below the point of leaf harvest. On 5, June 1997, two additional sets of 10 plants were sampled, 10 with fully developed inflorescences and 10 plants that did not produce inflorescences in 1997. Crowns were separated from roots in the lab and all parts were oven-dried at 37°C to constant weight then ground to a powder in a Wiley mill with a 0·5-mm mesh screen.

Samples of leaf, crown, root and inflorescences were analysed for glucose, fructose, sucrose, starch and fructan. A tissue sample was treated with 8 M HCl and dimethysulphoxide (DMSO) to solubilize the starch, which was then digested with amyloglucosidase using a Starch UV-test kit (Boeringer-Mannheim, GmbH #207748) to

produce fraction **A**, glucose from starch plus free glucose. Glucose, fructose, and sucrose were determined by enzymatic digestion with a Sucrose/D-Glucose/D-Fructose UV-test kit (Boeringer-Mannheim, GmbH #716260). A water extract was treated with invertase, hexokinase (HK), and glucose-6-phosphate dehydrogenase (G6PDH) to yield fraction **B**, gluocose from sucrose plus free glucose. A second water extract was treated with HK and G6PDH to yield fraction **C**, free glucose. Fraction **C** was further treated with phosphoglucoseisomerase (PGI) to yield fraction **D**, glucose from free fructose plus free glucose. Another tissue sample was treated with 0·005 M H_2SO_4 to digest fructans. This extract was treated with HK and G6PDH to yield fraction **E**, glucose from fructans plus free glucose. Fraction **E** was then treated with PGI to yield fraction **F**, glucose from free fructose, glucose from fructose in fructans, glucose from fructan, and free glucose. The percentages of the various carbohydrates are calculated as follows: free glucose = **C**, sucrose = **B**-**C**, free fructose = **D**-**C**, starch = **A**-**C**, and fructan = **F**-**D**. Total non-structural carbohydrate (TNC) was estimated as the sum of free glucose, sucrose, free fructose, starch, and fructan.

Differences in carbohydrate percentages within roots, crowns, and leaves between the three groups of plants (not flowering, initiating flower stalks, and fully-developed flower stalks) were analysed by ANOVA. Differences in carbohydrate levels in flower stalks between plants just initiating flower stalks and those with fully developed flower stalks were analysed with *t*-tests.

Carbohydrate requirement for flowering

Mean dry weights for flower stalks, flowers, capsules and seeds were measured or calculated for the samples of 32 inflorescences monitored for flower production in 1992 and for the sample of 228 inflorescences from 100 plants used to monitor fruit production in 1997. To determine the amounts of carbohydrates required to produce these flower stalks (as glucose requirements, Loomis & Conner, 1992), we assumed that flower stalks, flowers, capsules and seeds were composed entirely of carbohydrate, protein and lipid. Protein was determined as 6·25 time the nitrogen content (see below), lipid contents were measured by extraction of duplicate samples with hexane for 8 h in Soxhlet extractors, and the carbohydrate fractions were then determined by subtraction. Biochemical requirements to produce these fractions are 1·21 g glucose g^{-1} carbohydrate, 2·48 g glucose g^{-1} protein, and 2·71 g glucose g^{-1} lipid (Loomis & Connor, 1992).

Nitrogen determinations

Samples of leaves, crowns, roots, flowers, capsules, and seeds of *H. funifera* were analysed for total nitrogen at the University of Arizona Soil, Water, and Plant Testing Laboratory using an automated elemental NCS analyser (Carlo Erba NA-1500). Total inflorescence and whole-plant N levels were estimated by summing the products of the biomass of the different plant parts by their respective percentage N contents.

Results and discussion

Number of flowers produced per flower stalk

In the sample of 32 plants monitored for flower production throughout the 1992 growing season, flower stalk height was 352 ± 10 cm (mean ± S.E.), there were 10·3 ± 0·6 primary branches (including the terminal, flowering portion of the flower stalk) averaging 66·9 ± 2·4 cm in length, and there were 3·8 ± 0·8 secondary branches

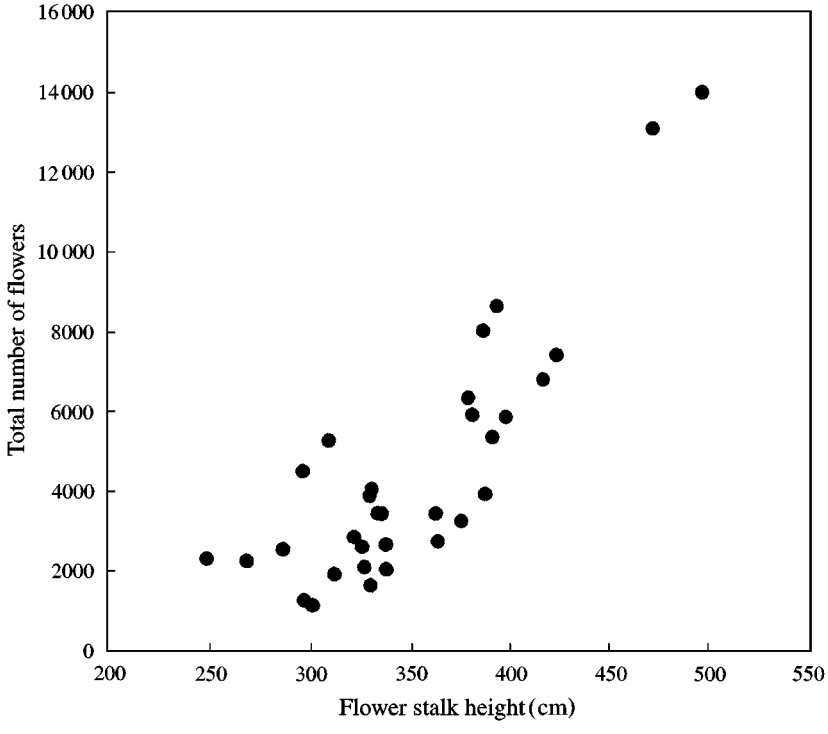

Figure 1. Plot showing the number of flowers versus flower stalk height in a sample of 32 inflorescences of *Hesperaloe funifera*.

averaging 28·9 ± 3·0 cm. Secondary branches occurred on 22 of the 32 flower stalks. Primary and secondary branches averaged 43·8 ± 1·8 and 21·3 ± 2·4 nodes per branch, and these nodes produced 8·6 ± 0·4 and 3·4 ± 0·7 flowers per node, respectively. Total numbers of flowers averaged 4081 ± 450 for primary branches, 673 ± 209 for secondary branches, and 4523 ± 548 for the entire inflorescence. In this sample, plants produced an average of 72·5 ± 9·1 capsules per inflorescence for an average fruit set of 1·96 ± 0·21%.

The number of flowers produced by an inflorescence is a function of its height (Fig. 1). Total flower number can be estimated with greater accuracy using a multiple regression with height of the flower stalk and the total length of flowering branches, characters that can easily be measured. Within the range of the 32 flower stalks shown in Figure 1, either a linear regression or a power curve provides a reasonable fit to the data. The power curve is more useful over a wider range of flower-stalk sizes, since the linear regression estimates a negative number of flowers for shorter inflorescences. The power curve more accurately estimates the number of flowers on small inflorescences but does underestimate the number of flowers produced on the larger inflorescences. The equation combining flower stalk height and branch length in a power curve is:

$$F = \exp\,[1{\cdot}121\ (\ln H) + 0{\cdot}992\ (\ln B) - 4{\cdot}752],\ r^2 = 0{\cdot}772\ (p < 0{\cdot}001)$$

where F is the total number of flowers, H is total flower stalk height in cm, and B is total length of flowering branches in cm.

Fruit production and fruit set

The 228 inflorescences produced by the sample of 100 plants monitored in 1997 at BRF encompassed a large range of variation in all traits measured. Heights of flower stalks ranged from 131 to 572 cm (370 $\pm$ 4, mean $\pm$ S.E.), estimated number of flowers ranged from 432 to 13 363 (3862 $\pm$ 145), number of capsules ranged from 0 to 125 (38·0 $\pm$ 1·5), and fruit set ranged from 0 to 4·6% (1·15 $\pm$ 0·05%). Mean number of fruits produced and fruit set were both lower in this sample than in the sample of 32 inflorescences monitored in 1992.

In the 1997 sample of 100 plants with 228 inflorescences, 31 plants had a single flowering rosette, 28 plants had two, 27 plants had three, 11 plants had four, two plants had five, and one plant had six flowering rosettes. The number of flowering rosettes on a plant was not related to mean flower stalk height ($r = 0{\cdot}101$, $p = 0{\cdot}316$), number of capsules per inflorescence ($r = -0{\cdot}050$, $p = 0{\cdot}623$), or fruit set ($r = -0{\cdot}086$, $p = 0{\cdot}393$). That is, larger plants—those with a larger number of rosettes—did not produce larger flower stalks with more fruits. This suggests that rosettes within a plant are essentially autonomous in their allocation of resources to sexual reproduction.

Carbohydrate analyses

Results of the carbohydrate analyses are summarized in Tables 1 and 2. Table 1 gives the percentages of starch, fructan, glucose, fructose, sucrose and total non-structural carbohydrates (TNC) determined in roots, crowns, leaves and flower stalks for plants not flowering (Group I), plants initiating flower stalks (Group II) and plants with fully developed flower stalks (Group III). Percentages of all carbohydrates, except glucose, differed significantly between groups; differences between plant parts within groups were significant for all carbohydrates. Percentages of TNC were highest in the roots, and fructan, a polymer of fructose with a terminal glucose unit, was the most abundant non-structural carbohydrate in the roots. Very high percentages of fructan and TNC were also found in the crowns of plants initiating flower stalks. Leaves had the lowest percentages of non-structural carbohydrates in all three groups.

Plants initiating flower stalks (Group II) had the highest percent TNC in roots, crowns and leaves. Percentages of most individual non-structural carbohydrates were highest in Group II plants for all plant parts, with few exceptions. Percent fructose was higher in the roots of Group III plants than in the roots of Group II plants. There were no significant differences between groups in percent glucose in roots. Flower stalks of Group II plants had higher percentages of all carbohydrates than flower stalks of Group III plants.

TNC pools (Table 2) were calculated by multiplying the percent TNC by the mass of each storage organ. Total plant dry weights and proportions of leaves, crowns and roots did not differ greatly among plants selected for inclusion in the three groups. Non-flowering plants averaged 598·3 g DM with 59·6% of the vegetative plant as leaves, 20·3% crowns, and 20·1% roots; plants initiating inflorescences averaged 611·5 g DM consisting of 53·2% leaves, 26·8% crowns, and 20·0% roots; and plants with fully developed flower stalks averaged 640·8 g DM consisting of 55·9% leaves, 24·2% crowns and 19·9% roots. The greatest change in the carbohydrate pool of the plants initiating inflorescences relative to the non-flowering plants was the substantial increase in the amount of TNC stored in the crowns (including the leaf bases). The total TNC pool in the plants initiating inflorescences averaged 146 g, which was depleted to 44 g TNC in plants with fully-developed flower stalks. In the latter group most of the remaining CH_2O occurred in the roots.

Fructan proved to be the major reserve CH_2O in *H. funifera*, accounting for 42% of the whole-plant TNC and 55% in the roots of plants initiating inflorescences. Fructan

Table 1. *Percentages of non-structural carbohydrates in Hesperaloe funifera roots, crowns, leaves, and flower stalks from non-flowering plants, plants initiating flower stalks, and plants with fully-developed flower stalks. Means within a row not followed by the same letter are significantly different ($p < 0{\cdot}05$)*

Plant part	Carbohydrate	Group I. Plants not flowering	Group II. Plants initiating flower stalks	Group III. Plants with fully-developed flower stalks
Roots	Starch	$2{\cdot}3 \pm 0{\cdot}3^{b}$	$3{\cdot}9 \pm 0{\cdot}3^{a}$	$1{\cdot}0 \pm 0{\cdot}3^{c}$
	Fructan	$17{\cdot}7 \pm 1{\cdot}9^{b}$	$24{\cdot}0 \pm 1{\cdot}9^{a}$	$9{\cdot}2 \pm 1{\cdot}3^{c}$
	Glucose	$4{\cdot}8 \pm 0{\cdot}7^{a}$	$5{\cdot}6 \pm 0{\cdot}5^{a}$	$4{\cdot}7 \pm 0{\cdot}3^{a}$
	Fructose	$3{\cdot}6 \pm 0{\cdot}4^{ab}$	$3{\cdot}2 \pm 0{\cdot}2^{b}$	$4{\cdot}5 \pm 0{\cdot}5^{a}$
	Sucrose	$4{\cdot}5 \pm 0{\cdot}5^{b}$	$6{\cdot}6 \pm 0{\cdot}4^{a}$	$3{\cdot}8 \pm 0{\cdot}4^{b}$
	TNC	$32{\cdot}5 \pm 1{\cdot}8^{b}$	$43{\cdot}4 \pm 1{\cdot}9^{a}$	$23{\cdot}3 \pm 2{\cdot}1^{c}$
Crowns	Starch	$0{\cdot}5 \pm 0{\cdot}2^{b}$	$2{\cdot}8 \pm 0{\cdot}2^{a}$	$0{\cdot}1 \pm 0{\cdot}1^{b}$
	Fructan	$1{\cdot}1 \pm 0{\cdot}4^{b}$	$18{\cdot}2 \pm 1{\cdot}4^{a}$	$0{\cdot}2 \pm 0{\cdot}4^{b}$
	Glucose	$1{\cdot}9 \pm 0{\cdot}1^{ab}$	$2{\cdot}2 \pm 0{\cdot}2^{a}$	$1{\cdot}5 \pm 0{\cdot}1^{b}$
	Fructose	$1{\cdot}9 \pm 0{\cdot}2^{b}$	$3{\cdot}3 \pm 0{\cdot}3^{a}$	$1{\cdot}3 \pm 0{\cdot}2^{b}$
	Sucrose	$0{\cdot}7 \pm 0{\cdot}3^{b}$	$4{\cdot}5 \pm 0{\cdot}2^{a}$	$0{\cdot}7 \pm 0{\cdot}1^{b}$
	TNC	$6{\cdot}2 \pm 0{\cdot}7^{b}$	$31{\cdot}0 \pm 1{\cdot}3^{a}$	$3{\cdot}8 \pm 0{\cdot}6^{b}$
Leaves	Starch	$0{\cdot}1 \pm 0{\cdot}1^{b}$	$1{\cdot}9 \pm 0{\cdot}4^{a}$	$0{\cdot}0 \pm 0{\cdot}1^{b}$
	Fructan	$-0{\cdot}1 \pm 0{\cdot}2^{b}$	$0{\cdot}4 \pm 0{\cdot}4^{a}$	$-0{\cdot}1 \pm 0{\cdot}1^{b}$
	Glucose	$1{\cdot}3 \pm 0{\cdot}1^{b}$	$2{\cdot}8 \pm 0{\cdot}2^{a}$	$1{\cdot}1 \pm 0{\cdot}1^{b}$
	Fructose	$1{\cdot}1 \pm 0{\cdot}2^{b}$	$2{\cdot}7 \pm 0{\cdot}2^{a}$	$0{\cdot}8 \pm 0{\cdot}1^{b}$
	Sucrose	$0{\cdot}2 \pm 0{\cdot}1^{b}$	$4{\cdot}6 \pm 0{\cdot}7^{a}$	$0{\cdot}2 \pm 0{\cdot}1^{b}$
	TNC	$2{\cdot}5 \pm 0{\cdot}2^{b}$	$12{\cdot}4 \pm 0{\cdot}9^{a}$	$2{\cdot}0 \pm 0{\cdot}2^{b}$
Flower stalks	Starch		$1{\cdot}3 \pm 0{\cdot}6^{a}$	$0{\cdot}1 \pm 0{\cdot}1^{b}$
	Fructan		$8{\cdot}3 \pm 1{\cdot}1^{a}$	$0{\cdot}0 \pm 0{\cdot}1^{b}$
	Glucose		$4{\cdot}8 \pm 0{\cdot}4^{a}$	$0{\cdot}1 \pm 0{\cdot}1^{b}$
	Fructose		$6{\cdot}6 \pm 0{\cdot}5^{a}$	$0{\cdot}1 \pm 0{\cdot}1^{b}$
	Sucrose		$5{\cdot}8 \pm 0{\cdot}5^{a}$	$0{\cdot}1 \pm 0{\cdot}1^{b}$
	TNC		$26{\cdot}9 \pm 2{\cdot}0^{a}$	$0{\cdot}3 \pm 0{\cdot}1^{b}$

has been reported for other Agavaceae, including *Agave americana* (Bhatia & Nandra, 1979), *A. deserti* (Wang & Nobel, 1998), *A. vera-cruz* Mill. (= *A. lurida* Aiton according to Gentry, 1982) (Dorland *et al.*, 1977), and *Furcraea humboldtiana* Trel. (Olivares & Medina, 1990). Apparently fructan, in particular inulin, is the major storage CH_2O in

Table 2. *Average carbohydrate pools in three-year-old* Hesperaloe funifera *plants. Table entries are amounts (g) of total non-structural carbohydrates. N = 10 plants per group*

Organs	Group I. Non-flowering plants	Group II. Plants initiating flower stalks	Group III. Plants with fully-developed flower stalks
Leaves	8·9	40·3	7·1
Crowns	7·5	50·8	5·9
Roots	39·0	52·9	29·8
Flower stalks	—	2·4	0·8
Total	55·4	146·4	43·6

Agave tequilana Weber, for which this species is exploited commercially (Valenzuela Zapata, 1994). *Hesperaloe esceraloe funifera* differs from *A. deserti* and most other Agavaceae spp. in its use of roots for CH_2O storage. Tissue and Nobel (1988) reported 26·5 to 30·5% TNC in the leaves, 27·4 to 44·2% TNC in the stem + rhizome and just 4·3 to 4·4% TNC in the roots of unshaded *A. deserti* plants. For the whole *Agave* plant, 64·9 to 72·5% of the TNC reserves occurred in unfolded leaves, 12·7 to 21·5% in the stem + rhizome and just 0·9 to 1·5% in the roots (Tissue & Nobel, 1988). In *H. funifera* the highest concentration of TNC occurs in the roots (Table 1), which contain about one-third of the whole plant TNC reserves (Table 2).

Carbohydrate requirement for flowering

The dry weight of senescent flower stalks at the end of the flowering season for the 228 inflorescences monitored in 1997 averaged 330 $\pm$ 10 g. Mean dry weights per plant for capsules and seeds were 59·4 $\pm$ 2·3 g and 69·6 $\pm$ 2·9 g, respectively. Samples of 157 fresh flowers obtained from May 7-13, 1997 and 271 fresh flowers obtained from May 13-22, 1997, were 0·164 g and 0·142 g per flower, respectively. Aborted flowers obtained at the same times weighed 0·084 and 0·085, respectively. The differences in dry matter between fresh and aborted flowers could represent either dry matter lost from the flowers (in pollen and nectar, or flower parts not recovered with aborted flowers), or dry matter recovered by the inflorescence prior to dehiscence of the aborted flowers. Howell and Roth (1981), for example, found that pollen and nectar accounted for 13·5% of the energy content of flowers of *Agave palmeri* Engelm. As our estimate of dry matter irretrievably invested per flower we used the average difference between the lower fresh flower dry weight and the dry weight of aborted flowers—0·113 g per flower. Estimates for total dry weights of flowers produced per inflorescence were then 436·7 $\pm$ 16·4 g. Total inflorescence dry weights were 895 $\pm$ 28 g. Flower stalks, flowers, capsules and seeds accounted for 36·9%, 48·7%, 6·6% and 7·8%, respectively, of the total inflorescence dry weight.

For the 32 inflorescences studied in 1992, dry weight averaged 1111 $\pm$ 108 g distributed as follows: stalks, 357 $\pm$ 33 g; flowers 511 $\pm$ 62 g; and capsules and seeds, 243 $\pm$ 31 g. In this sample, flower stalks, flowers, and capsules + seeds accounted for 32, 46 and 22%, respectively, of the total dry weight of the inflorescences.

Estimated CH_2O requirements in *Hesperaloe* inflorescences were: 1·24 g glucose g^{-1} flower stalk, 1·42 g glucose g^{-1} flowers, 1·37 g glucose g^{-1} capsules and 1·72 g glucose g^{-1} seed. Reynolds & Cunningham (1980) found similar values for flowers, capsules, and seeds in *Yucca baccata* and *Y. elata* Engelm.; their estimates of CH_2O for the stalks of these *Yucca* species were considerably higher (1·50 g glucose g^{-1}), however.

Estimated total CH_2O requirements for the 32 inflorescences monitored in 1992 and the 228 inflorescences monitored in 1997 are shown in Table 3. Estimated total CH_2O requirements were higher in 1992, averaging 1429 $\pm$ 139 g, than in 1997, which averaged 1230 $\pm$ 38 g. The estimated amounts of CH_2O invested in the flower stalk were similar in the two samples. Because of the higher fruit set in the 1992 sample, more CH_2O was invested in the capsules and seeds for that sample. Most of the CH_2O was invested in the flower stalks and flowers for both samples. Just 218·9 $\pm$ 27·5 g and 116·3 $\pm$ 4·9 g of CH_2O went to seed production in the 1992 and 1997 samples—about 15·7 and 9·8%, respectively, of the total CH_2O invested in flowering.

The CH_2O reserves in the leaves, crown and roots (Table 2) fall far short of that required by the inflorescence during the flowering season. In fact, plants that have produced a fully-expanded flower stalk and are just beginning to produce flowers have depleted most of their CH_2O reserves (Table 1, Group III). Plants initiating inflorescences had a total carbohydrate pool of just 146 g (Table 2). These plants (rosettes) averaged just over 600 g dry weight, which is typical for 3-year-old plants. Few plants

Table 3. *Estimated carbohydrate requirements for inflorescences of* Hesperaloe funifera

	Carbohydrate requirement (g) Mean ± S.E. (range)				
Study	Stalk	Flowers	Capsules	Seeds	Total
1992, 32 inflorescences	324 ± 30 (96 −737)	726 ± 88 (181 − 2250)	153 ± 19 (32 −519)	225 ± 28 (47 − 765)	1429 ± 139 (433 − 3879)
1997, 228 inflorescences	410 ± 12 (54 −1456)	620 ± 23 (69 − 2188)	81 ± 3 (0 −238)	120 ± 5 (0 − 374)	1230 ± 38 (157 − 3166)

actually flower at this early age, even under cultivation with irrigation and fertilization; many more come into flower after their third growing season when average dry weight of the primary rosette is approximately 2400 g, of which leaves constitute about 55%, crowns 25% and roots 20%. Assuming that maximum CH_2O pools prior to flowering are approximately 40% of the root mass, 30% of the crown mass and 15% of the leaf mass, the TNC pool of rosettes averaging 2400 g DW would be 198 g in the leaves, 180 g in the crowns and 192 g in the roots, or 570 g CH_2O total, or about 40% of the CH_2O required to produce an average-size inflorescence.

The remaining carbohydrate must come from current photosynthesis. During the summer months (May–August) mean daily rates of photosynthesis in *H. funifera* are about 200–250 mmol CO_2 m^{-2} day^{-1}, or 2·4–3·0 g C m^{-2} day^{-1} on a 1-sided leaf basis (Ravetta & McLaughlin, 1996). A 2400 g DW plant would have a leaf surface (1-sided basis) of about 1·15 m^2. Photosynthesis over 120 days during the summer would thus fix about 331 to 414 g C, sufficient to produce 827 to 1050 g CH_2O (as glucose). Current photosynthesis plus the estimated TNC comes to 1397 to 1605 g CHO, approximately equal to the estimated 1430 g CHO invested in the average inflorescence (Table 3) with just 1–2% fruit set.

In species of Agavaceae which produce secondary rosettes prior to flowering, the secondary rosettes can contribute CH_2O to the flowering primary rosette (Tissue & Nobel, 1988; Huxman & Loik, 1997). Secondary rosettes of *H. funifera*, however, cannot contribute to flowering in the parent rosette since they are produced while the parent rosette is still flowering and producing fruit; in fact, their growth would be competing with the inflorescence for CH_2O. From three to six secondary rosettes emerge aboveground in August and September from the crown of each flowering primary rosette and expand rapidly from September through December (McLaughlin, 1995). Photosynthesis during the autumn (September–October), when night-time temperatures are cooler, is higher than in summer, averaging closer to 400 mmol CO_2 m^{-2} day^{-1} or 4·8 g C m^{-2} day^{-1} (Ravetta & McLaughlin, 1996), resulting in the production of an additional 830 g of CH_2O. Most of the CH_2O produced after August probably is allocated to growth of these secondary rosettes.

Nitrogen determinations and nitrogen requirements for flowering

Total nitrogen contents of different plant parts are given in Table 4. Leaves sampled in November of 1994 were older and presumably more representative of leaves on plants at the time of flowering. There was little difference in N content between fresh and senescent flower stalks, but there were substantial differences between fresh flowers and aborted flowers, and between green capsules and brown capsules. The main axis of the stalk averages 90% of its dry matter and the lateral branches average 10%, which gives a weighted average N content of 0·30% for the entire stalk. Much of

Table 4. *Nitrogen contents of* Hesperaloe funifera *organs*

Plant part	Date sampled	Sample size	% N ($\bar{x} \pm$ S.E.)
Leaves	November 1991	12	1·42 ± 0·06
Leaves	November 1994	12	1·16 ± 0·05
Crowns	September 1996	5	0·85 ± 0·10
Roots	September 1996	5	0·27 ± 0·03
Main axis, fresh stalks	September 1996	5	0·29 ± 0·02
Main axis, senescent stalks	September 1996	5	0·26 ± 0·03
Lateral branches, fresh stalks	September 1996	5	0·73 ± 0·07
Lateral branches, senescent stalks	September 1996	5	0·67 ± 0·01
Fresh flowers	September 1996	5	2·33 ± 0·04
Fresh flowers	October 1996	5	2·26 ± 0·03
Aborted flowers	October 1996	5	1·79 ± 0·04
Green capsules	September 1996	5	2·45 ± 0·03
Brown capsules	September 1996	5	1·28 ± 0·04
Seeds	September 1996	5	3·16 ± 0·02

the nitrogen contained in flowers is probably incorporated into the pollen and would be lost following anther dehiscence and pollen dispersal. In estimating an N-budget for inflorescences we used a value of 2·0% N in dry matter irretrievably invested in flowers. It is assumed that the difference in N between green capsules and brown capsules represents N in chlorophyll and photosynthetic enzymes that is redistributed to developing seeds as the fruit matures.

Table 5 shows the estimated N invested in flowering in the samples of 32 and 228 inflorescences monitored during 1992 and 1997, respectively. N invested in flowering averaged 16·9 ± 1·7 g per inflorescence in the 1992 sample and 12·7 ± 0·4 g per inflorescence in the 1997 sample. For the largest inflorescences with the greatest number of capsules, N requirements were over 40 g N per inflorescences in 1992 and over 35 g N per inflorescence in 1997. Flowers had the highest N requirements. N invested in seeds represented 24·6% of total N for the 1992 sample and 17·4% of total N for the 1997 sample.

The total N requirement for the inflorescence is 12·7 to 16·9 g. A 600-g 3-year-old plant would have a total N content of just 5·4 g and a 2 400-g four-year-old plant would have a total N content of 21·7 g, somewhat higher than the N needs of an average inflorescence. Very little of the N in these vegetative parts, however, can be mobilized if the leaves are to remain photosynthetically active (although flowering plants of

Table 5. *Nitrogen invested in inflorescences of* Hesperaloe funifera

	Nitrogen Content (g) Mean ± S.E. (range)				
Study	Stalk	Flowers	Capsules	Seeds	Total
1992, 32 inflorescences	1·07 ± 0·10 (0·3 – 2·4)	10·22 ± 1·24 (2·5 – 31·7)	1·43 ± 0·18 (0·3 – 4·9)	4·14 ± 0·52 (0·9 – 14·1)	16·9 ± 1·7 (5·1 – 47·4)
1997, 228 inflorescences	0·99 ± 0·03 (0·1 – 3·5)	8·73 ± 0·33 (1·0 – 30·8)	0·76 ± 0·03 (0 – 2·23)	2·20 ± 0·09 (0 – 6·88)	12·7 ± 0·4 (1·6 – 36·0)

H. funifera often appear chlorotic in mid-summer, suggesting some temporary loss of N). Therefore significant uptake of N from the soil is required to meet the N demand of the inflorescence. In the third year of a stand's growth about 20% of the plants flower; approximately 60% flower during the fourth year. Total N required for flowering and fruit set would amount to 55 to 75 kg N ha^{-1} in year 3 and 165 to 220 kg N ha^{-1} in year 4 for a stand planted to 21 500 plants ha^{-1}.

Conclusions

There is considerable error involved in estimating the number of flowers produced by an inflorescence (Fig. 1). Given the large number of flowers produced by *H. funifera*, uncertainty in the exact amount of dry matter (and hence CH_2O and N) irretrievably invested in flowers represents a significant potential error in our estimates. We used an estimate of 0·113 g dry weight per flower as the average dry weight irretrievably invested in flowers. This is less than that observed for fresh flowers (0·142 to 0·164 g) but more than that for aborted flowers (0·084 g). Dry weights of aborted flowers do not account for carbon and nitrogen lost in nectar and pollen, which could be substantial.

Flowering in *Hesperaloe funifera* required stored CH_2O as well as currently assimilated CH_2O and considerable amounts of N. Rosettes within a plant appeared to be autonomous in their allocation of CH_2O and N to flowering and fruit production. Of the CH_2O required for sexual reproduction, most was produced by photosynthesis during the 4-month period of flowering and fruit set. Removal of the flower stalk at an early stage in its bolting should thus free-up these resources for allocation to growth of secondary rosettes, accelerating production of new leaves and potentially reducing the harvest cycle significantly.

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