Elizabeth A. Newell · Stephen S. Mulkey
S. Joseph Wright

Seasonal patterns of carbohydrate storage in four tropical tree species

Abstract We examined the seasonal variation in total non-structural carbohydrate (TNC) concentrations in branch, trunk, and root tissues of *Anacardium excelsum*, *Luehea seemannii*, *Cecropia longipes*, and *Urera caracasana* growing in a seasonally dry forest in Panama. Our main goals were: (1) to determine the main sites of carbohydrate storage, and (2) to determine if seasonal patterns of carbohydrate storage are related to seasonal asynchronies in carbon supply and demand. We expected asynchronies to be related to seasonal variation in water and light availability and to foliar and reproductive phenology. *Cecropia* and *Urera* are fully drought-deciduous and so we expected them to exhibit the most dramatic seasonal variation in TNC concentrations. We predicted that maximum carbon supply would occur when canopies were at their fullest and that maximum carbon demand would occur when leaves, flowers, and fruits were produced. The concentration of total non-structural carbohydrates was assessed monthly in wood tissue of roots and in wood and bark tissue of terminal branches. Trunk tissue was sampled bimonthly. All tissues sampled served as storage sites for carbohydrates. As predicted, TNC concentrations varied most dramatically in branches of *Cecropia* and *Urera*: a 4-fold difference was observed between dry season maxima and wet season minima in branch wood tissue. Peak concentrations exceeded 25% in *Urera* and 30% in *Cecropia*. Less dramatic but significant seasonal variation was observed in *Anacardium* and *Luehea*. In all species, minimum branch TNC concentrations were measured during canopy rebuilding. In *Anacardium*, maximum branch TNC concentrations occurred when canopies were at their fullest. In *Cecropia*, *Urera*, and *Luehea*, TNC concentrations continued to increase even as canopies thinned in the early dry season. The greater photosynthetic capacity of leaves produced at the beginning of the dry season and the potential for the export of carbohydrates from senescing leaves may explain this pattern. In all species, the phenology of carbon gain was more important than the phenology of reproduction in influencing seasonal carbohydrate patterns. The combination of high TNC concentrations and the large biomass of branches, trunks, and roots indicates these species are storing and moving large quantities of carbohydrates.

Keywords Total non-structural carbohydrates · *Anacardium excelsum* · *Cecropia longipes* · *Luehea seemannii* · *Urera caracasana*

E.A. Newell (✉)
Department of Biology, Hobart and William Smith Colleges,
Geneva, NY 14456, USA
e-mail: newell@hws.edu
Tel.: +1-315-7813590, Fax: +1-315-7813860

S.S. Mulkey
Department of Botany, University of Florida, Gainesville,
FL 32611, USA

S.J. Wright
Smithsonian Tropical Research Institute, Apartado 2072, Balboa,
Ancon, Panama

Introduction

While temperatures in tropical forests are generally conducive to plant growth year-round, seasonal variation in the availability of water, light, and nutrients has the potential to limit plant productivity. For example, photosynthetic rates may be limited by low light intensities during rainy seasons when water is plentiful or by drought during dry seasons when light intensities are at their highest (Wright and Van Schaik 1994; Mulkey et al. 1996). The great variety of leaf longevity and patterns of leaf production observed in tropical trees may result in part from this contrasting seasonality of water and light availability (Wright 1996). Plants may also adapt to this seasonal variation in resource availability at the level of leaf morphology and physiology. There is evidence that some species produce seasonal leaf phenotypes with characteristics that optimize the allocation of resources for carbon gain during different seasons (Kitajima et al. 1997). Another response to temporal variation in resource availability is to acquire a resource when it is plentiful and then store it until it is required.

Whenever species experience seasonal asynchronies in resource supply and demand, we should expect stored reserves to play an important role in the plant's resource budget (Chapin et al. 1990). Tropical deciduous species should be no different from temperate species in accumulating carbon when leaf canopies are full and drawing from stored carbohydrates while leafless for respiratory costs and for the flushing of new leaves. Three species from Neotropical forests were found to follow this pattern, whether they were leafless during the dry season (*Jacaratia mexicana*, *Spondias purpurea*; Bullock 1992) or during the rainy season (*Jacquinia pungens*; Janzen and Wilson 1974). While seasonal variation in carbon gain may be less common for evergreen species in tropical forests than in temperate forests, there still may be periods when demand for carbon does not match supply. For example, in three understory *Psychotria* shrub species, the costs of leaf production are paid in part by non-structural carbohydrates stored in shoot tissues (Tissue and Wright 1995). In *Piper arieianum*, an understory shrub of wet tropical forests, the costs of reproduction require the use of stored reserves in addition to current photosynthate (Marquis et al. 1997).

The importance of carbohydrate storage in temperate trees has been well-documented (Kramer and Kozlowski 1979), but we know little about its role in the productivity and reproduction of tropical trees. Most studies on the seasonal patterns of carbohydrate storage in tropical trees have measured carbohydrate concentrations in one organ or another (e.g. canopy branches: Bhatt and Appukuttan 1986; trunk tissue: Olofinboba 1969; Newell 1994), but rarely has storage been examined in multiple organs simultaneously. When branch and trunk tissues have been sampled together (e.g. Bullock 1992), a limited number of sampling dates made a detailed description of annual patterns difficult.

This study addresses the following questions for tropical trees: (1) What are the main sites of carbohydrate storage? and (2) Are seasonal patterns in carbohydrate concentrations related to predictable seasonal asynchronies in carbon supply and demand? Although the main conducting cells in wood (secondary xylem) lack protoplasts, living parenchyma cells intermingled with tracheids and vessel members do serve as sites of carbohydrate storage (Kramer and Kozlowski 1979). We hypothesize that the woody tissue of canopy branches will exhibit the greatest seasonal changes in carbohydrate concentration simply because canopy branches are closest to the carbon supply provided by sun leaves and the carbon demand of distal reproductive structures. Roots and trunks are also expected to store carbohydrates, but with less extreme seasonal variation. We also hypothesize that: (1) greatest seasonal fluctuations in total non-structural carbohydrate (TNC) concentrations will occur in deciduous species, with maximum and minimum concentrations when canopies are full and rebuilding, respectively, and (2) TNC concentrations will drop during reproduction, especially if reproduction occurs when current photosynthate is unlikely to meet the demands of flower or fruit production. These hypotheses were tested by measuring TNC concentrations monthly in roots and terminal branch tissues and bimonthly in trunk tissues of four common species growing in a seasonally dry forest in Panama. The species differed in leaf phenology, reproductive phenology, and successional status.

This study of the seasonality of carbohydrate storage in four tropical tree species is unique for three reasons. First, we examine carbohydrates in canopy branch, trunk, and root tissues. Secondly, we assess these carbohydrates on a monthly basis, allowing for a more detailed picture of the seasonality of carbohydrate storage than possible in most other studies. Thirdly, detailed data from previous and concurrent studies on canopy leaf physiology and reproductive and vegetative phenology for the same four tree species (Kitajima et al. 1997) are combined with information on carbohydrate storage to produce a comprehensive picture of the role carbohydrate storage plays in the carbon budget of tropical trees.

Table 1 General information on the species studied. Nomenclature follows D'Arcy (1987) and mature height and successional status are based on Croat (1978) and personal observation. Diameter at breast height (*DBH*, mean with range) is for trees from which canopy branch tissues were sampled (*n*=5) and from which root and trunk tissues were sampled (*n*=5)

Species	*Cecropia longipes* Pitt.	*Urera caracasana* (Jacq.) Griseb.	*Anacardium excelsum* (Bert. & Balb.) Skeels	*Luehea seemannii* Tr. & Pl.
General information				
Family	Moraceae	Urticaceae	Anacardiaceae	Tiliaceae
Mature height (m)	10–15	5–10	20–40	15–30
Successional status	Pioneer	Pioneer	Early-Late	Early-Late
Leafless period	February–March	January–March	December/January (<1 week)	April/June (4–10 weeks)
Leaf production	April–December	April–November	December–June	June–December
Reproduction	May–November	April–May	January–May	January–May
DBH (cm) of trees sampled				
Branch samples	27.2 (23.5–31.5)	16.8 (12.0–22.0)	85.2 (65.0–103.0)	47.9 (34.5–47.6)
Trunk and root samples	18.3 (14.5–22.0)	16.8 (12.0–22.0)	76.6 (36.5–133.0)	62.3 (40.0–110.0)

Materials and methods

Site and canopy approach

The study was conducted in a seasonally dry forest in the Parque Natural Metropolitana near Panama City, Panama. Annual rainfall averages 1,740 mm with most precipitation occurring between May and December. The forest is a stand of 75- to 150-year-old second growth, with tree heights up to 40 m. We used a 42-m-tall tower crane with a 51-m jib to reach the upper canopy (Parker et al. 1992).

Species

The four focal species varied in stature, successional status, and phenology (Table 1, Fig. 1). Phenology was documented each month from January 1992 through April 1995 for *Anacardium excelsum* and *Luehea seemannii* and from November 1992 through April 1995 for *Urera caracasana* and *Cecropia longipes*. The presence of floral buds, flowers, and fruits was recorded for 8–20 individuals of each species. New leaves were marked with an indelible marker and the status of old leaves was evaluated on three branches each for three to eight individuals of each species. Figure 1 presents phenological data recorded from October 1994 through April 1995 followed by data representative of the two previous years for May through September 1995.

C. longipes and *U. caracasana* are both deciduous, with *Urera* leafless for a longer period during the dry season. *L. seemannii* is facultatively drought deciduous, losing leaves in the second half of the dry season in March and April and becoming entirely deciduous in early April during severe dry seasons. Following mild dry seasons, *Luehea* is deciduous for the first 4–6 weeks of the rainy season with a first peak of leaf production in June and July and a second peak from October through December. *A. excelsum* is brevideciduous; peak leaf exchange occurs at the beginning of the dry season, December or January, followed by ongoing leaf production throughout the dry season. In this paper, *Anacardium* and *Luehea* will be referred to as brevideciduous species, to distinguish them from the distinctly deciduous *Cecropia* and *Urera*.

Given the phenology of these species, we predicted that *Cecropia* and *Urera* would have the greatest seasonal variation in TNC concentrations, with peaks at the beginning of the dry season, just prior to leaf senescence. Given *Urera*'s longer period of leaflessness and the coincidence of leaf flush with reproduction, we predicted it would have a more dramatic drop in TNC concentrations than *Cecropia*. We predicted that *Anacardium* would have the least seasonal variation in TNC concentrations because its canopy remains relatively full year-round, suggesting the potential for more consistency in carbon gain than in *Luehea*.

Tissue sampling

Branch samples from five individuals of each species were collected monthly for 1 year (1994–1995). At the beginning of the study, 15 branches were marked and numbered in each canopy and one number was randomly selected for harvest each month. Access to branches of *Anacardium*, *Cecropia*, and *Luehea* was via the crane; terminal branches of *Urera* were sampled from the ground or from a ladder. The trees were all reproductively mature but varied in diameter at breast height (Table 1). Samples included shoot wood and bark tissue. To document any branch characteristics that might influence carbohydrate concentrations in branch tissue, we noted leaf number, leaf age (expanding, young, mature,
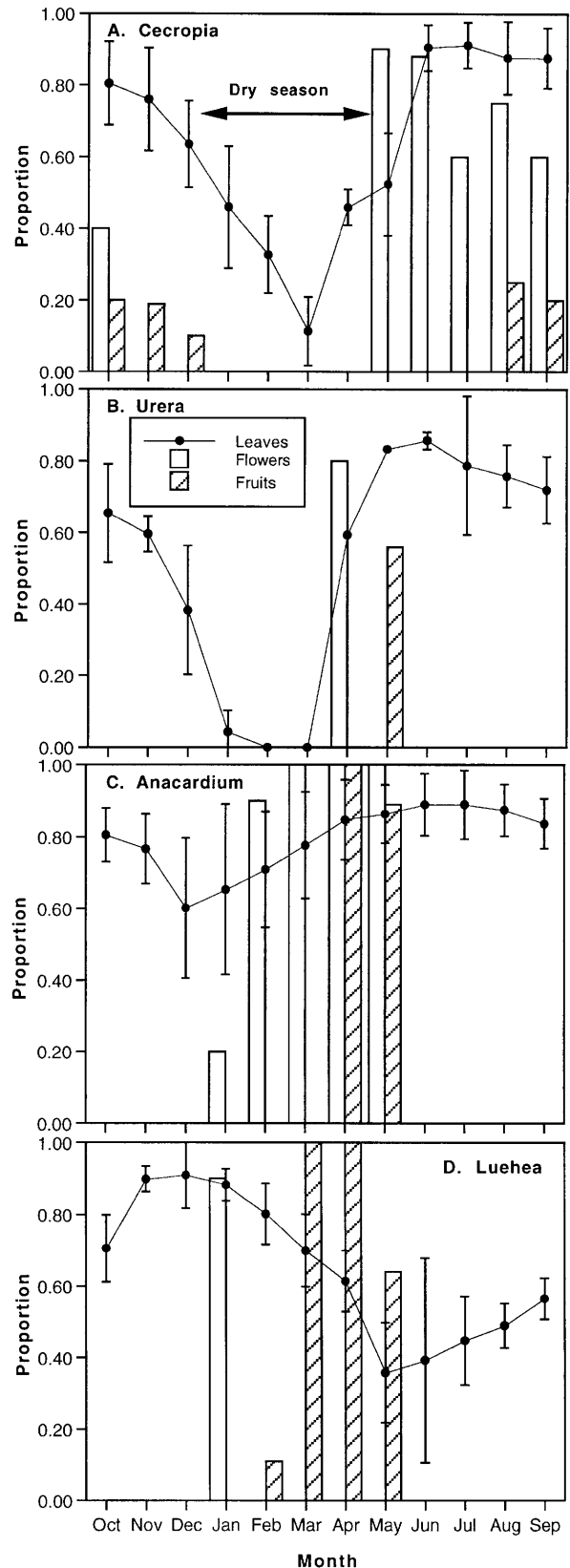

Fig. 1 Leaf and reproductive phenology for *Cecropia*, *Urera*, *Anacardium*, and *Luehea*. Leaf phenology (*lines*) is expressed as the proportion of the annual maximum leaf number present each month. Values are means (±SD). Asynchrony among individual trees of *Cecropia* and *Luehea* accounts for the fact that the mean proportion of maximum leaf number never reaches zero even though each tree censused was leafless at some point during the season. Reproductive phenology is expressed as the proportion of trees with flowers and with fruits as measured in the same survey. The extent of the dry season is marked with an *arrow*

old, or a mixture of ages), branch diameter at point of sampling, total length of stems above the point of sampling, and presence of any reproductive structures for each branch sampled.

On *Luehea* and *Urera*, terminal branches were removed and wood and bark samples were collected from the cut end of the branch. The length of stem, including side branches, above the sampled section averaged 165 (±10 SE) cm for *Luehea* and 84 (±7) cm for *Urera* and included multiple years of growth. To minimize damage to canopies of *Cecropia* and *Anacardium*, which have many fewer larger terminal branches, small sections of bark and wood were cut from each shoot without removing the terminal branch. For *Cecropia*, a rectangular section of bark and wood approximately 2 by 3 cm was removed, creating a "window" into *Cecropia'* s hollow shoots, with an average branch diameter of 3.6 (±0.1) cm at the site of sampling and an average of 70 (±7) cm of stem above the sample. Wood samples removed from *Anacardium* did not extend to the center of the shoot and so did not include the oldest wood tissue present. In *Anacardium*, stem diameter at the site of sampling averaged 2.2 (±0.1) cm with an average of 245 (±16) cm stem length above the point of sampling.

To avoid potential damage to trees within reach of the crane, samples of trunk and root tissue of *Anacardium*, *Cecropia*, and *Luehea* were collected from five different individuals than those utilized for shoot samples. Although these trees were outside of the crane's reach, they were similar in diameter and stature to those sampled from the crane (Table 1). Trunk and root samples of *Urera* came from the same trees as did shoot samples.

An increment borer (5 mm diameter) was used to extract a core of trunk tissue at least 6 cm in length. Samples were taken from approximately breast height with the exact position varying across the year to avoid sampling in the same area twice. Lengths of cores typically ranged from 6 cm in *Cecropia* to 10 cm in *Anacardium* and *Luehea*. Only in *Urera* and in *Cecropia*'s hollow stems did sampling reach the center of the tree. The goal was to focus on potential variation in the concentration of carbohydrates in what were presumed to be the most active tissues (the youngest secondary xylem) rather than to document carbohydrate concentrations to the center of the heartwood. Once dried, cores were divided into sections to determine the radial distribution of carbohydrates. Section 1 was the outermost 1 cm of trunk tissue, including bark. Inner sections were each 1.5 cm in length, with section 2 being the tissue 1–2.5 cm from the exterior, section 3 the tissue 2.5–4 cm from the exterior, and section 4 the tissue 4–5.5 cm from the exterior. These four sections represented the extent of trunk tissue available in *Cecropia* and *Urera* and were the ones analyzed for carbohydrates; *Anacardium* and *Luehea* samples from deeper into the trunk were analyzed only in October. While it would have been preferable to divide trunk samples by age of wood produced, a lack of consistent annual growth rings made this impossible.

To facilitate the collection of root tissue and to minimize damage to root systems, we removed wood samples from large surface roots; bark tissue was not analyzed. In *Cecropia*, samples came from adventitious prop roots. In *Anacardium* and *Luehea*, we sampled from buttress roots right at the soil surface, often using the increment borer to get a sufficient sample of wood tissue from beneath the thick bark. In *Urera*, we dug near the base of the tree to find large surface roots. While concentrations of carbohydrates in prop roots and large surface roots may not be representative of the entire root system, collecting woody tissue in this manner was necessary to allow for the repetitive sampling we desired in this study.

Carbohydrate analyses

Samples were put on ice in the field, dried at 80°C as soon as possible, and then either ground in a Wiley Mill (Thomas Scientific) to pass through a 40-mesh screen or ground in a Wig-L-Bug (an apparatus designed to pulverize dental filling material; Crescent Dental). Prepared samples were analyzed first for simple sugars and then for starch and other sugars. Simple sugars were extracted twice from 15-mg samples in 1.5 ml 80% (v/v) ethanol. The ex-

traction was done in a shaking water bath at 27°C. Supernatants were combined and diluted to 10 ml in volumetric flasks. Sugar concentrations were determined colorimetrically at 487 nm following a reaction with 80% phenol and concentrated sulfuric acid (Ashwell 1966). Duplicate glucose standards were run with each set of samples.

Starch and complex sugars remaining in the undissolved sample pellet were enzymatically reduced to glucose (Hewitt and Marrush 1986). Samples were incubated in 2.5 ml sodium acetate buffer (0.2 M) in a 100°C steam bath for 1 h. After cooling to room temperature, 2 ml of the buffer and 1 ml of amyloglucosidase (0.5% by weight, Sigma A-7255) were added. This particular amyloglucosidase preparation contains sugars and other impurities which were removed prior to use by placing the enzyme solution in dialysis tubing under running deionized water for at least 6 h and then filtering the solution through Whatman no. 1 filter paper. The sample and enzyme solutions were incubated for at least 8 h at 55°C, filtered through Whatman no. 1 paper, and diluted to 25 ml in volumetric flasks. Enzyme blanks and starch standards were included with each set of samples. Following the enzyme treatment, the concentration of starch and complex sugars in glucose equivalents was determined as described above. At least 2 replicates of each sample were analyzed for both sugars and starch.

Throughout the paper, carbohydrates measured after the ethanol extraction are referred to as sugars, carbohydrates measured after the enzymatic digestion are referred to as starch, and the sum of sugars and starch are referred to as total non-structural carbohydrates (TNC). Starch concentrations are presented in glucose equivalents.

Statistical analyses

To test for species differences across the year of measurement, repeated measures analyses of variance were performed (Systat 8.0). Individual trees were subjects and monthly observations were the repeated measures. The Greenhouse–Geisser adjustment was used to correct for violations of the assumption of compound symmetry, and probability levels presented reflect this adjustment.

Results

Dramatic seasonal variation in the concentration of non-structural carbohydrates in branch wood tissue distinguished the deciduous species from the brevideciduous species (Fig. 2A). TNC concentrations in both *Cecropia* and *Urera* were 4-fold greater during the dry season (December through March) than during the rainy season (May through September). Significant, but smaller, seasonal variation in TNC concentrations occurred in *Anacardium* and *Luehea*. TNC concentrations peaked at the end of the dry season (April) for *Luehea* and during the rainy season (August/September) for *Anacardium*. A repeated-measures ANOVA confirms what Fig. 2A illustrates: there were significant effects of month and species on branch wood %TNC and a significant interaction between these factors (Table 2).

Bark tissue %TNC was much less variable across the year (Fig. 2B). Bark TNC concentrations were lower than branch wood concentrations in *Cecropia* and *Urera* but greater than branch wood concentrations in *Anacardium* and *Luehea*. Seasonal patterns varied significantly among the four species, but there were no distinct differences in seasonal variation between the brevideciduous
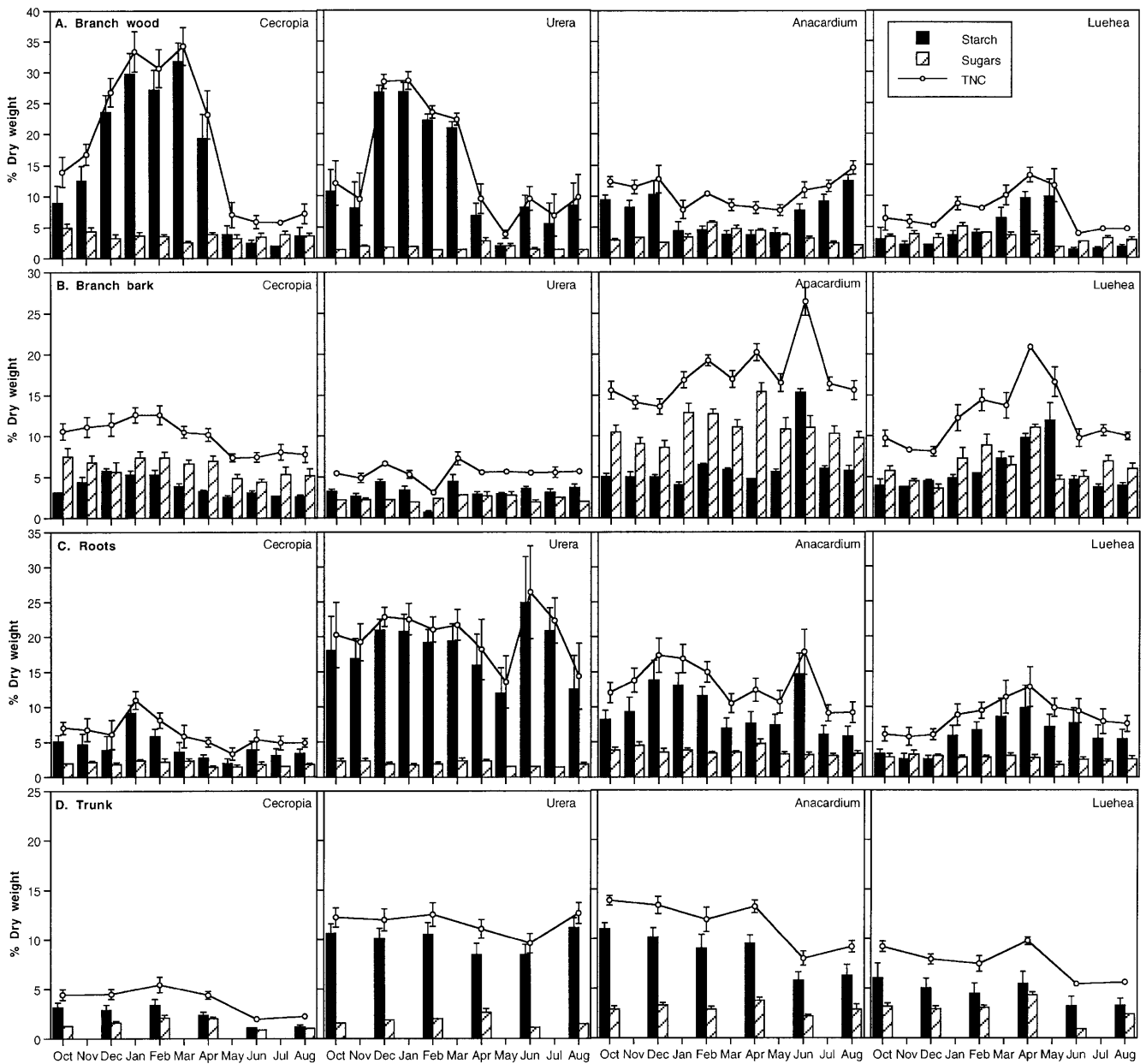
Fig. 2 Monthly means (+ SE) for starch, simple sugars, and TNC concentrations in branch wood (**A**), branch bark (**B**), and root (**C**) tissue of *Cecropia*, *Urera*, *Anacardium*, and *Luehea*. Bimonthly means (±SE) for trunk tissue (**D**) are weighted averages of the concentration in each of four radial sections

and deciduous species. Significant positive correlations between %TNC in wood and bark tissue were observed in *Cecropia* ($r=0.553$; $n=59$; $P<0.001$) and in *Luehea* ($r=0.761$; $n=60$; $P<0.001$).

Species differed significantly in root TNC concentrations, but not as predicted on the basis of phenology (Fig. 2C; Table 2). For example, *Urera* root carbohydrate concentrations did not vary significantly over time, despite the fact that trees were leafless in February and March. In *Anacardium*, *Cecropia*, and *Luehea*, root %TNC was much more variable across the year with

maximum and minimum monthly averages differing by 80–125%.

An analysis of trunk tissue TNC concentration, weighted by section length and averaged across the four sections, indicates significant species and month effects (Fig. 2D; Table 2). *Anacardium* and *Urera* had the highest trunk %TNC and *Cecropia* had the lowest. Overall, measurements made during June and August tended to be lower than those made in other months. The decrease in trunk carbohydrate concentrations between April and June corresponds to the timing of leaf production in all four species and to reproduction in *Anacardium*, *Cecropia*, and *Urera*. Trunk and root carbohydrate concentrations were not significantly related.

Examining separately the components of TNC (simple sugars and starch), we find that changes in starch concentration drive the seasonal variation in %TNC ob-

Table 2 Repeated measures ANOVA for concentrations of TNC in tree tissues. Repeated measures occur on month. *P*-values have been modified in accordance with the Greenhouse-Geisser Epsilon
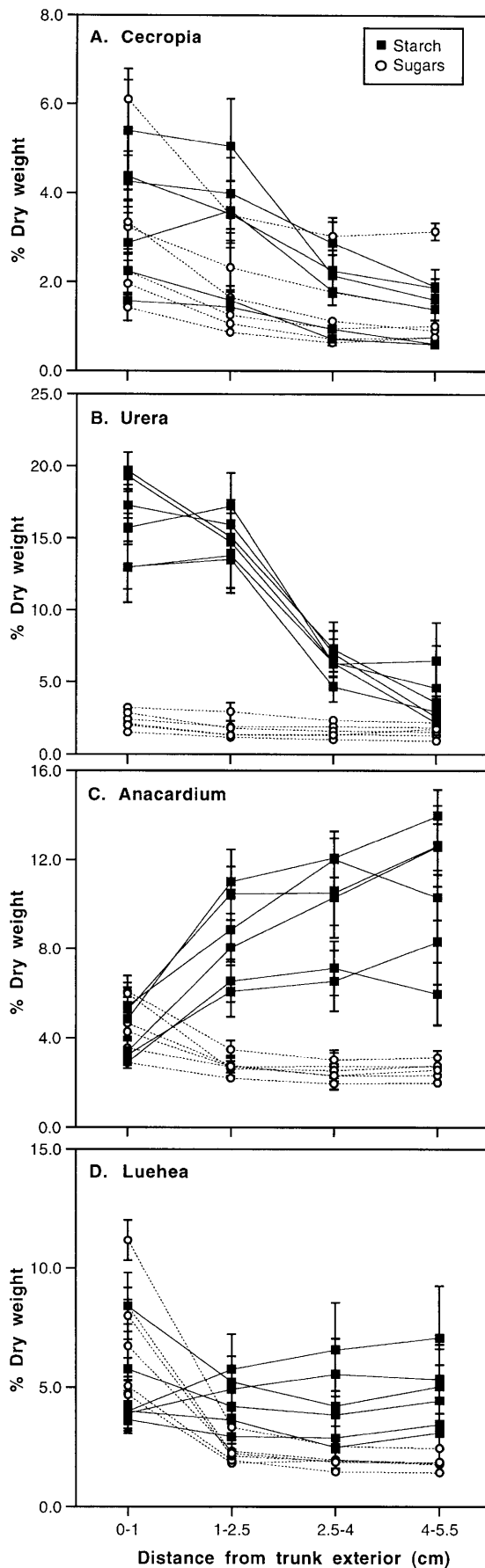
	df	SS	MS	F	P
Branch wood					
Between subjects					
Species	3	2,768.02	922.67	24.90	<0.001
Error	15	555.91	37.06		
Within subjects					
Month	11	3,703.10	336.65	10.37	<0.001
Month×Species	33	7,184.21	217.70	6.71	<0.001
Error	165	5,356.22	32.46		
Branch bark					
Between subjects					
Species	3	4,477.15	1,492.38	138.50	<0.001
Error	15	161.63	10.78		
Within subjects					
Month	11	3,377.90	34.355	9.22	<0.001
Month×Species	33	1,266.63	38.38	10.30	<0.001
Error	165	615.04	3.73		
Root					
Between subjects					
Species	3	564.08	188.03	3.39	0.048
Error	14	776.37	55.46		
Within subjects					
Month	11	793.46	72.13	3.01	0.032
Month×Species	33	4,569.17	138.46	5.78	<0.001
Error	154	3,688.40	23.95		
Weighted trunk					
Between subjects					
Species	3	1,231.70	410.57	34.18	<0.001
Error	15	180.19	12.01		
Within subjects					
Month	5	40.14	22.69	22.69	<0.001
Month×Species	15	5.82	3.29	3.29	0.002
Error	75				

served in the wood of branches and roots (Fig. 2A, C). For example, in *Cecropia* and *Urera*, seasonal maxima in wood %TNC were due solely to increases in starch; sugar concentrations remained low during these peaks. In bark tissue, on the other hand, simple sugars accounted for a larger fraction of TNC and contributed more to its seasonal variation (Fig. 2B). In trunk tissues, starch concentrations exceeded those of simple sugars, but sugars did contribute to seasonal TNC variation, especially in *Leuhea* (Fig. 2D).

More obvious than the seasonal variations in trunk TNC concentration were differences among species in both the radial distribution of carbohydrates and the overall concentration (Fig. 3). While concentrations of simple sugars were consistently highest in the outermost trunk tissues, patterns of starch storage varied dramatically among species. Starch concentrations were highest in the youngest tissues of *Cecropia* and *Urera* (Fig. 3A, B). In *Anacardium* and *Luehea*, starch concentrations

were lower in bark and young secondary xylem and reached their maximum in the innermost section analyzed across the seasons (4–5.5 cm; Fig. 3C, D). Three sections more to the interior of the trunk (5.5 cm–10.0 cm) were collected and analyzed from each of the *Anacardium* trees in October; they did not differ significantly and averaged 12.6% TNC, less than the mean of 16.6% TNC measured that month in the 4–5.5 cm section. From *Luehea*, sections 5.5–8.5 cm from the trunk surface were analyzed and their mean TNC concentration (6.9%) was also less than the mean for the 4–5.5 cm section (9.0%).

Branch carbohydrate concentrations were related to leaf phenology, but not quite as predicted. Our prediction that maximum TNC concentrations would occur when canopies were at their fullest was correct only for *Anacardium*. In the deciduous species, branch TNC concentrations reached their peak when canopies were already thinning during the early dry season (Fig. 4). As predict-
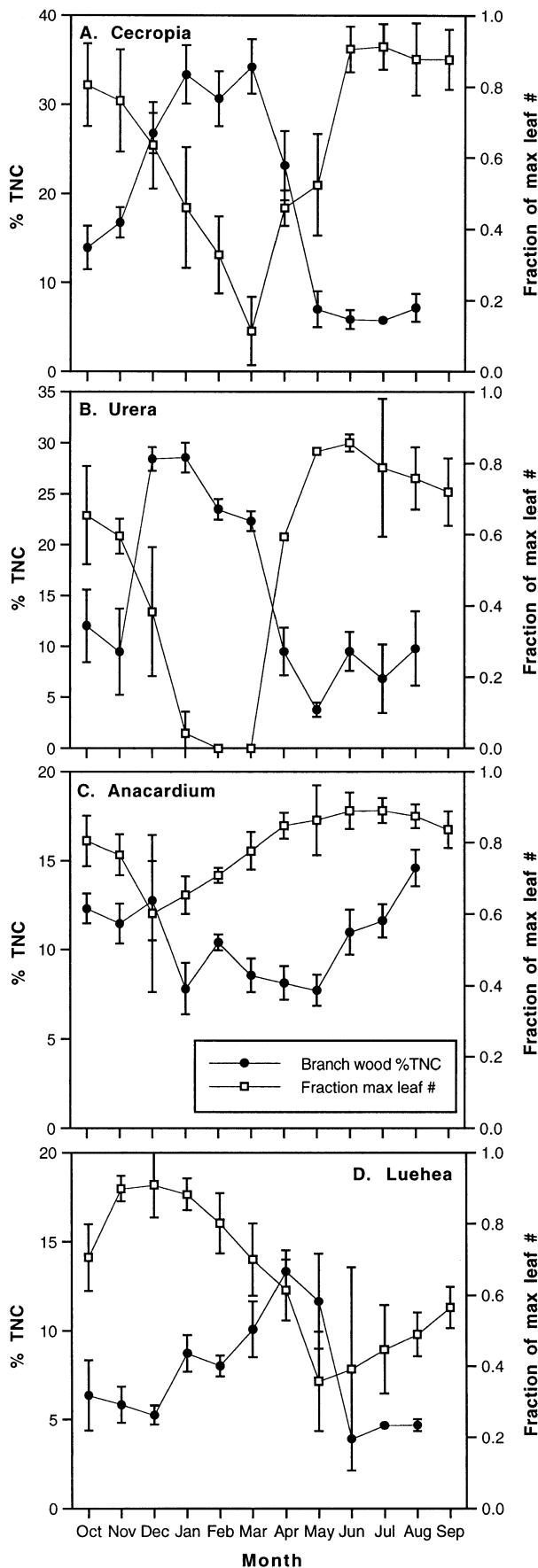
ed, canopy rebuilding at the beginning of the wet season was accompanied by a steep decline in branch wood TNC concentrations. An inverse relationship between leaf number (as a proportion of the maximum) and branch wood %TNC was statistically significant in *Cecropia* ($r=-0.835$; $P<0.001$; $n=12$) and *Urera* ($r=-0.875$; $P<0.001$; $n=12$). *Anacardium* and *Luehea* each had a major period of leaf turnover during which branch TNC concentrations dropped: December through January for *Anacardium* and April though July for *Luehea* (Fig. 4C, D). The overall decrease in %TNC during leaf turnover was greater for *Luehea* (from 13.3 to 3.9%) than for *Anacardium* (from 12.7 to 7.8%) which may be related to the coincidence of fruit-filling (March through May) with leaf exchange in *Luehea*. Seasonal patterns of root TNC concentrations were unrelated to leaf phenology.

Discussion

As predicted, the most dynamic pool of non-structural carbohydrates was in the woody tissues of terminal branches. The dramatic difference between minimum and maximum monthly mean % TNC in branch wood of the two deciduous species exceeds that measured in most other tropical species (e.g., vines of a tropical deciduous forest, Mooney et al. 1992; understory shrubs, Tissue and Wright 1995; Marquis et al. 1997). Coming closest are two deciduous species whose fruit production coincides with their leafless period (*Spondias purpurea*, Bullock 1992; *Ceiba pentandra*, Bhatt and Appukuttan 1986).

The dramatic seasonal variation in the concentration of TNC in shoot tissues may be due in part to the relative autonomy of individual branches. If within-branch source-sink relationships predominantly control the accumulation and depletion of shoot TNC stores, then dramatic fluctuations in TNC concentrations should be expected, while a buffering of fluctuations in branches would be expected if branches, trunk, and roots are completely integrated (Sprugel et al. 1991). Results from a CO_2 enrichment experiment suggest that individual *Luehea* branches are relatively autonomous in carbon allocation (Lovelock et al. 1999). For example, the TNC concentration of woody tissue in branches exposed to elevated CO_2 was significantly greater than in nearby control branches and there was a positive correlation between leaf area and flower bud production on individual branches. Branch autonomy in *Anacardium*, *Cecropia*, and *Urera* has not been examined but given their canopy architecture, it is likely that mature individuals of these species also have fairly autonomous branches in terms of carbon.

Fig. 3 Radial distribution of starch and simple sugars in trunk tissue of *Cecropia*, *Urera*, *Anacardium*, and *Luehea*. Values are bimonthly means (±SE) measured in 5-mm diameter core samples cut into sections based on distance from trunk exterior. Lines connects means from the same bimonthly sample

Fig. 4 Monthly means (±SE) of TNC concentration in branch wood tissue and monthly mean fraction of maximum leaf number (±SD) for *Cecropia*, *Urera*, *Anacardium*, and *Luehea*

Seasonal patterns in carbohydrate concentrations can be explained in large part by leaf phenology; reproductive phenology appeared to have a minimal impact. As predicted, branch wood TNC concentrations in all species were lowest as canopies were being rebuilt. Unexpectedly, the highest concentrations in all species but *Anacardium* were recorded after leaves began senescing in the early dry season (Fig. 4). This may be due to a combination of two factors: (1) translocation of non-structural carbohydrates from senescing leaves, and (2) higher rates of photosynthesis in leaves present at the beginning of the dry season. TNC concentrations were measured in mature leaves for one date in October. Concentrations ranged from 7% for *Urera* to between 13% and 14% for the other species. Carbohydrates translocated from senescing leaves may have contributed to the increase in branch tissue concentrations observed during canopy thinning. A second source may be photosynthesis early in the dry season. Leaves in *Cecropia*, *Luehea* and *Urera* continue to be produced even as their canopies thin. These new leaves expand just prior to the dry season and have significantly higher maximum rates of photosynthesis than those produced at other times of the year (Kitajima et al. 1997). This may enable these species to take advantage of the higher light levels available during the early dry season and add to carbohydrate stores being accumulated in branch tissues. To determine the relative importance of translocation during senescence versus accumulation due to early dry season photosynthesis, the carbohydrate content of leaves should be measured during senescence.

This study's data on the spatial distribution of carbohydrates in trunk tissue indicate the need for more research on the role these tissues play in carbohydrate storage in tropical trees. Starch was concentrated in the youngest wood of *Urera* and *Cecropia* (a pattern typical of woody species; Hillis 1987; Magel et al. 1994) but in *Anacardium* and *Luehea* starch concentrations remained high through the oldest wood sampled (8.5 – 10 cm from trunk surface). Axial and radial parenchyma cells that run throughout the sapwood of a tree are the most likely site for the carbohydrates assayed in these inner trunk sections (Hillis 1987; Kozlowski 1992) but because core sampling did not reach the center of *Anacardium* and *Luehea* stems, we do not know the extent of carbohydrate storage across the entire trunk. While most researchers consider the heartwood to be void of accessible storage compounds, starch-containing cells have been observed in the heartwood of trees such as *Shorea* spp. and *Fagus sylvatica* (Dietrichs 1964 as cited in Hillis 1987). The temporal variation in % TNC observed in each radial section (compare individual lines in Fig. 3) hints at seasonal variation in source-sink relationships across trunk tissues, but a larger number of trees would need to be sampled to confirm this.

At this point we can only speculate on the causes of the seasonal variation measured in trunk TNC concentrations (Fig. 2D). The coincidence of a decrease in trunk carbohydrate concentrations between April and June with the period of leaf production in all species and of reproduction in *Cecropia*, *Urera*, and *Anacardium* suggests that demands in the canopy may have drawn carbohydrates from trunk tissue. However, energy needs in the trunk itself are also likely to affect trunk carbohydrate concentrations. For example, trunk carbohydrate reserves may be used locally in cell division at the vascular cambium (Venugopal and Krishnamurthy 1987), in maintenance respiration (Kozlowski 1992), and in the synthesis of compounds, such as polyphenols, associated with heartwood formation (Magel et al. 1994). Root growth may also draw upon trunk carbohydrates (Kozlowski 1992). Clearly a more detailed study of the deposition and retrieval of carbohydrates in trunk tissues must be combined with measurements of trunk, root and shoot growth before conclusions can be drawn about the main effects of whole plant sources and sinks on trunk carbohydrate reserves. What this study demonstrates is that trunks do act as seasonal storage organs in tropical trees.

Roots stored significant amounts of carbohydrates in all four species, however the high concentrations in the roots of *Urera* deserve special note. *Urera*'s roots averaged 20.8% TNC across the year, a much higher concentration than found in the other three species (Fig. 2C). One hypothesis for the maintenance of such high TNC concentrations in its roots is that these carbohydrates may support resprouting after fire damage. *Urera* grows in areas where dry-season fires are common and, unlike *Cecropia*, *Urera* has the capacity to resprout. Species that respond to damage by resprouting often have high carbohydrate concentrations in their roots (Pate et al. 1990; McPherson and Williams 1998; Bollmark et al. 1999). The thick bark of *Anacardium* and *Luehea* probably protects them from fire intensities sufficient to severely damage the above-ground tissues of *Urera* and *Cecropia*. *Urera* appears to have a pattern of allocation to storage that reflects not only its phenology of vegetative growth and reproduction, but also its evolutionary history in a fire-prone environment.

The combination of high TNC concentrations and the large amount of dry weight in branches, trunks, and roots indicate these species are storing and moving immense quantities of carbohydrates. Multiplying TNC concentrations by trunk, root, and branch biomass would yield an estimate of the mass of carbohydrates being accumulated, transported, and utilized over the year. At this point, we lack good estimates of the relative biomass of trunk, root, and branch tissues for these species, and so can only speculate on the enormity of the TNC pools and fluxes in these trees.

This work points to the need for more research on the role of storage in the carbon budget of tropical trees. Yet to be determined is the role respiration, diameter growth, root growth, and shoot extension play in the seasonal patterns of storage in these trees. In addition, little is known about the impact increasing atmospheric CO_2 concentrations may have on carbohydrate storage in tropical trees. Terminal branches of *Luehea* exposed to elevated CO_2 accumulated more non-structural carbohydrates in their woody tissues (Lovelock et al. 1999) but the potential for increased storage in larger branches, trunk, and roots is unexplored. The size and labile nature of the pools of stored carbohydrates in tropical trees are likely to complicate estimates for the long-term storage of carbon in tropical forests.

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