

# Ecological functions of carbohydrates stored in corms of *Tipularia discolor* (Orchidaceae)

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## Summary

1. The orchid *Tipularia discolor* possesses two to five subterranean corms containing a high concentration of total non-structural carbohydrates (TNC). We investigated the role of corms in the initiation of new growth following seasonal dormancy, in reproduction, and in the response of plants to artificial defoliation.
2. Severance of older corms (representing c. 30% of total corm biomass) influenced new shoot initiation, but had little or no effect on plants during fruit production or in their response to defoliation.
3. Shading of plants during growth initiation had no detectable impact on shoot growth or storage use. Growth initiation caused a reduction in corm mass but no change in per cent TNC in corms. Reproduction was associated with reductions in both corm mass and per cent TNC.
4. Artificial defoliation had little impact on the utilization of existing carbohydrate stores.
5. It is concluded that carbohydrate storage in corms was relatively unimportant for the recovery of plants from herbivory in comparison to its role in growth initiation and reproduction.

*Key-words:* Accumulation, artificial defoliation, corms, herbivory, phenology, reproduction, reserves, storage, total non-structural carbohydrates

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## Introduction

Storage organs are a common attribute of perennial herbaceous plants, yet few studies have considered their ecological function (Chapin, Shultze & Mooney 1990). Storage structures represent reserves and thus directly compete with the allocation of resources to other plant functions; consequently the cost of storage can be high and ecologically important. If storage competes with resource allocation to leaves, it will have a direct cost associated with the allocation of reserves away from leaves and an indirect cost associated with the loss of the compounded benefit (i.e. future growth) which accrues to resources allocated to leaves (Bloom, Chapin & Mooney 1985). Storage does not serve as a reserve function if it does not compete with other plant functions (Chapin *et al.* 1990). Resources can simply accumulate in storage if their external supply exceeds the immediate demand.

As reserves, storage organs may: (1) support the initiation of growth following seasonal dormancy; (2) support reproduction; or (3) allow plants to respond to tissue losses to herbivores, pathogens, or catastrophe (risk aversion). These reserve functions are not mutually exclusive and have the common feature

that reserves provide resources when demand outstrips external supply (Chapin *et al.* 1990). Most evidence for functions 1 and 2 comes from observational studies of seasonal variation in nutrient and carbohydrate levels in storage organs (e.g. Fonda & Bliss 1966; Chapin, Johnson & McKendrick 1980; Abrahamson & McCrea 1985; Defoliart *et al.* 1988). Some manipulative studies have emphasized the importance of storage organs for reproduction (Lubbers & Lechowicz 1989; Zimmerman 1990). However, other studies have found no effect of artificial reductions in storage on plant growth or reproduction (Lovett Doust 1980; de Kroon, Whigham & Watson 1991) suggesting that storage organs are important for risk aversion or that they represent accumulation and do not function as reserves.

We have investigated carbohydrate storage in corms of the woodland orchid *Tipularia discolor* (Pursh) Nuttall with respect to the three proposed reserve functions. Approximately 80% of biomass is allocated to below-ground storage in *T. discolor* (Whigham 1984). We focused on carbohydrate storage because Whigham (1984) found that corms were only marginally important for nutrient storage

and that direct uptake and retranslocation of nutrients from senescing tissues played the largest role in supporting growth initiation and reproduction.

A role of carbohydrate storage in support of new growth in *T. discolor* is suggested by the observation that growth is initiated in early autumn when light levels on the forest floor are still very low (Whigham & O'Neill 1991). Flowering and fruit production occur in the summer when plants are leafless and occur at the expense of future corm growth (Snow & Whigham 1989). The role of current storage in mitigating reproductive costs is unknown. Finally, Whigham (1990) showed that artificial defoliation in *T. discolor* has a much greater impact on below-ground than above-ground biomass, suggesting that below-ground stores were being utilized to maintain long-term growth. Thus, there is evidence to suggest that carbohydrate storage in the corms of *T. discolor* may play a role in all three proposed reserve functions. Our objective was to quantify the relative importance of stored carbohydrates in each of these functions.

### Materials and methods

*Tipularia discolor* is a common winter-evergreen orchid in woodlands of the south-eastern USA (Luer 1975). Plants produce a single leaf during September–October and a single corm is produced at the base of each leaf. Leaves senesce in May, flowering occurs in early August, and fruits mature by late September (Whigham & McWethy 1980). The shallowly rooted corms persist for one to several years such that plants have a standing crop of two to five corms (Whigham 1984; Efrid 1987). We refer to corms of differing ages as  $C_1$ ,  $C_2$ ,  $C_3$ , etc., beginning with the youngest, fully formed corm. Vegetative reproduction occurs when large flowering plants produce a second leaf and corm on the youngest, fully formed corm (Snow & Whigham 1989). New plants become independent after several years when the connection between old and new plants disintegrates (Efrid 1987). Herbivores, usually whitetail deer (*Odocoileus virginianus* Zimmermann), frequently eat entire leaves of *T. discolor* and plants do not resume growth until the following autumn when a new leaf is produced (Whigham 1990). Our studies were conducted in two upland hardwood forest sites at the Smithsonian Environmental Research Center near Annapolis, Maryland, USA (see Whigham & McWethy 1980 and Whigham 1984 for details).

#### EFFECTS OF SHADING AND CORM SEVERANCE ON GROWTH INITIATION AND FRUIT SET

On 31 August 1989 clones of *T. discolor* were located that contained at least one independent vegetative and reproductive individual. Reproductive plants

had flowered and initiated fruit filling. Pairs of plants were assigned, in turn, to four treatments: (1) unmanipulated control plants; (2) shading to 6.5% of ambient understorey total daily photosynthetic photon flux density (PPFD); (3) severance of the youngest, fully formed corm ( $C_1$ ) from older corms ( $C_2$ ,  $C_3$ , etc.); and (4) the combination of treatments (2) and (3). Each treatment was replicated four times at each site. Shading was provided by three layers of shade cloth 90 cm in diameter suspended 25 cm above the ground.

At the start of the experiment each plant was gently excavated and the length ( $L$ ), width ( $W$ ), and height ( $H$ ) of each corm was measured with calipers. A separate set of harvests indicated that  $\ln$  dry mass of  $C_1 = -3.670 + 0.073 \times L + 0.121 \times H$  ( $r^2 = 0.47$ ,  $n = 29$ ). The  $\ln$  dry mass of  $C_2$  and older corms =  $-5.729 + 0.052 \times L + 0.075 \times W + 0.185 \times H$  ( $r^2 = 0.73$ ,  $n = 92$ ). The severance of older corms removed, on average, 29.9% (SD = 14.9,  $n = 30$ ) of the estimated dry corm mass per plant.

Experimental plants were harvested on 11 and 12 October 1989. Data were recovered for 27 of the potential 32 pairs of plants. Following measurement of the length of the primary leaf (petiole + blade), plants were separated into new shoots (leaves, developing corms and new roots), secondary shoots (if present),  $C_1$  corms,  $C_2$  and older corms (if present), old roots, and (if present) reproductive structures. These were dried in a forced-air oven (SC-350, Grieve Corp., Illinois, USA) at 60°C for at least 72 h before weighing. Dry masses of primary and secondary shoots were combined for data analysis.

Corms and leaves were stored in a desiccator before being ground (Wiley Mill, A.H. Thomas Co., Pennsylvania, USA) to pass through a 40-mesh screen. Ground samples were sealed in plastic vials until analysis for total non-structural carbohydrates (TNC) using the anthrone method (Spiro 1966) following extraction and hydrolysis of starch using amylase (Smith 1981). Where sample size permitted (>90% of samples), analyses for TNC were run in duplicate. Roots contained <10% TNC and are only a small component of plant biomass (Whigham 1984).

#### DETERMINATION OF FLOWERING

On 17 April 1990 we located and marked 47 independent plants at both sites, measured the size of their leaves (length  $\times$  width) and determined whether these plants had developed floral primordia on the  $C_1$  corm. On 7 June 1990 we harvested a random subset of plants within a range of leaf sizes which included plants with ( $n = 8$ ) and without ( $n = 8$ ) floral primordia. Among flowering plants, noticeable elongation of the floral primordia had begun with the

exception of two plants in which flowering is referred to as 'arrested'. Harvested plants were separated into  $C_1$ ,  $C_2$  plus older corms, and roots, and dried, weighed, stored, ground and analysed for TNC as previously described.

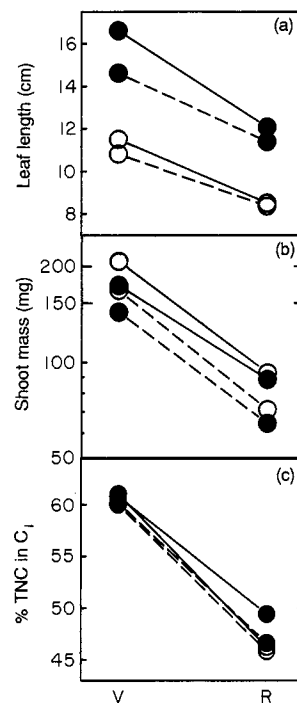
#### EFFECTS OF CORM SEVERANCE ON RECOVERY FROM HERBIVORY

Beginning on 24 October 1989 we excavated and measured corms and leaves of 36 plants at each site. Plants were randomly assigned to three treatments: (1) unmanipulated; (2) artificial defoliation; (3) artificial defoliation plus severance of  $C_1$  from older corms. Artificial defoliation was conducted by removing the leaf blade, mimicking the pattern of natural herbivory (Whigham 1990). The severed leaves were used to estimate the leaf area (LI-3050A area meter, Li-Cor, Lincoln, Nebraska, USA) of the unmanipulated plants from measurements of blade length ( $L$ ) and width ( $W$ ). The resultant equation was  $\sqrt{\text{leaf area}} = -0.068 + 0.270 \times L + 0.611 \times W$  ( $r^2 = 0.98$ ,  $n = 47$ ). The corm severance procedure removed an average of 27.6% (SD = 0.15,  $n = 18$ ) of the total estimated corm mass.

Plants were harvested nearly 1 year later (10 October 1990). Plants that had flowered (relatively few) and those which suffered natural herbivory were not sampled. Eight unmanipulated plants were recovered from the experimental design. Ten randomly chosen plants from the artificial defoliation treatment were harvested for comparison, along with eight plants in which defoliation and corm severance were combined. Plants were measured for leaf area, dry mass of new shoots (leaf + developing corm + new roots),  $C_1$  corm (produced during the course of the experiment),  $C_2$  corm (most recent, fully developed corm at the start of the experiment),  $C_3$  and older corms (if present) and roots, and TNC in corms.

#### STATISTICAL ANALYSES

Where possible, plant responses to experimental treatments were examined using analysis of covariance (ANCOVA; SAS 1987). In some cases no available covariate improved the statistical models or the data did not satisfy the assumptions of ANCOVA. Where ANCOVA was used, corrected treatment means are presented and the covariate used is indicated in the text. Biomass data were subject to  $\ln$  transformation and per cent TNC data were subject to arcsin-square root transformation. Because site distinctions were of secondary importance to the overall results, site effects were included in ANOVA and ANCOVA models but interaction terms involving site and other treatments were not. Site effects were only occasionally significant.

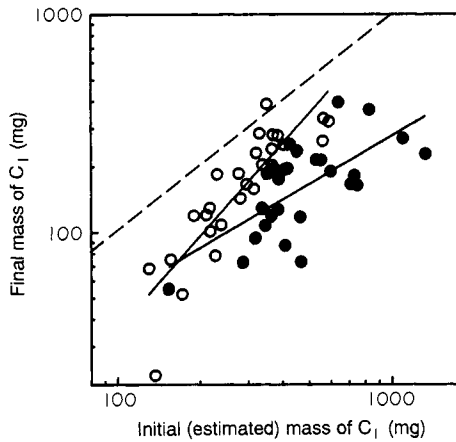


**Fig. 1.** Interaction plots for the responses of vegetative (V) and reproductive (R) plants of *Tipularia discolor* during shoot development. Experimental treatments are: control (○—○); shading, no severance of older corms from the youngest ( $C_1$ ) corm (●—●); corm severance, no shading (○- -○); and shading plus corm severance (●- -●). (a) Mean leaf length, corrected for  $\ln$  initial total corm mass (estimated, see Materials and methods); (b) mean shoot mass, which includes secondary shoots (if present), corrected for  $\ln$  initial total corm mass; (c) mean TNC (% dry mass) in  $C_1$  corm, corrected for  $\ln$  initial mass.

## Results

#### EFFECTS OF SHADING AND CORM SEVERANCE ON GROWTH INITIATION AND FRUIT SET

The responses of plants to the factorial shading and corm severance experiment are presented as a series of interaction plots (Fig. 1) exhibiting the differences in means between vegetative and reproductive plants in each treatment. Because vegetative and reproductive plants were paired within a clone, the data were analysed using repeated measures ANOVA following correction for differences in initial plant size. For leaf length (Fig. 1a), the strongest response appeared to be due to shading ( $F_{1,21} = 104$ ,  $P << 0.001$ ). Leaves of shaded plants were much longer than those of unshaded plants owing to aetiolation of the petioles ( $F_{1,21} = 61$ ,  $P << 0.001$ ). Leaves of reproductive plants were significantly shorter than those of vegetative plants ( $F_{1,21} = 36$ ,  $P << 0.001$ ) and plants with their older corms removed were shorter than unmanipulated plants ( $F_{1,21} = 7.6$ ,  $P = 0.012$ ). In addition, there was a significant interaction between



**Fig. 2.** Relationship of initial estimated mass (see Materials and methods) of youngest, fully formed corm ( $C_1$ ) to final  $C_1$  mass in vegetative ( $\circ$ ) and reproductive ( $\bullet$ ) *Tipularia discolor*. For vegetative plants,  $\ln$  final mass =  $-0.066 + 1.417 \times \ln$  initial mass; for reproductive plants,  $\ln$  final mass =  $-1.318 + 0.708 \times \ln$  initial mass. Dotted line denotes 1:1 relationship for initial and final  $C_1$  mass.

the shading and corm severance treatments ( $F_{1,21} = 5.4$ ,  $P = 0.030$ ), indicating that corm severance influenced the leaf length of shaded plants more than unshaded plants (Fig. 1a).

Despite the effects of shading on leaf length, there was no detectable effect of shading on new shoot mass (Fig. 1b;  $F_{1,21} = 1.9$ ,  $P = 0.17$ ). However, shoot masses of vegetative plants were significantly greater than those for reproductive plants ( $F_{1,21} = 106$ ,  $P \ll 0.001$ ) and shoot mass was significantly reduced by corm severance ( $F_{1,21} = 11.1$ ,  $P = 0.003$ ). There was also a significant interaction between reproductive status and corm severance ( $F_{1,21} = 6.1$ ,  $P = 0.022$ ), indicating that shoot masses of reproductive plants were more strongly influenced by corm severance than vegetative plants (Fig. 1b).

The concentration of TNC in the youngest, fully formed corm ( $C_1$ ; Fig. 1c), the only corm remaining following corm severance, was significantly influenced only by the comparison of vegetative and reproductive plants ( $F_{1,22} = 47.4$ ,  $P \ll 0.001$ ). Similarly, per cent TNC in leaves of vegetative plants (20.3% of dry weight) was significantly higher than that of reproductive plants (15.2%;  $F_{1,19} = 31.8$ ,  $P \ll 0.001$ ).

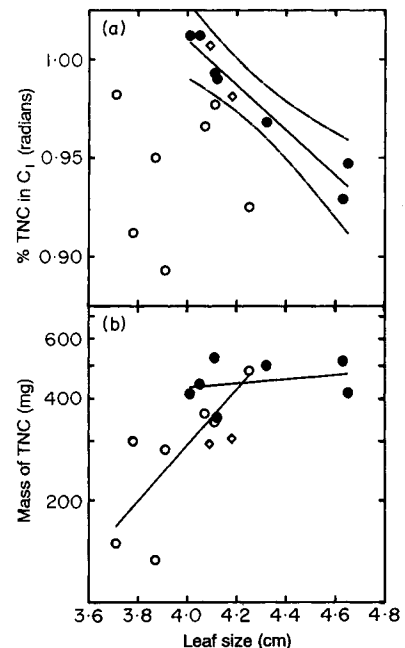
The final mass of the  $C_1$  corm (Fig. 2) could not be analysed by ANCOVA because the relationships between estimated initial corm mass and the final mass in vegetative and reproductive plants were not statistically parallel ( $F_{1,50} = 9.2$ ,  $P = 0.004$ ). Nevertheless, the data show a clear separation of vegetative and reproductive plants. Reproductive plants exhibited a stronger decline in corm mass than vegetative plants when compared to initial (estimated) values. Within groups of vegetative and reproductive plants, the effects of shading or severance on  $C_1$  mass

following shoot development were not significant (NS).

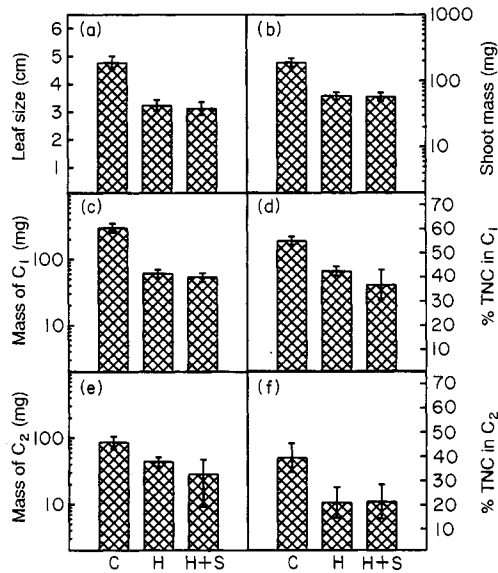
#### DETERMINATION OF FLOWERING

Plants which had initiated flowering by early summer of 1990 displayed a significant negative relationship ( $r^2 = 0.94$ ,  $P < 0.001$ ) between per cent TNC in  $C_1$  and leaf size (Fig. 3a). Values of per cent TNC ranged from 64 to 72%. This relationship was NS in vegetative plants ( $r^2 = 0.0$ ,  $P = 0.99$ ) and these plants exhibited an average per cent TNC of 66%. The data points for vegetative plants fell below and to the left of the 99% confidence level CL for the regression involving reproductive plants. Data for two plants in which flowering was arrested following development of a floral meristem fell within the 99% CL of reproductive plants.

The mass of TNC in the  $C_1$  corm of plants initiating reproduction (Fig. 3b) was statistically constant across the range of leaf sizes sampled ( $r^2 = 0.07$ ,  $P = 0.57$ ), but there was a significant positive relationship for vegetative plants ( $r^2 = 0.60$ ,  $P = 0.04$ ). Two plants which had arrested inflorescence development fell below the area of scatter for reproductive plants. The single vegetative plant with the largest leaf size



**Fig. 3.** Relationships of (a) per cent TNC in the  $C_1$  corm (in radians) and (b) the mass of TNC in  $C_1$  with respect to leaf size ( $\sqrt{\text{leaf area}}$ ) in vegetative ( $\circ$ ) and reproductive ( $\bullet$ ) *Tipularia discolor*. In (a) 99% CL are provided for the regression for reproductive plants, which excludes two plants ( $\diamond$ ) in which flowering was arrested following development of reproductive meristems. The regression equation was: per cent TNC (radians) =  $-0.115 - 0.013 \times$  leaf size. For (b) the regression equation for vegetative plants was:  $\ln$  mass TNC =  $-8.82 + 1.89 \times$  leaf size. The regression equation for reproductive plants was NS and is presented only for comparison.



**Fig. 4.** Responses of *Tipularia discolor* to artificial defoliation (H) and artificial defoliation plus severance of connection to old corms (H+S) in comparison to unmanipulated plants (C). Plants were harvested 1 year later: (a) Mean leaf size ( $\sqrt{\text{leaf area}}$ ), corrected for initial leaf size; (b) mean shoot mass (leaf + developing corm + new roots), corrected for  $\ln$  initial total corm mass (estimated, see Materials and methods); (c) mean mass of C<sub>1</sub> corm, corrected for  $\ln$  initial mass of C<sub>2</sub> corm; (d) mean TNC (% dry mass) in C<sub>1</sub>, corrected for  $\ln$  initial mass of C<sub>2</sub>; (e) mean mass of C<sub>2</sub>; (f) mean per cent TNC in C<sub>2</sub>. Error bars are SE.

fell well within the relationship for reproductive plants (Fig. 3b), but exhibited a relatively low level of per cent TNC in the C<sub>1</sub> corm (Fig. 3a).

#### EFFECT OF CORM SEVERANCE ON RECOVERY FROM HERBIVORY

Responses of vegetative *T. discolor* to defoliation and corm severance (Fig. 4) were analysed using one-way ANOVA and two pre-planned contrasts comparing control (C) and defoliated plants and, among defoliated plants, those in which older corms were severed away (H+S) vs those with unmanipulated corms (H). Leaf size in the year following the manipulations (Fig. 4a) was significantly reduced by defoliation ( $F_{1,21} = 32.0$ ,  $P << 0.001$ ), but corm severance had no additional influence on the leaf size of defoliated plants ( $F_{1,21} = 0.13$ ,  $P = 0.72$ ). Similarly, the contrast of new shoot mass (Fig. 4b) of control and defoliated plants was highly significant ( $F_{1,21} = 23.9$ ,  $P << 0.001$ ), but the difference between H and H+S treatments was NS ( $F_{1,21} = 0.04$ ,  $P = 0.83$ ). Similar patterns were displayed by the mass and carbohydrate storage in corms produced during the course of the experiment (C<sub>1</sub>; Fig. 4c,d) and in the mass of corms present at the start of the experiment (C<sub>2</sub>; Fig. 4e). The overall influence of the treatments on per cent TNC in C<sub>2</sub> (Fig. 4f) was NS

( $F_{1,21} = 2.37$ ,  $P = 0.11$ ), but the pattern of response was similar to that seen for other variables.

#### Discussion

Our results suggest that carbohydrate reserves in corms of *T. discolor* serve multiple ecological functions but differ in their relative importance for these functions. Stored carbohydrates appeared of relatively equal importance for supporting the initiation of new growth and reproduction and were relatively unimportant for supporting the recovery of plants from herbivory. While some of the observed responses may involve nutrient storage, Whigham's (1984) previous study of nutrient allocation in *T. discolor* suggested that nutrients present in corms are not likely to serve as a reserve function for growth initiation and reproduction. Implications of nutrients for responses to herbivory are discussed below.

The importance of corms to growth initiation is underscored by the fact that this was the only aspect of reserve utilization that was clearly influenced by the severance of older corms from the youngest, C<sub>1</sub> corm. During the 6 weeks when new growth was initiated, vegetative plants lost, on average, about 120mg of mass from the youngest, fully formed (C<sub>1</sub>) corm, about 45% of the initial mass. However, following shoot initiation, per cent TNC in the youngest corms was 61% in vegetative plants (Fig. 1c), not much less than the 66% measured following dormancy (measured the following summer, Fig. 3a). Yet, a net export of carbohydrates must have occurred to maintain their concentration in the C<sub>1</sub> corm during mass loss.

Curiously, shoot mass following growth initiation was not strongly influenced by shading to very low levels of light availability. Shaded plants were etiolated, which is a typical response to light stress (Salisbury & Ross 1978). In the related winter-evergreen orchid *Aplectrum hyemale* (Adams 1970), leaves are physiologically adapted to high light levels and low temperatures such that photosynthetic rates in the autumn are relatively low. If leaves of *T. discolor* are similar, then the contrast of ambient understorey light levels and the shade treatment may not have had a large impact on photosynthetic carbon gain. These photosynthetic characteristics would emphasize the importance of carbohydrate reserves for supporting growth initiation in the autumn. However, *T. discolor* may also acquire carbon through mycorrhizal associations with saprophytic fungi as in some orchids which are achlorophyllous (e.g. members of the related genus *Corallorhiza*; Dressler 1981).

Shoots initiated by reproductive plants were much smaller than those produced by vegetative plants, supporting the results of Snow & Whigham (1989) which show that plants suffer a cost of reproduction

affecting both future growth and reproduction. Our results show that carbohydrate storage alleviates these reproductive costs to some degree. During fruit set and shoot initiation the  $C_1$  corms of reproductive plants lost an average of 67% of their initial mass (c. 350 mg of corm mass), a greater loss than observed in vegetative plants. The loss of corm mass during reproduction was coupled with a decline in the concentration of storage carbohydrates in both corms and leaves.

While plant size is an important determinant of flowering in *T. discolor*, large plants do not always flower (Snow & Whigham 1989). Our results indicate that the status of carbohydrate storage in the youngest corms (Fig. 3) appears to be an added determinant of flowering that is independent of plant size (Tissue & Nobel 1990).

Few studies of wild plants have explicitly considered the comparative role of storage in growth initiation and reproduction. Several studies of temperate and arctic perennial herbs suggest that below-ground reserves are more important for spring regrowth than for reproduction (Fonda & Bliss 1966; Bradbury & Hofstra 1977; Mark & Chapin 1989). In horticulturally grown tulips, translocation studies indicate that growth initiation is supported by stored carbohydrates but that subsequent growth and flowering are supported by current photosynthesis (Ho & Rees 1976, 1977). By contrast, Zimmerman (1990) reported a pattern opposite to this in the deciduous, tropical orchid *Catasetum viridiflavum*. Artificial reduction of the number of pseudobulbs in *C. viridiflavum* influenced growth in only the smallest plants, but caused a large reduction in the number of flowers produced by plants of all sizes.

Our results suggest that carbohydrate reserves of *T. discolor* are relatively unimportant for their recovery from herbivory. After 1 year, defoliation caused a reduction in the mass and per cent TNC in the newest corm ( $C_1$ ) representing a difference of about 140 mg TNC between control and defoliated plants (Fig. 4c,d). The effect on existing storage ( $C_2$ ) represented at most 25 mg of corm TNC (Fig. 4e,f). Thus, artificial defoliation has a much larger impact on the production of new carbohydrate storage than on existing storage. Moreover, severance of the connection to older corms in conjunction with defoliation had no apparent effect on the ability of the plant to respond to herbivory. Thus, while carbohydrates stored in corms of *T. discolor* appear to play some role in the response of plants to herbivory, their role appears to be smaller than first suspected (Whigham 1990).

These results are in accord with other studies which have shown a reduction in carbohydrate reserves following artificial defoliation, but which also frequently show that large proportions of stored carbohydrates remain during regrowth (Chapin *et al.* 1990). One explanation for this pattern is that

regrowth is limited by nitrogen and phosphorus to a greater extent than by access to carbon. During the growing season, leaves of *T. discolor* represent about 20% of plant biomass, but contain up to 40% of total nitrogen and phosphorus (Whigham 1984). Thus, defoliation must have a relatively large impact on the nutrient budget of these plants.

We have demonstrated that carbohydrates stored in the corms of *T. discolor* provide a reserve function and are more important for supporting growth initiation and reproduction than for recovery from severe herbivory. However, the possibility that some of the stored carbohydrates are not reserves, but represent accumulation that does not compete with allocation to growth or other processes, needs to be considered. This is suggested by the fact that, even when statistically significant, removal of the older corms had only a small impact on the plants. If some corm carbohydrates represent accumulation, then plants should respond to increased nutrient availability (e.g. artificial fertilization) by reducing carbohydrate storage (Chapin *et al.* 1980) as the factors limiting growth are brought into closer balance. Similarly, elevated nutrient availability should strongly influence the ability of plants to recover from herbivory if this response is limited more by nutrients than carbohydrates as our results imply.

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