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The role of carbohydrate reserves in the growth, resilience, and persistence of cabbage palm seedlings (*Sabal palmetto*)

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Abstract *Sabal palmetto* (Walt.) Lodd. ex Schultes (cabbage palm) is an arborescent palm common in many plant communities throughout Florida, U.S.A., and the Caribbean. Although its seedlings grow very slowly in forest understories, they survive damage and defoliation well, and the species may increase in dominance following disturbances such as fire, logging, and hurricanes. We investigated the potential importance of total nonstructural carbohydrate (TNC) pools in the ability of cabbage palm seedlings to recover from the loss of aboveground tissue such as that caused by fire, grazing, or shallow burial by storm debris. TNC concentrations in belowground organs of seedlings from a forest understory were high, and TNC pools were sufficient to theoretically replace >50% of a seedling's canopy. The largest fraction of the belowground TNC pool was in stem tissue, where TNC in unclipped plants accounted for 26–54% of stem dry mass. Experimental reduction of TNC pools by repeated defoliation slowed seedling regrowth, and seedlings with inherently smaller pools (smaller seedlings) suffered higher mortality after repeated defoliation than did larger seedlings. Although regrowth and recovery after the loss of aboveground tissue was related to the size of the TNC pool in belowground organs, even the smallest seedlings with the smallest pools had sufficient stores to withstand at least two defoliations at frequent (7-week) intervals. Large belowground TNC pools in *S. palmetto* seedlings appear to enable them to survive all but the most frequent defoliations (e.g., frequent grazing or mowing). Allocation of resources to these stores, however, may contribute to the slow growth rates of *S. palmetto* seedlings in natural communities.

Key words *Sabal palmetto* · Cabbage palm · Nonstructural carbohydrates · Defoliation · Seedling growth

Introduction

Sabal palmetto (Walt.) Lodd. ex Schultes (cabbage palm), a palm tree common throughout Florida, Georgia and the Caribbean, is highly tolerant of many forms of disturbance and stress (Brown 1973; Perry and Williams 1996; Williams et al. 1998). Disturbances such as fire, hurricanes, and logging appear to favor the palm and have been credited with increasing *S. palmetto* dominance in many areas (Duever et al. 1979; Wade et al. 1980). Although the high tolerance of mature *S. palmetto* to fire and hurricane winds contributes to the tolerance of this species to such disturbances, characteristics of the juvenile palms appear to render *S. palmetto* populations resilient to a wide variety of disturbances (McPherson 1997; McPherson and Williams, in press).

S. palmetto seedlings undergo an establishment phase during which the stem apex grows downward for a time in the soil before growing back toward the soil surface (Tomlinson 1990; McPherson 1997). During this phase, the stem increases in girth until the diameter of the mature tree is achieved. Leaf size also increases, with young seedlings producing narrow strap-shaped leaves of three plicate segments and larger juveniles producing large fan-shaped leaves of >40 segments. Seedling growth is slow, and the duration of the establishment phase in natural, unfertilized systems is generally ≥ 20 years (McPherson and Williams 1996). During this phase, all but the very youngest plants are tolerant of fire (McPherson 1997) and even fairly severe logging damage (personal observation). Thus, even disturbances that destroy mature palms and all aboveground tissue may leave a bank of juvenile palms, containing >20 years of seedling cohorts, to repopulate the tree stand.

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In this study we investigated the role of total non-structural carbohydrate (TNC) pools in the ability of seedlings to recover from the loss of aboveground biomass. TNC reserves have often been suggested to enable plants to recover from tissue loss (e.g., Chapin et al. 1990; Rodgers et al. 1995), but many have questioned their importance. Several studies have found that bud availability was as important or more important than carbohydrate stores in limiting regrowth (Richards and Caldwell 1985; Zammit 1988; Lloret and Lopez-Soria 1993). Additionally, studies linking deficient carbohydrate stores directly to mortality are few (Miyanishi and Kellman 1986; Bowen and Pate 1993). It has been shown that nonstructural carbohydrates decline in plants experiencing tissue removal and regrowth (Caldwell et al. 1981; Orodho and Trlica 1990; Bowen and Pate 1993; Lacey et al. 1994; Rodgers et al. 1995; Cralle and Bovey 1996), and carbohydrate stores have been shown to be mobilized to support regrowth and maintenance of surviving organs (Dankwerts and Gordon 1987, 1989). However, the magnitude of contributions from storage carbohydrates may be small. Contributions of carbohydrate stores to new growth are commonly short-lived, lasting only a few days in grasses and some shrubs (Richards and Caldwell 1985; Dankwerts 1993; Cralle and Bovey 1996), but longer in woody, deciduous species (Loescher et al. 1990). Current photosynthate commonly contributes more carbon to regrowth after defoliation than do carbohydrate stores (Davidson and Milthorpe 1966; Richards and Caldwell 1985; Meney et al. 1990; Dankwerts 1993; Pendery et al. 1993). For plants that experience frequent tissue loss to grazing and evolved under such conditions, low storage levels may pose little limitation to regrowth, due to compensatory mechanisms (Caldwell 1986) or plasticity in allocation patterns (Richards 1984).

For many plants, however, repeated defoliation reduces growth and may ultimately affect survival. Dankwerts (1993) found that, although the contribution of current photosynthate outweighed that of stored carbon in the regrowth of *Themeda triandra*, individuals with larger stores were able to initially flush more leaf area and ultimately grow more rapidly than plants with smaller stores. Defoliation may temporarily stop or reduce root growth (Cridler 1955; Davidson and Milthorpe 1966; Richards 1984; Eissenstat and Duncan 1992), presumably because plant resources are used to replace lost leaf tissue, and such curtailed growth may affect subsequent survival. Although leaves of *S. palmetto* are fairly unpalatable, cattle graze young tissue, and repeated defoliation may partly account for the absence of *S. palmetto* from most pastures.

Some evidence suggests that carbohydrate stores are important for survival of even infrequent tissue loss, such as that suffered in fire. Two hypotheses commonly proposed to explain the mechanism of fire-induced mortality include lethal heating of buds and meristems, and a lack of carbohydrate stores for regrowth (Zedler et al. 1983; Rundel et al. 1987; Malanson and Trabaud

1988; Moreno and Oechel 1993; Bond and Van Wilgen 1996). While protection of meristematic tissue is undoubtedly necessary for fire survival, the importance of storage reserves has been largely assumed. Pate et al. (1990) found that species that resprouted following fire stored large amounts of starch in root tissue, whereas species in the same ecosystem that persisted by seeding after fires generally stored little starch. Such findings suggest an important role for TNC storage in the survival of fires by individual plants.

Due to the nature of its establishment phase, the apical meristem of a juvenile *S. palmetto* is located underground, and is generally well protected from heat and other damage. Thus, although *S. palmetto* is monopodial, with only one shoot apical meristem, that meristem is rarely damaged and is generally available for regrowth. McPherson and Williams (in press) found that only the smallest of *S. palmetto* seedlings died in fires. The apical meristems of these seedlings were closer to the soil surface and less well insulated by soil and leaf bases than were meristems of larger juveniles. Because these seedlings were small, however, it is likely that they also had the smallest TNC pools. This study was carried out, in part, to elucidate the role of TNC pools in seedling mortality during fire.

We examine the role of nonstructural carbohydrates in the resilience of *S. palmetto* seedlings to damage and disturbance, and discuss implications of these storage reserves for seedling growth rates. The objectives of this study were (1) to assess the size of the belowground TNC pool in seedlings, (2) to determine if defoliation reduced TNC pools and concentrations, (3) to determine if reduced TNC pools and concentrations were associated with increased seedling mortality, and (4) to determine if plant vigor (growth and size) decreased with reduced TNC pools. To determine the effects of TNC pool size on plant performance, we studied (1) plants in which TNC pools had been experimentally reduced through repeated defoliation and (2) plants that varied naturally in TNC pool due to variation in size.

Methods

Study site and plant material

The *S. palmetto* used in these experiments were small plants (hereafter, "seedlings") with strap-shaped (undivided) leaves of three to five plicate segments. Seedlings with narrow three-segment leaves may have been 1st-year seedlings. Based on prior demographic research in north central Florida, we estimate that seedlings with three-segment leaves ≥ 1.0 cm wide were ≥ 1 year old, and seedlings with five-segment leaves were ≥ 2 years old (McPherson and Williams 1996). Seedlings were growing in the understory of a mature planted pine (*Pinus elliottii* var. *elliottii*) forest with a sparse oak (*Quercus* spp.) midstory near Micanopy, Florida (29°30' N, 82°15' W). Soils were entisols and spodosols (US Soil Conservation Service 1985). Light transmission to the understory ranged from 3 to 39%. Mean maximum air temperature in the area fluctuates seasonally between about 19°C in January and 32°C in July (National Oceanographic and Atmospheric Administration 1997).

Seasonal leaf drop by midstory oaks may slightly increase light transmission to the understory during cool winter months.

Experimental carbohydrate depletion

Small palms were defoliated zero to three times to determine whether defoliation influenced carbohydrate status. Mortality and subsequent regrowth were monitored to determine the effects of reduced carbohydrate pools on seedling performance. Eighty seedlings with undivided leaves of five plicate segments (leaf dimensions ranging from 1.8 to 3.1 cm wide and from 30 to 60 cm long) were randomly selected and marked on 22 and 23 June 1995. Twenty seedlings were assigned to each of four clipping treatments (0, 1, 2, and 3 defoliations) in a stratified random manner based on leaf size. Plants were defoliated on 23 June, 11 August, and 29 September 1995. A 7-week interval was chosen because leaves on plants defoliated once were approximately half of their original length at 7 weeks following defoliation. [Because leaves of most species are not self-sufficient for carbon until they are 1/3–1/2 fully expanded (Sesták 1985), half-expanded leaves were unlikely to have exported much carbon to belowground stores.] The defoliation schedule was designed such that all plants could be harvested on the same date to avoid potential confounding effects of seasonal fluctuation in carbohydrate content. Thus, for plants defoliated three times, the initial defoliation occurred 7 weeks before the initial defoliation for plants defoliated twice, and 14 weeks before plants defoliated only once.

On 28 November 1995, a subset of 8 plants in each group was harvested to determine biomass, TNC concentrations and TNC pools in belowground organs. Due to incomplete root recovery, only TNC concentration but not TNC pool was measured in roots. The unharvested plants were monitored for mortality and leaf area production at 3 months and 1 year after harvesting. Leaf area was calculated by multiplying the total leaf length regrown by the maximum leaf width and this value was added to the projected area of petiole. Petiole area was calculated by multiplying the total petiole length by 0.2 cm (the average width of petioles).

Repeated defoliation of plants differing in size and TNC pool

To determine how belowground TNC stores varied with seedling size (and, presumably, age), we quantified TNC storage pools for seedlings of three size classes. To determine the potential magnitude of the contribution of these stores to regrowth, we calculated the amount of leaf material that could theoretically be constructed from these stores if all stored TNC were allocated to leaf regrowth and biosynthetic processes were maximally efficient. To determine how sensitivity to repeated defoliation varied with plant size and associated belowground TNC pools, we subjected seedlings in these three size classes to repeated defoliation for a year and monitored them for mortality and regrowth. The three size classes studied included seedlings with leaves of three plications <1.0 cm in width, larger plants with leaves of three plications >1.0 cm width, and plants with leaves of five plications (hereafter, small, medium, and large seedlings).

To estimate initial belowground TNC pools in plants of each size class at the beginning of the defoliation experiments described below, four plants in each size class were harvested. TNC concentrations in roots, stems, and leaf bases were measured. Additionally, biomass of stems and leaf bases were measured. However, because full excavation of the root system would have severely disturbed the study site, initial root biomass was estimated from full excavations that were conducted after the defoliation experiments were completed. At that time, four additional undefoliated plants in each size class were fully excavated to determine relative biomass distributions among roots, stems, and leaf bases. These proportions were used to estimate root biomass and root TNC pools in seedlings harvested at the beginning of the defoliation study.

To estimate the maximum amount of leaf area that could be produced from belowground stores of TNC, total belowground TNC pools in each size class (g glucose equivalents/plant) were divided by the average construction cost of leaf tissue (1.5 g glucose/g dry mass) and converted to leaf area using specific leaf areas of 76.5, 79.2, and 95.4 g dry mass/m² for small, medium, and large seedlings, respectively. The energetic construction costs of leaves have been calculated based on biosynthetic pathway analysis and methods derived therefrom (Penning de Vries et al. 1974; McDermitt and Loomis 1981; Williams et al. 1987), and on assumptions that biosynthesis occurs with maximal energetic efficiency. The construction cost of leaf tissue has been found to vary little among species (Chapin 1989). We used a mean value (1.5 g glucose/g dry mass) found for species from a wide range of habitats (Williams et al. 1987; Chapin 1989). Specific leaf area was measured on a subset of seedlings at the study site.

To determine how sensitivity to repeated defoliation varied with plant size and associated belowground TNC pool, twenty palms in each of the three size classes were defoliated every 7 weeks for a year. To document mortality rates in the absence of defoliation, 20 additional plants in each of three size classes were monitored for mortality but were not defoliated. At the time of each defoliation, the number of dead plants and the total length of regrown leaf blade and petiole were recorded. Leaf width was periodically measured. Leaf area was calculated as above, but different petiole widths were used for each size class.

Carbohydrate analysis

Plants were placed on ice immediately after harvest. Before drying, plants were cleaned of sand, debris, and dead plant material. All plants were dried at 100°C for 1 h then at 70°C until constant weight was reached (Smith 1969). Plants were then placed in a freezer until further analysis. All parts were pulverized in a Wig-L-Bug bead pulverizer (Crescent Dental Co., Lyons, Ill.) set on the highest speed for 1.5–2 min. Plant parts too large for the pulverizer were ground first in a Wiley mill.

Carbohydrate pools of each organ were calculated by multiplying the concentration of nonstructural carbohydrates in each organ by the dry mass of the organ. For plants defoliated zero and three times in the carbohydrate depletion experiment, leaf bases and stems were analyzed for nonstructural carbohydrates separately. For all other plants in the carbohydrate depletion experiment, mass and TNC concentrations in leaf bases and stems were physically averaged by grinding and analyzing them together. To determine the initial TNC status of plants used in the repeated-defoliation experiment, tissue from the four plants in each size class was combined to obtain mass, TNC concentrations, and pools in leaf bases plus stems and TNC concentrations in roots. Pooling plants was necessary for the smallest size class because individual plants were too small to analyze separately.

To determine total TNC concentration in each sample, starch was hydrolyzed enzymatically and resulting sugars were quantified with a phenol-sulfuric color reaction (R. Kobe and E. Latty, personal communication). Between 0.05 and 0.10 g plant material (depending on the plant part and the respective potential carbohydrate concentration) was weighed and placed in 5.0 ml 0.2 M acetate buffer solution (pH 4.8). Cell membranes of samples were then ruptured with a Vibra Cell Sonic Dismembrator (Sonics and Materials, Danbury, Conn.) by sonicating for 3 min. Another 5.0 ml of acetate buffer solution was then added. Starch was then gelatinized by placing samples with heat-tolerant alpha-amylase (Sigma A-3403) solution in a shaking hot water bath at 80–85°C for 1 h. Gelatinized starch was then hydrolyzed with amyloglucosidase (Sigma A-3042) solution by placing samples in a shaking hot water bath at 55–60°C overnight. Samples were then centrifuged for 10 min at 10,000 g (force) to separate unhydrolyzable material. A 1.0-ml subsample was removed and diluted with 10 ml deionized water.

The phenol-sulfuric acid method for detecting sugars was then used in colorimetric analysis (Dubois et al. 1956). Glucose solu-

tions were used as a standard. Absorbance was read at 487 nm on a Sequoia Turner model 690-310 Spectrophotometer (Abbott Laboratories, Abbott Park, Ill.).

Data analysis

Analyses of variance (ANOVAs, SAS 1989) were used to test for effects of defoliation history (0, 1, 2, and 3 defoliations) on TNC concentrations in roots, TNC concentrations in stems + leaf bases, and TNC pools in stems + leaf bases. Following ANOVAs, preplanned contrasts were used to determine if number of defoliations was linearly related to dependent variables (Montgomery 1991). TNC concentration in roots, TNC concentration of stems + leaf bases, and TNC pool in stems + leaf bases were analyzed separately.

For plants that survived the three defoliation treatments, effects of defoliation history on leaf areas 3 months and 1 year after the final defoliation were analyzed using one-way ANOVAs (SAS 1989). Regression analysis was used to analyze the relationship between estimated TNC pools in stems + leaf bases at the end of the defoliation treatments and the amount of leaf area subsequently produced. The mean TNC pool in each treatment was taken as the best estimate of initial pools for plants subsequently monitored for regrowth, yielding regression analyses with multiple values of y per x . The relationship between TNC concentrations in stems + leaf bases and subsequent leaf area growth was analyzed in a similar manner.

In the repeated-defoliation experiment, the overall difference in number of live versus dead plants of each size group at approximately 1 year after the initial defoliation was analyzed with a likelihood-ratio test. Two more independent contrasts were made with the likelihood-ratio test comparing mortality between the two smaller size classes and the two larger size classes (SAS 1989).

Results

Experimental carbohydrate depletion

TNC concentrations in small cabbage palms were high especially in stem tissue. Up to 54% of the dry mass of stem tissue in undefoliated plants consisted of TNC, and large amounts of starch were observed in parenchyma ground tissues of the stem. Where seedlings were separated into stems, leaf bases, and roots, stems had the highest TNC concentration. In undefoliated plants, TNC (measured as g glucose equivalents) accounted for $39.6 \pm 10.1\%$ (mean \pm SD, $n = 8$) of stem dry mass, $16.2 \pm 3.5\%$ of leaf base dry mass, and $9.0 \pm 1.7\%$ of root dry mass. In seedlings defoliated three times, TNC accounted for $14.9 \pm 4.4\%$ of stem dry mass, $7.9 \pm 4.1\%$ of leaf base dry mass, and $4.9 \pm 1.7\%$ of root dry mass.

Tissue removal reduced TNC concentrations in all tissues. The number of defoliations had a highly significant effect on carbohydrate concentration in stems + leaf bases (ANOVA, $F = 8.50$, $df = 3$, $P = 0.0004$), with increasing numbers of defoliations reducing TNC concentration ($F = 24.38$, $df = 1$, $P = 0.0001$, Fig. 1A). Likewise, defoliation had a highly significant effect on TNC concentration in roots (ANOVA, $F = 7.84$, $df = 3$, $P = 0.0006$), and there was a negative relationship between number of defoliations and root TNC concentration ($F = 11.24$, $df = 1$,

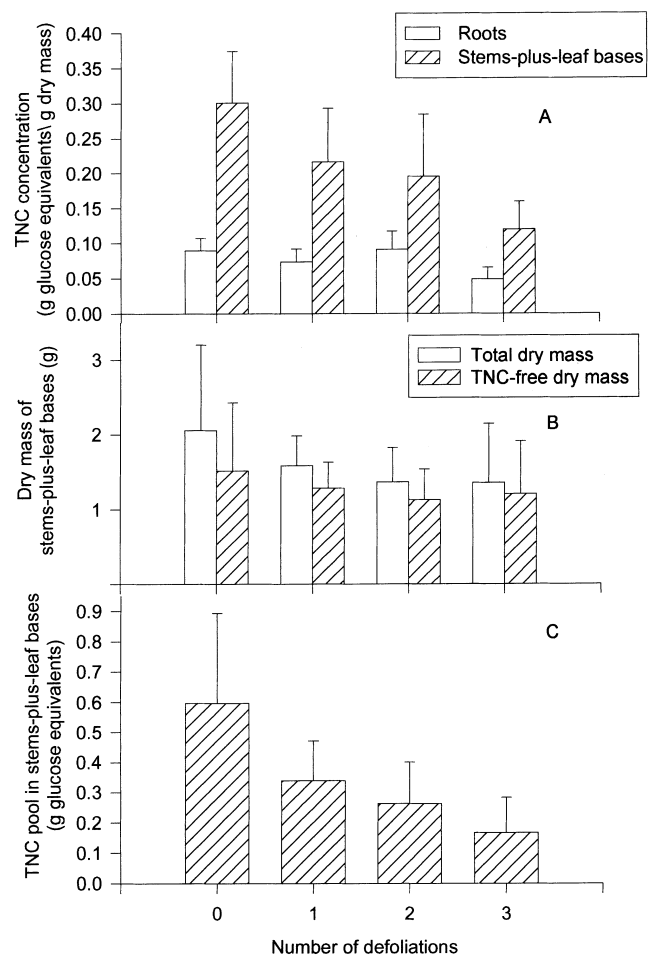


Fig. 1 Effect of defoliation history on total nonstructural carbohydrate (TNC) concentrations in belowground organs (A), dry mass of belowground stems and leaf bases (B), and TNC pools in belowground stems+leaf bases of large seedlings (seedlings with leaves of five plicate segments) (C) (mean \pm SD, $n = 8$)

$P = 0.0023$, Fig. 1A). Withdrawal of TNC from stems and leaf bases appeared to precede withdrawal from roots, as the concentration in roots did not decline appreciably in any plants except those defoliated three times, whereas declines in concentration in stem + leaf base were apparent in plants experiencing one, two, and three defoliations (Fig. 1A).

Defoliation appeared to reduce growth as reflected in the mean final biomass of stems + leaf bases (Fig. 1B). However, this reduction was not statistically significant when analyzed as either total dry mass (ANOVA, $F = 1.48$, $df = 3$, $P = 0.24$) or TNC-free dry mass (ANOVA, $F = 0.56$, $df = 3$, $P = 0.65$). Root mass changes were not quantified due to incomplete recovery of root tissues.

Defoliation significantly reduced the pool of TNC in stems + leaf bases (ANOVA, $F = 7.90$, $df = 3$, $P = 0.0006$, Fig. 1C). This change in TNC pool size was more influenced by a reduction in TNC concentration than by a reduction in plant size: the difference in average biomass between plants defoliated zero and three times was

only 34% (and statistically insignificant) compared to a 66% change in TNC concentration in the same plants. The carbohydrate pool was negatively related to number of defoliations ($F = 21.70$, $df = 1$, $P = 0.0001$).

The consequences of reduced TNC pools for small cabbage palms defoliated up to three times did not seem severe if measured as change in survival rates, but changes in plant vigor were apparent. Mortality among all defoliated plants was surprisingly low. Only 1 plant of 80 died; it had been defoliated three times. Defoliation intensity (one, two, and three defoliations) affected plant vigor as measured by leaf area produced after the last defoliation. This effect was significant at 3 months after the final defoliation (ANOVA, $F = 4.88$, $df = 2$, $P = 0.014$) and persisted for at least a year after the last defoliation (ANOVA, $F = 5.48$, $df = 2$, $P = 0.009$). The amount of leaf area produced in the first 3 months after the cessation of defoliation treatments was significantly related to both estimated initial TNC pools and estimated initial TNC concentrations in stems+leaf bases (Fig. 2). Similar results were obtained for leaf area measured 1 year after defoliation treatments. Despite the significance of these relationships, R^2 values were low (all < 0.21), indicating the importance of other factors in leaf area production and/or the weaknesses inherent in using treatment means as estimates of TNC concentration and pool in each plant. The significance of the slopes of these relationships increased with time (3 months to 1 year). As expected, the linear relationship between initial TNC pool and the amount of leaf area subsequently produced was stronger than that between initial TNC concentration and the amount of leaf area produced (Fig. 2).

Repeated defoliation of plants differing in size and TNC pool

Plants of the three different size classes had similarly high TNC concentrations in stems+leaf bases, but the con-

centration in root tissues seemed to decrease with increasing plant size (Table 1). Plant dry mass differed so much among the three size classes (Table 2) that the belowground TNC pool in the medium-sized plants was approximately 5.5 times that of small plants. Large plants (with five plicate leaf segments) had pools approximately 3.4 times those of medium plants and 18.8 times those of small plants (Table 1). In all size classes, however, the belowground TNC pool was large enough to theoretically replace 56–58% of a seedling's canopy (Table 1).

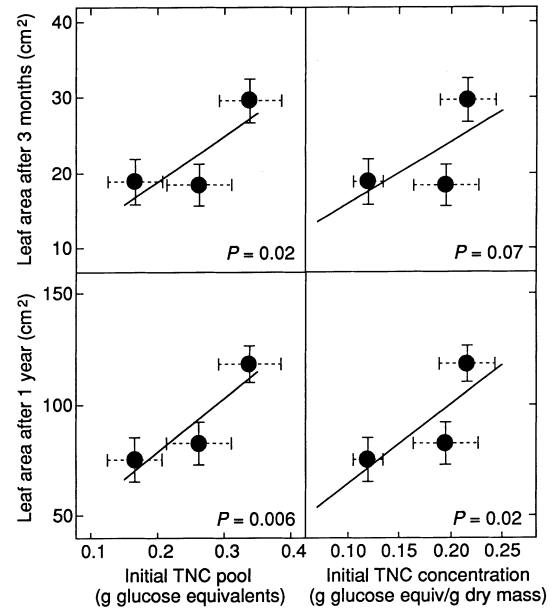


Fig. 2 Relationship between initial TNC (pools or concentrations) in stems+leaf bases and subsequent leaf area production. Leaf area at 3 months and 1 year after defoliation treatments ceased are shown (mean \pm SE). Results of regressions of leaf production vs mean TNC pools or concentrations in the three clipping treatments are shown (seven to eight y values per x). Regression lines and P values are indicated. SEs of TNC pools and concentrations, although not used in regression analyses, are shown to indicate variation (*dashed lines*)

Table 1 Initial belowground TNC concentrations and pools in plants of three size classes. Plants were defoliated every 7 weeks

	Seedling size class		
	Small	Medium	Large
TNC concentration (g glucose equivalents/g dry mass)			
Roots	0.24	0.14	0.12
Stems plus leaf bases	0.44	0.53	0.47
Belowground TNC pools (g glucose equivalents):			
Roots	0.042	0.094	0.411
Stems plus leaf bases	0.055	0.445	1.410
Total belowground pool	0.097	0.539	1.821
Maximum leaf area that could be produced from TNC pool ^a (cm ²)	8	45	127
Average leaf area flushed over 1 year (cm ² /year)	8	36	101
Standing canopy before defoliation ^b (cm ²)	15	80	218
Percent of standing canopy potentially produced from TNC pool	56%	57%	58%

^a Theoretical, based on assumption of maximally efficient biosynthesis

^b Estimated from leaf dimensions of plants before clipping

Table 2 Dry mass of roots, stems, and leaf bases of small, medium, and large seedlings that were completely excavated (g, mean \pm SD, $n = 4$)

	Seedling size class:		
	Small	Medium	Large
Stems	0.031 \pm 0.024	0.220 \pm 0.158	1.450 \pm 0.451
Leaf bases	0.035 \pm 0.009	0.129 \pm 0.025	0.607 \pm 0.203
Roots	0.084 \pm 0.016	0.272 \pm 0.108	2.400 \pm 0.698

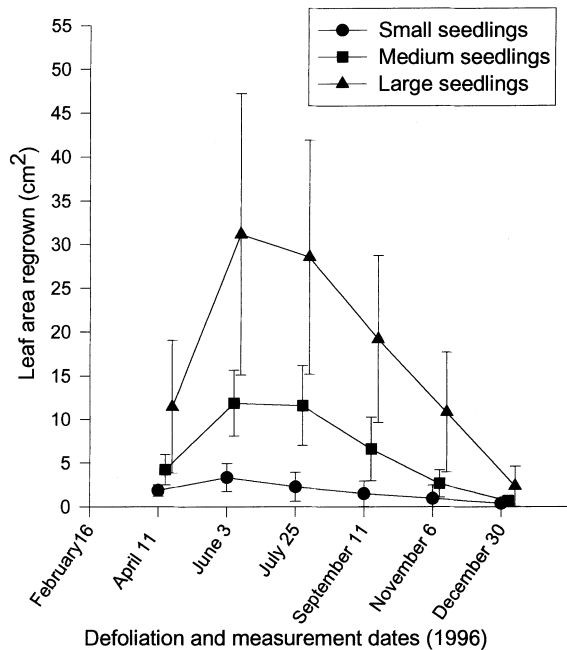


Fig. 3 Leaf area produced by surviving seedlings between defoliations (mean \pm SD). The initial defoliation occurred on 16 February 1996, and at 7-week intervals thereafter. Initial sample size, prior to mortality, was $n = 20$ in each seedling size class

Larger plants flushed more leaf area after defoliation than did smaller plants (Fig. 3). Leaf area flushed by all size classes was low after the first defoliation, peaked after the second defoliation (mid-summer) and declined after subsequent defoliations (Fig. 3). Over the course of the year, small, medium, and large plants produced an average of 8.2 (± 4.7 SD), 36.4 (± 12.6 SD), and 101.5 (± 47.4 SD) cm^2 of leaf area, respectively, or 56%, 48%, and 47% of the initial seedling canopies, respectively (Table 1). The amount of leaf area produced by small plants was very close to the maximum they could have produced from belowground TNC pools. The amount of leaf area produced by medium and large plants was below this theoretical maximum (Table 1).

Small plants were more sensitive to tissue loss than larger plants. Small plants showed higher mortality than larger plants after 1 year of successive defoliations (Fig. 4). At 1 year after the initial defoliation, there was an overall difference in the proportion of live and dead plants among size classes ($\chi^2 = 13.74$, $df = 2$,

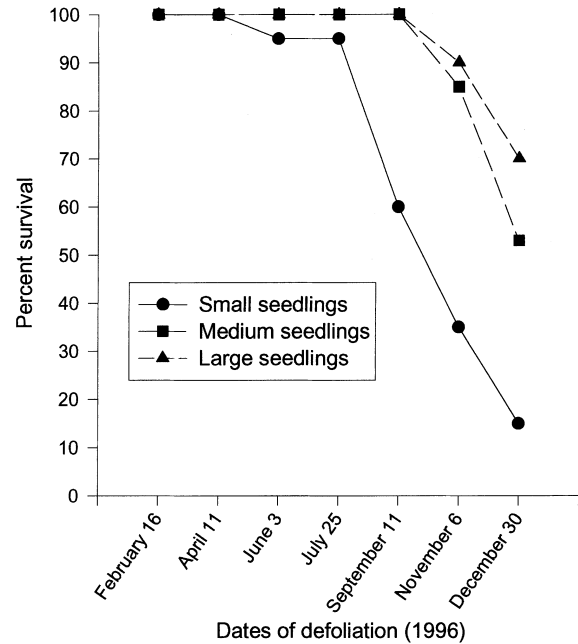


Fig. 4 Percent survival of *Sabal palmetto* seedlings of three size classes subjected to repeated defoliation at 7-week intervals ($n = 20$ in each seedling size class)

$P = 0.001$). The smallest size class had significantly more dead plants than did the medium size class ($\chi^2 = 6.45$, $df = 1$, $P = 0.011$); however, the proportions of dead plants in the medium and large size classes were not significantly different ($\chi^2 = 1.25$, $df = 1$, $P = 0.26$). Among plants that were monitored for mortality but not defoliated, none died.

Discussion

The formation of large belowground reserves of non-structural carbohydrate appears to play a major role in the noted ability of *S. palmetto* seedlings to withstand disturbance and loss of aboveground tissue. The seedlings studied set aside large belowground reserves of TNC at very early stages of development. These stores were drawn upon, and appeared to be necessary, for regrowth.

Concentrations of TNC were highest in stem tissue and lower in roots and leaf bases. High concentrations of TNC have also been found in other palm species. Hough (1968) found that unburned stems of the fire-tolerant saw-palmetto, *Serenoa repens*, contained up to about 40% TNC. Eighty percent of this TNC was starch, and although we did not quantify the percent starch versus sugars in *S. palmetto*, observation of starch grains in stem cross-sections suggested that a large portion of storage carbohydrate in *S. palmetto* was in the form of starch. As in *S. palmetto*, starch storage in date palm, *Phoenix dactylifera*, was found to occur primarily in the trunk, rather than the roots or leaf bases (Aldrich and Young 1941). For long-term reserve formation, this is a logical pattern of allocation because,

presumably, stem tissue is much longer-lived than roots or leaf-bases in these plants.

Over the range of seedling sizes studied, seedlings continued to build belowground pools of TNC. For plants that were completely excavated and harvested, 65–74% of total plant biomass was belowground, and TNC pools accounted for a large fraction of total plant dry mass in all size classes (21.5, 24.3, and 16.6%, for small, medium, and large seedlings, respectively). Despite the small apparent decrease in TNC concentration with increasing size, the large increase in size (a 33-fold increase in belowground mass between small and large seedlings) indicates that seedlings continued to allocate carbon to TNC stores as they grew.

These belowground stores were drawn upon to replace lost tissue. Successive clipping treatments progressively reduced belowground concentrations and pools of TNC below those of control plants (Fig. 1A, C). Our experimental TNC depletion treatments were not severe enough to fully deplete belowground reserves, and it is unknown if all measured belowground reserves were available for regrowth (Chapin et al. 1990). However, three clips reduced TNC concentrations to approximately 40% of those in unclipped controls, and some plants subjected to three clips had TNC concentrations in stems + leaf bases only 27% of the average found for unclipped controls. One plant that was clipped three times died; we do not know how low its TNC concentration had dropped. Thus, a substantial fraction, if not all, of the large belowground TNC pool in these seedlings can be remobilized for regrowth.

Environmental conditions appeared to affect the amount of leaf area produced after defoliation. In plants defoliated every 7 weeks for a year, leaf flush was slow after the first defoliation, peaked after the second defoliation and declined thereafter (Fig. 3). Cool winter temperatures after the first defoliation may have contributed to the slow rate at which leaf area was flushed. Declines following the second and third defoliations were likely due to carbohydrate depletion and reduced ability to gain carbon. Overall, however, responses to environmental variation in our study did not mask responses to defoliation or relationships between TNC stores and plant performance.

The belowground TNC reserves in *S. palmetto* seedlings appear necessary for their recovery from defoliation. Seedlings with smaller TNC pools, whether experimentally reduced or a natural consequence of small plant size, suffered greater mortality and/or reduced regrowth following defoliation compared to seedlings with larger pools. Small seedlings suffered greater mortality when repeatedly defoliated than did larger plants (Fig. 4). This difference in survival appeared to be largely attributable to differences in TNC pool size: for small seedlings, the mass of leaf tissue produced over the course of the study was very close to that which theoretically could have been produced from belowground stores; for larger plants, leaf production had not exhausted this theoretical capacity by the end of the study

(Table 1). While this coincidence suggests that exhaustion of belowground TNC stores caused the mortality observed in defoliated plants, a more detailed seedling carbon budget would be required to fully analyze its role. Obviously, regrowing leaf tissue fixed some carbon in the weeks between clips, augmenting the supply from stores. Conversely, respiratory demands of belowground plant parts provided an additional drain on TNC stores that was not accounted for in our analysis. Chapin et al. (1990) pointed out that plants must store more resources than are required to simply replace lost canopy tissue, because they must also supply respiratory demands of the remaining plant body while the canopy is replaced. At a minimum, our results suggest that those plants that suffered most from repeated clipping were much nearer to exhausting their reserves than larger plants with higher survival rates and larger TNC pools.

Although, as predicted, smaller seedlings had smaller TNC pools and consequently suffered greater mortality from repeated defoliation than larger seedlings, even the smallest seedlings had sufficient reserves to replace about 56% of their canopy. No seedling of any size died as a result of a single defoliation. Therefore, although frequent disturbances such as grazing or mowing may eliminate *S. palmetto* seedlings, a single fire should not reduce cabbage palm numbers due to carbohydrate depletion. Even frequent fires, occurring at 2-year intervals, would be insufficient to exhaust carbohydrate reserves. Although defoliation slows seedling growth, increased levels of light, soil nutrients, and water availability following fire (Whelan 1995) may more than compensate for this setback, increasing *S. palmetto* growth. The observed susceptibility of very small *S. palmetto* seedlings to fire (McPherson and Williams, in press) appears to be caused by lethal heating of their shallow buds, since exhaustion of TNC reserves cannot explain it.

The formation of large TNC reserves early in seedling development may ensure recovery from disturbance, and perhaps survival of periods with low carbon gain, but may also carry a cost. Allocation of resources to belowground TNC stores undoubtedly reduces growth by detracting from the construction of resource-gaining organs (roots and leaves), thereby reducing the potential for further growth (e.g., Chapin et al. 1990). *S. palmetto* seedlings also allocate a large fraction of their resources to the construction of structural stem tissue; the belowground stems must increase in diameter to approximately the girth of a mature tree before emerging aboveground. Both allocation to stem structural tissue and TNC stores must slow seedling growth rates, and may contribute to the long duration of the *S. palmetto* establishment phase in natural communities (McPherson and Williams 1996). High allocation to belowground stem tissue is an unavoidable requirement of the mode of establishment of *S. palmetto*. Growth rates would be higher, however, if the large fraction of resources allocated to storage were allocated to leaves, roots, and structural stem tissue instead.

In their slow growth rates, *S. palmetto* seedlings are similar to other shade-tolerant seedlings. *S. palmetto* seedlings inhabit a wide range of light environments but are common in dark forest understories (McPherson and Williams 1996). They may be opportunistic, with plastic growth rates and seem to respond to disturbances and high light conditions by increasing growth rates (K. Williams, unpublished data). Slow growth rates are associated with shade-tolerant species (Bazzaz 1979), and seedlings that survive well in shaded environments may not allocate their resources to maximize carbon gain (Kitajima 1994). Kitajima (1994) showed that, among 13 tropical tree seedlings, species with higher relative growth rates experienced greater mortality in the shade than species with low relative growth rates. She found that species with high survival in the shade had higher root:shoot ratios and leaf mass per unit area than those with lower survival, speculating that, in the shade, allocation of resources to defense and storage may benefit seedlings more than allocation to photosynthetic functions. Kobe (1997) found that, among four temperate tree species, allocation to TNC stores was associated with higher survival in the shade. Both the shade tolerance and slow growth rates of *S. palmetto* seedlings may be due, in part, to allocation to belowground TNC stores.

Both Chapin et al. (1990) and Kobe (1997) have noted that, although allocation to TNC stores reduces plant growth rates, such opportunity costs are much smaller in low-resource environments than in high-resource environments. *S. palmetto* occurs in habitats and microsites where unfavorable conditions for photosynthesis may be common. These conditions could include periods of drought, flooding by fresh and salt water, tissue loss due to hurricanes, partial burial by falling vegetation, periodic fires, and deep shade. Our results suggest that early allocation of carbon to large storage pools helps allow them to tolerate such conditions, despite the growth costs of such storage.

Conclusions

Although small *S. palmetto* seedlings necessarily have small pools of TNC, rendering them more susceptible than larger seedlings to death from defoliation and perhaps other stresses, even the smallest seedlings set aside sufficient stores to completely replace more than half of their canopy. Fractional partitioning of carbon to storage was as great, if not greater, in young seedlings than in older seedlings. We interpret these patterns as a strategy enabling *S. palmetto* seedlings to withstand defoliation and periods of stress, despite potential growth costs.

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