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Non-structural carbohydrate pools in a tropical forest

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Abstract The pool size of mobile, i.e. non-structural carbohydrates (NSC) in trees reflects the balance between net photosynthetic carbon uptake (source) and irreversible investments in structures or loss of carbon (sink). The seasonal variation of NSC concentration should reflect the sink/source relationship, provided all tissues from root to crown tops are considered. Using the Smithsonian canopy crane in Panama we studied NSC concentrations in a semi-deciduous tropical forest over 22 months. In the 9 most intensively studied species (out of the 17 investigated), we found higher NSC concentrations (starch, glucose, fructose, sucrose) across all species and organs in the dry season than in the wet season (NSC 7.2% vs 5.8% of dry matter in leaves, 8.8/6.0 in branches, 9.7/8.5 in stems, 8.3/6.4 in coarse and 3.9/2.2 in fine roots). Since this increase was due to starch only, we attribute this to drought-constrained growth (photosynthesis less affected by drought than sink activity). Species-specific phenological rhythms (leafing or fruiting) did not overturn these seasonal trends. Most of the stem volume (diameter at breast height around 40 cm) stores NSC. We present the first whole forest estimate of NSC pool size, assuming a 200 t ha^{-1} forest biomass: 8% of this i.e. ca. 16 t ha^{-1} is NSC, with ca. 13 t ha^{-1} in stems and branches, ca. 0.5 and 2.8 t ha^{-1} in leaves and roots. Starch alone (ca. 10.5 t ha^{-1}) accounts for far more C than would be needed to replace the total leaf canopy without additional photosynthesis. NSC never passed through a period of significant depletion. Leaf flushing did not draw heavily upon NSC pools. Overall, the data imply a high carbon supply status of this forest and that growth during the dry season is not carbon limited. Rather, water shortage seems to limit carbon investment (new tissue formation) directly, leaving little leeway for a direct CO_2 fertilization effects.

Keywords Biodiversity · Carbon balance · Global change · Seasonality · Wood reserves

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Introduction

Plants produce, store, invest and lose carbon compounds. The size of the mobile fraction of these compounds at a given time may (1) reflect passive accumulation for no other reason than a periodic disparity between net-uptake and need; (2) it may represent a required, in part transitory pool of solutes (transport, metabolic and osmotic requirements); (3) it may be tied to defense compounds; or (4) represent ''intentionally'' stored reserves (Chapin et al. 1990). Except perhaps for defense compounds and osmotics, the size of the mobile C-pool is always likely to mirror a plant's overall carbon supply status, with the greatest fraction of this pool commonly present as non-structural carbohydrates (NSC, largely starch and sugars). It is well established (review by Chapin and Wardlaw 1988) that this pool becomes larger when active sinks are removed, for instance when trees are debudded or girdled, or when sources become stronger, for instance through photosynthetic stimulation by atmospheric CO_2-enrichment or high compared to low light (Wong 1990; Körner and Arnone 1992; Graham et al. 2003). Sink limitation causes source activity to decline ('end product inhibition'), whereas active sinks stimulate source activity (e.g., Neals and Incoll 1968; Wardlaw 1990; Stitt and Knapp 1999; Fig. 1).

On a whole tree basis, NSC concentrations indicate a tree's actual C-supply status and reflect its capital for

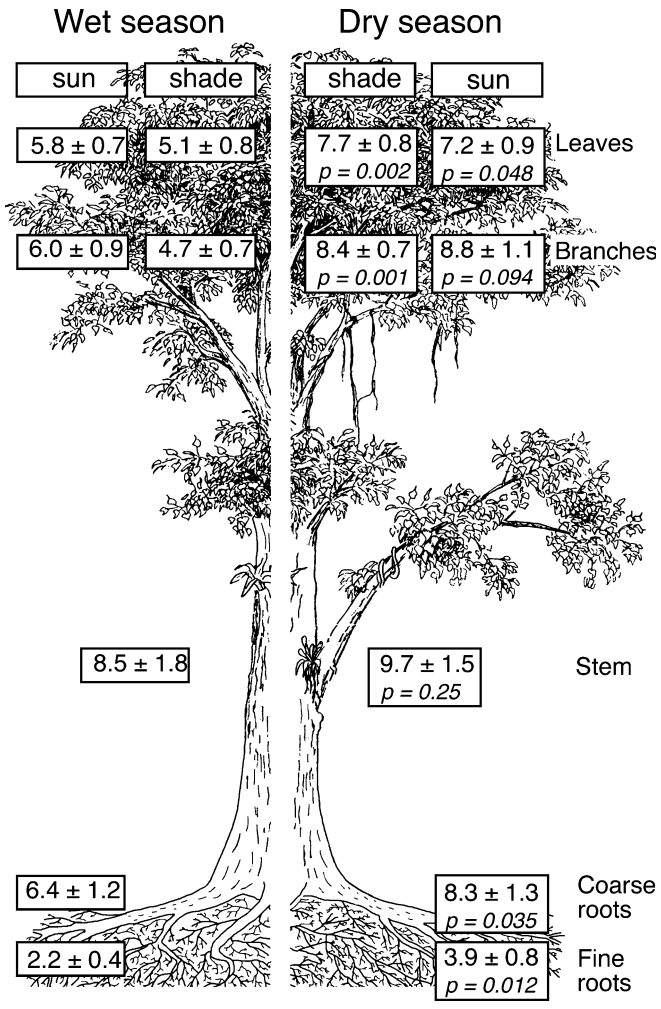


Fig. 1 Wet and dry season means of concentrations in non-structural carbohydrates (dry matter % ± SE, in large starch) for those nine tree species in which all tissues at all seasons were sampled in at least two trees (data for 2 years pooled before statistics; *P*-values for season effects)

flushing and reproduction and its buffering capacity with respect to replacement of lost tissue (e.g., after massive herbivory or wind damage). Given that almost half of the world's forests are in the tropics (Brown and Lugo 1982) and that these forests have been supposed to represent a net C-sink in response to atmospheric CO_2-enrichment (e.g., Taylor 1993; Malhi and Grace 2000; Canadell and Pataki 2002), knowing their current C-supply status is of particular interest. Here we apply this approach to a broad sample of tree species in a tall tropical forest in central Panama and make use of the climate-induced seasonal variation of source and sink activity.

Tree carbon reserves are known to exhibit seasonal trends (Kramer and Kozlowski 1979) , although the amplitude of such variations may have diminished in recent decades as a consequence of higher atmospheric CO_2 concentrations (Hoch et al. 2003). Seasonal NSC variations can be induced by seasonal temperature or water regimes or by phenological patterns these regimes induce. In the case presented here, water is the overarching driver. It is often difficult to separate effects of climate and phenology, because they typically are correlated and relationships differ widely across species. For example, in branch-wood of the drought-deciduous, Mediterranean *Aesculus californica*, NSC concentration dropped during fruit production in fall and re-growth in early spring, whereas evergreen *Quercus agrifolia* showed little change throughout the year (Mooney and Hays 1973). For a subtropical seasonal climate, Bullock (1992) reports an increase in stem NSC at the end of the wet season for *Jacaratia mexicana*, in contrast to *Spondias purpurea* which showed hardly any change across seasons. In a tropical seasonal climate vines showed increasing NSC in stems as seasonal drought developed (Mooney et al. 1992). Similarly, Tissue and Wright (1995) report for evergreen *Psychotria* species maximum NSC early in the dry season. Young trees of five agro-forestry tree species in Nigeria showed a dry season maximum and a wet season minimum of NSC in stems (Latt et al. 2001). In the forest where the present survey was conducted, two fast growing, distinctly drought-deciduous pioneer species entered their dormant period with maximum stem NSC concentrations (with a massive drop at re-sprouting), whereas two later succession evergreen species showed smaller or no significant seasonal changes in NSC (Newell et al. 2002).

It is not a priori clear whether carbon sinks or carbon sources are more limited during dry weather. We first explored this question in situ using small scale source manipulation experiments in the same forest investigated here. In these experiments, leaf NSC varied surprisingly little with irradiance within the canopy or in shading treatments in three evergreen species, but increased significantly in CO_2-enriched leaves, irrespective of season and the large sink represented by the mature trees to which the manipulated branches were attached (Würth et al. 1998a) . Artificial light, added above the same forest and throughout the cloudy wet season, led to up-regulation of photosynthesis, increased branch extension growth, and increased seed production but had no consistent effect on NSC for an upper canopy tree species at the forest considered here (Graham et al. 2003). The CO_2 response of leaf NSC is in line with in situ observations in Mediterranean trees (Körner and Miglietta 1994), understory plants in the Canal Zone of Panama (Würth et al. 1998b), tree seedlings of this area grown in open top chambers (Winter et al. 2000), and an earlier greenhouse test with complex communities of tropical plants (Körner and Arnone 1992). From the forest canopy studies we concluded, that leaf NSC is tightly coupled to the surrounding CO_2 concentration in a not fully understood way, but does not appear to reflect the tree carbon balance as such. CO_2– enriched leaves in tall forest trees responded individualistically, irrespective of the large sink size of the mature trees they were attached to. Lovelock et al. (1999) further

showed that even terminal branchlets accumulate NSC when exposed to high CO_2, again pointing at an autonomous response (no dilution through tree demand).

NSC in leaves or terminal branches, thus seems like an insufficient measure of a tree's overall carbon supply status. Though very laborious, a complete, whole tree representation of tissue samples across seasons is crucial, as is a broad coverage of species of contrasting phenologies given the variability seen in the above examples. To our knowledge such a complete 'inventory' of the carbon reserves of a forest has not yet been obtained for the tropics, and we know of only one such study in a temperate forest (Hoch et al. 2003). This field study was thus guided by three ideas: (1) we assumed that species differ widely in their resource use, hence, whatever overall picture we might arrive at, it should be based on as broad as possible a sample of species; (2) since trees allocate resources among compartments, all major tree compartments need to be sampled (whole tree approach); and (3) we further assumed that changes in NSC (relative differences) over periods of contrasting supply/demand ratios will hint at the seasonal C-supply status, requiring repeated sampling over a longer period. Seasonality may be seen as a sensitivity test of NSC to variation in moisture driven changes in the carbon relations and phenorhythms of the various species.

Specifically, we asked whether there is any evidence of carbon shortage or of a seasonal and/or phenologically driven depletion of whole tree NSC pools. We expected a progressive draw down of NSC stores during prolonged periods of drought. In order to test this, we quantified important NSC per unit dry mass of tissue of leaves, branch-wood, stems, and coarse and fine roots in 17 canopy tree species and extrapolated these data to a unit land area basis, using estimates of forest biomass.

Materials and methods

Study site

The study site is located in the Parque Natural Metropolitano (8°58′N, 79°34′W and 15–20 m elevation) near Panama City, Republic of Panama. The tropical climate of Panama is driven by the seasonality of precipitation and opposing trends in radiation (Wright and Van Schaik 1994), which induces characteristic phenological rhythms in trees. Water is abundant during the wet season, but due to greater cloud cover and greater canopy density (LAI) light availability is reduced. Most trees flush new leaves around the beginning of the wet season and continue to produce leaves late into the wet season, when they reach the maximum leaf area. Leaf area is reduced as the dry season advances, but remarkable exceptions to this pattern do exist (Wright 1996, see also Table 1). Annual precipitation averaged 2,120 mm (SD ±160 mm) for the years 1993–1995 at a site 1.6 km from the canopy crane (data from the Panama Canal Commis-

Table 1 List of study species (sorted by phenology), their common mature height, measured diameter at breast height (*Dbh*), specific leaf area (fully sunlit leaves only), phenological characteristics (based on J. Wright, unpublished data) and successional status (Croat 1978). Nomenclature follows D'Arcy (1987). Season was defined as *wet* for June to November, *dry* for January to March, transition periods (*trans.*) for April, May, and December

Species and author	Family	Height (m)	Dbh (cm)	SLA ($cm^2\ g^{-1}$)	Leafing	Flowers	Fruit filling	Successional status
Cecropia longipes Pitt.	Moraceae	20	17–30	85 ± 5	Wet	Wet	Wet	Pioneer
Cecropia peltata L.	Moraceae	20	15–36	104 ± 3	Wet	Wet	Wet	Early-late
Annona spraguei Saff.	Annonaceae	20–25	17–36	131 ± 8	Wet	Trans.	Wet	Early
Castilla elastica Sessé in Cerv.	Moraceae	ca. 25	14–29	115 ± 9	Wet	Trans.	Trans.	Early
Antirrhoea trichantha Griseb. (Hemsl.)	Rubiaceae	ca. 20	17–32	118 ± 8	Wet	Trans.	Trans.	Early
Ficus insipida Willd.	Moraceae	30–35	64–76	73 ± 3	Wet	Trans.	Dry	Early
Cordia alliodora ®.& P.) Cham.	Boraginaceae	20–25	15–29	99 ± 7	Wet	Dry	Trans.	Early-late
Anacardium excelsum (Bert.& Balb.) Skeels	Anacardiaceae	35–40	60–127	95 ± 6	Wet	Dry	Dry	Early-late
Luehea seemannii Tr.& Pl.	Tiliaceae	25–30	27–93	79 ± 5	Wet	Dry	Dry	Early-late
Spondias mombin L.	Anacardiaceae	25–30	15–48	91 ± 5	Trans.	Trans.	Wet	Early-late
Astronium graveolens Jacq.	Anacardiaceae	20–25	18–35	111 ± 2	Trans.	Trans.	Trans.	Early-late
Pseudobombax septenatum (Jacq.) Dug.	Bombacaceae	ca. 35	124–155	–	Trans.	Dry	Trans.	Early-late
Nectandra gentlei Lundell	Lauraceae	ca. 20	29	102 ± 7	Dry	Wet	Wet	Early-late
Phoebe cinnamomifolia (H.B.K.)	Lauraceae	ca. 20	13–19	95 ± 4	Dry	Wet	Wet	Early-late
Albizia adinocephala Britt.& Rose	Mimosoideae	ca. 25	12–26	111 ± 2	Dry	Wet	Wet	Early
Schefflera morototoni (Aubl.) Dec.& Planch.	Araliaceae	30–35	15–44	68 ± 3	Dry	Dry	Wet	pioneer
Enterolobium cyclocarpum (Jacq.) Griseb.	Mimosoideae	ca. 35	108–138	–	Dry	Dry	Dry	Early-late

sion, meteorological and hydrological branch). The precipitation pattern for the sampling period is shown in the top of Fig. 4. Season was defined as dry for January to March, and wet for June to November, with transition periods from April to May and in December. The annual mean temperature is 27°C (Kitajima et al. 1997).

Study species

We studied 17 tree species in a 75 to 150-year-old secondary forest stand (Table 1). The species composition is characteristic for this type of forest and successional status in Panama. The canopy is around 30 m tall, diameter at breast height (dbh) of canopy individuals is around 40 cm, with a few very large individuals of dbh between 1 and 1.5 m (Fig. 3). Specific leaf area varies from 61 to 131 cm^2 g^{-1} (a mean of 100); variation among species in SLA is not related to leafing season. We subsequently refer to species by genus except for *Cecropia* where we have two species.

Sampling

Roots, stems, leaves and branch-wood were sampled between October 1993 and July 1995. Leaf and branch-wood was collected from both, fully sunlit and shaded parts of the crown 11 times (for sampling dates see Fig. 4). Root and stem-wood was collected four times, (April and September 1994, January and February 1995). We selected these dates to cover the early and late dry season and the core of the wet season. We first sampled leaf and branch tissue in October 1993 and first cored trunks and excavated roots in April 1994. The exact hour of sampling, which is relevant for leaf data only, was noted. However, given the very small diurnal variation of NSC in leaves and their surprisingly small contribution to the forest NSC pool, we do not present data with diurnal resolution (for detail see Würth et al. 1998a). Hence leaf data presented here are pooled across sampling hours.

Samples were collected from one to three (mostly three) mature trees of each species. Canopy leaf and branch samples were obtained from a set of marked individuals, using a 42 m tall construction crane with a 51 m jib for canopy access. To avoid damage to trees under the crane, we sampled root and stem tissue from a second set of individuals (1–3) just outside the reach of the crane's jib.

For leaf and branch-wood, we always sampled two sets of tissues, one from the sunlit and one from the shaded part of the canopy. 'Sunlit' is defined as top canopy, 'shaded' is defined as the most shaded branches found in the interior of the upper canopy. For leaf tissue 10–15 punches, from at least five different fully expanded mature leaves were sampled with a cork borer (13 or 18 mm diameter), avoiding major veins. For branch-wood we sampled young, ca. 10 mm diameter terminal shoots (pieces of 20 mm length; including the cortex).

Stem-wood tissue was obtained at breast height or above adventitious roots if there were any. We used a 5 mm diameter wood corer and cored to the center of stems or up to 30 cm depth, in stems exceeding a radius of 30 cm. The cores were subdivided in sequential segments of 12 mm length. We averaged the data for the outer 3–4 segments (4–5 cm) to calculate seasonal and other summary statistics (Figs. 1, 4, Table 3), but we show the full stem depth profile in Fig. 3 for one sampling date. For root tissue we followed main roots until roots appeared with a diameter of 10–15 mm ('coarse roots') and 3–5 mm ('fine roots'). Pieces of 20 mm length were cut and rinsed before drying. Samples from terminal branches, stems and roots included bark. In branches and roots, the dry matter contribution by bark was negligible, but in stems the inclusion of the bark in the outermost 12 mm core segment lowered NSC concentrations.

All samples were killed and pre-dried at the crane site in a microwave oven (5 min at 800 W, with a glass of water inside the oven to avoid overheating). Final drying was done in a convection oven at 65°C for 24 h, starting on the evening of the sampling day.

Biochemical analysis

The enzymatic method used requires grinding samples to fine powder (in a ball mill) and boiling samples for 30 min in distilled water. The soluble fraction was then treated with invertase and isomerase and analyzed for glucose using a hexosekinase reaction kit (Sigma Diagnostics, St. Louis, Mo., USA). In a second step, the insoluble material (including starch) was incubated for 20 h at 40°C with the crude enzyme 'Clarase' (a fungal a-amylase from *Aspergillus oryzae;* Miles Laboratory, Elkhart, Ind., USA), which was dialyzed at 4°C for 12 h immediately before application in order to remove any mobile carbohydrate compounds. After centrifugation, the supernatant plant extract was treated and analyzed in the same way as the soluble fraction. Starch and sugar standards as well as a laboratory standard of plant powder were used as controls for all analyses. We also cross-checked our results with a gas chromatographic assay (M. Popp, Vienna), which yielded identical results and also illustrated that the suite of other mobile carbon compounds found in these tree tissues commonly contributed less than 10% to the total mobile pool. Hence, carbohydrates other than starch, sucrose, fructose and glucose are not covered here. For more methodological detail on the NSC assay see Wong

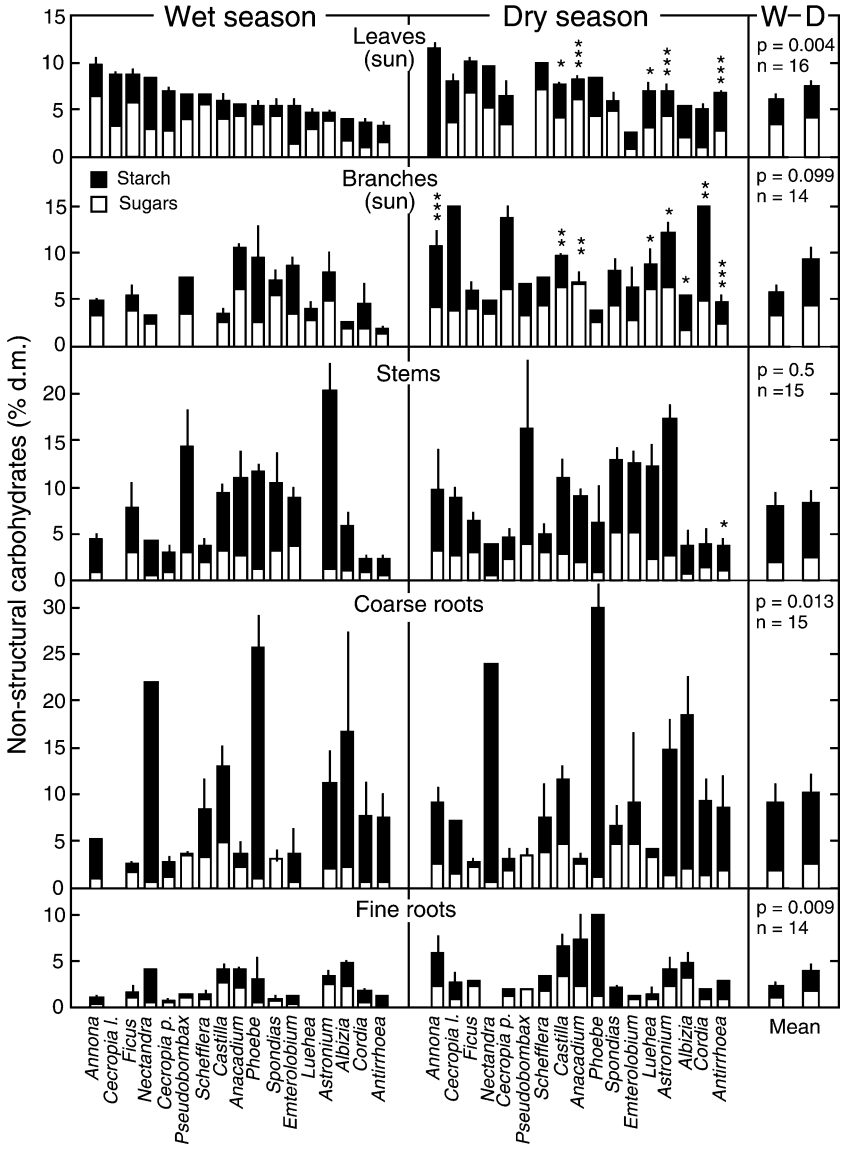


Fig. 2 Wet and dry season means of starch (*shaded area*), sugars (*unshaded area*) and total non structural carbohydrates (NSC) for each of 17 tree species of the semi-deciduous forest under the Smithsonian crane in Panama. Species are ranked by the wet season NSC concentration in leaves. Means across species (*right-most bars*) were calculated for only those species sampled in both seasons. *Error bars* indicate standard errors for two to four, mostly three tree individuals. *No error bar* means there was only one individual. *Asterisks* indicate significant season effects at the species level (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). Note, *P*-values for dry versus wet season means differ from Fig. 1 because the number of tree species sampled year-round is greater than $n = 9$ for specific tissue types

(1980), Körner and Miglietta (1994) and Hoch et al. (2003).

Data handling and statistics

We present species, tissue and season specific data and whole forest estimates on a land area basis. All statistical tests treat individual trees as replicates. Data from repeated sampling of one individual were pooled for sample dates within seasons. Hence our test of seasonality is a most conservative approach because variation within seasons and between years is uncontrolled. It was impossible to sample all tissues for all species at each sampling date. Some species lack leaves at certain periods. Root sampling and stem coring would be too destructive if done at the same frequency as leaf and branch sampling. For some species roots are not accessible. For these reasons the sample size of different tree species (n) differs among analyses.

We analyzed all data by hierarchical ANOVA (JMP version 3.1 released by SAS Institute, Cary, N.C., USA). The main model was: species and season. All statistical tests were done for each tissue type separately. As can be seen from Fig. 4, some samples were taken in the wet/dry or dry/wet transition periods, hence they could not be assigned to either the wet or the dry season. Therefore, we used "transition period" as a third season (hence, $df = 2$ for season in Table 3). For clarity, we present wet and dry season data only in Figs. 1 and 2. In leaves and branches we also determined NSC in sunlit and shaded crown parts. These data were analyzed with a *t*-test at the species level.

In our attempt to provide as broad as possible a picture of NSC patterns in this forest, we report all available data (except for seasonal variation of specific

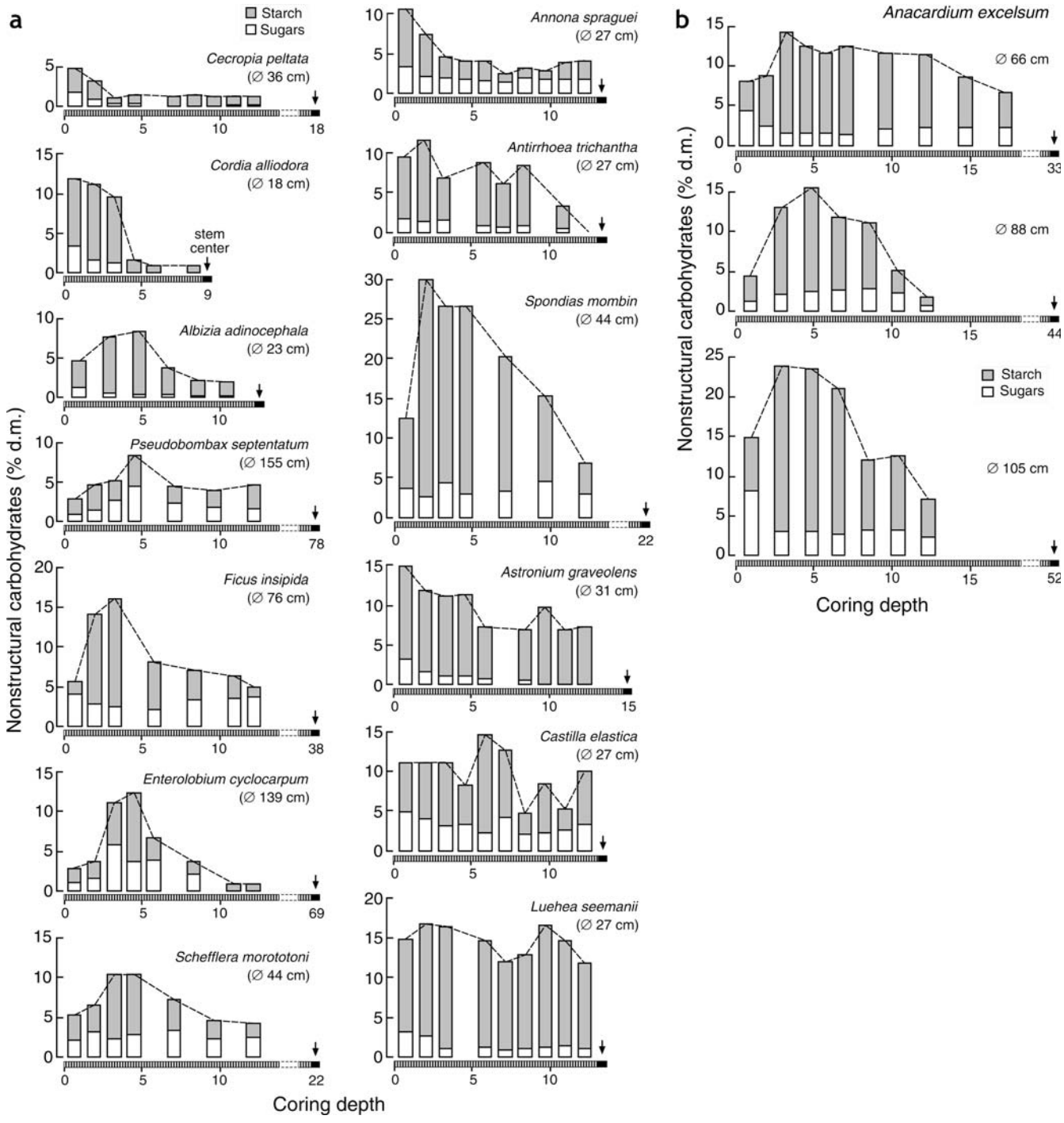


Fig. 3 Examples of radial profiles (12 mm segments of 5 mm cores taken with an increment corer) of NS C in stems of 14 tree species for April 1994, except for *Albizia* and *Anacardium* (b), which were cored in September 1994. Given that we present these details for one date only, we selected the samples from the transition season. Repeated coring (not shown here for space reasons) did not change this picture. For the dominant *Anacardium*, we present data for three individuals. The *horizontal bars* indicate coring depth in centimeters, with the *arrows* indicating the stem center. *Shaded bars* for starch, *open bars* for sugars. The total tree diameter of the cored tree specimen is given with the species name

stem depth segments) and we refer to this complete data set when reporting extremes, ranges and variability in general. However, when we discuss interspecific differences and report means for each of the five tissue types (and forest NSC pools derived from these), we consider species only for which all tissues and both wet and dry seasons were represented in the data set by at least two trees each (a species was dismissed even when a single data point in the matrix was missing). This reduces the number of species from 17 to 9, but permits a sound

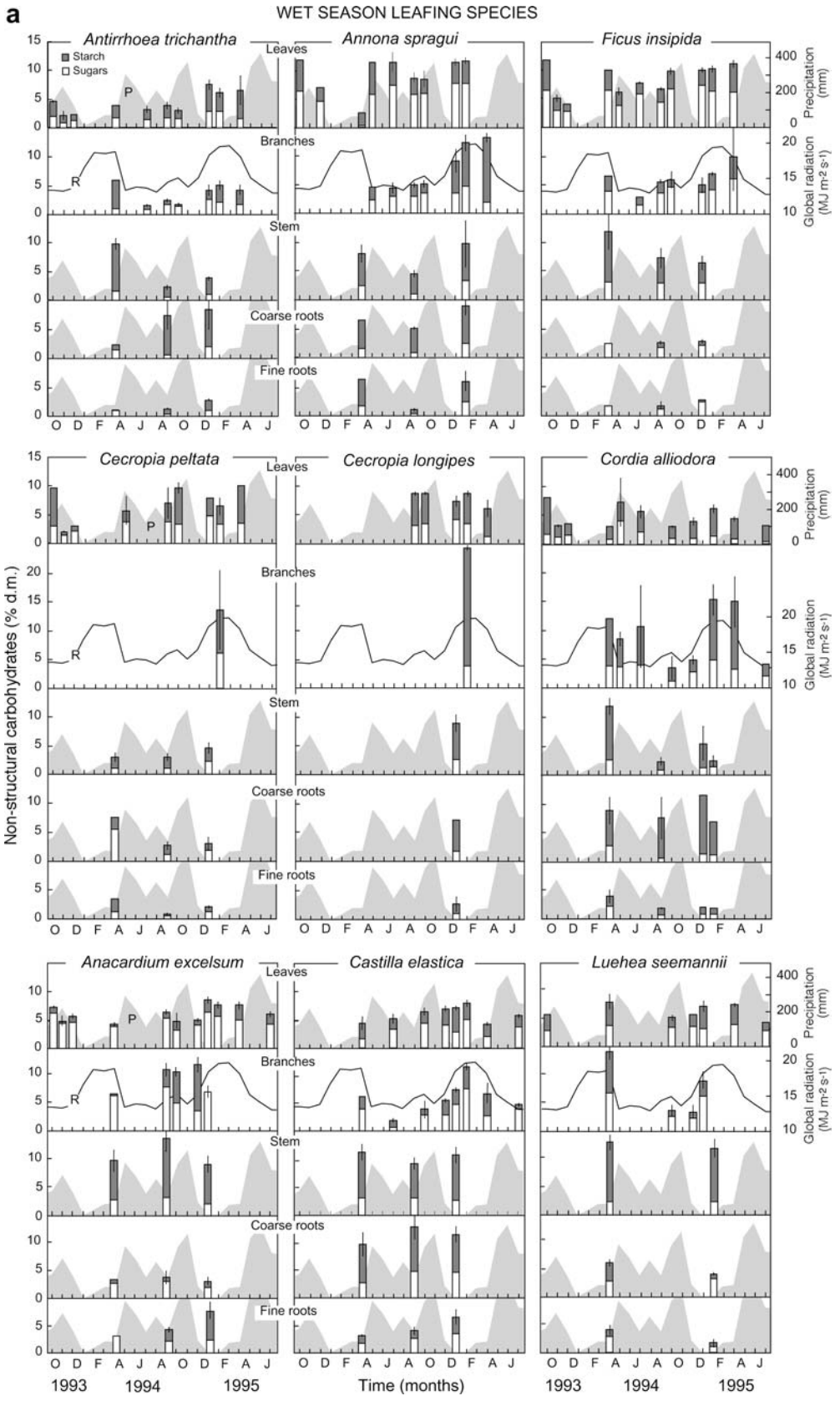
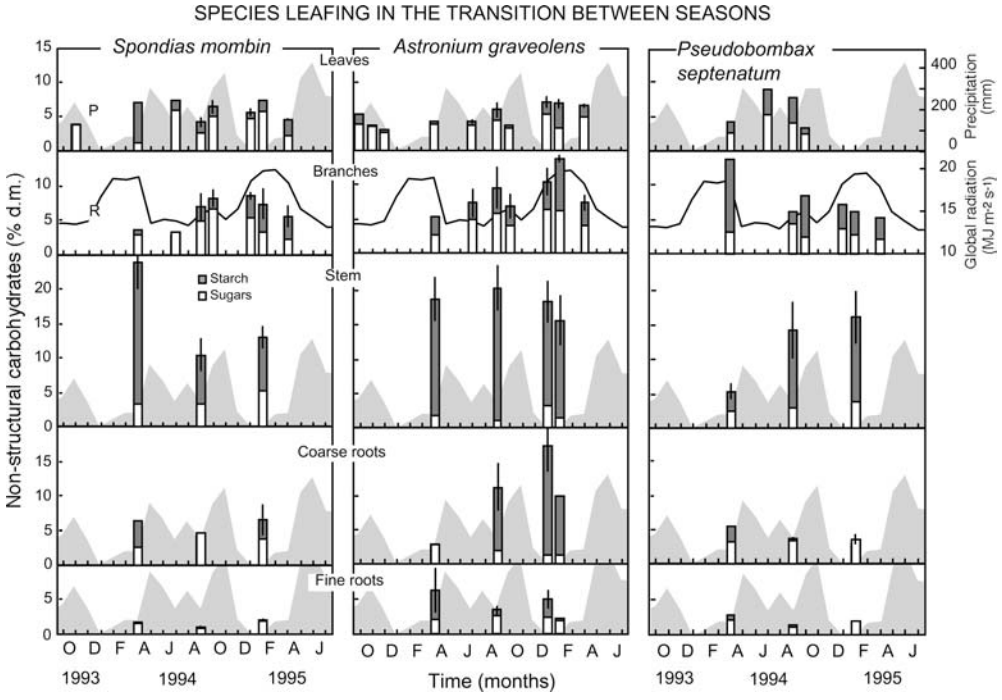


Fig. 4 The seasonal variation of NSC concentration for 17 tropical trees species. Means and standard errors for each sampling date for two to four, mostly three tree individuals. No error bar means there was only one individual. *black parts* of bars for starch, *open parts* for sugars. The *shaded curve* illustrates the course of precipitation over the 22 months sampling period, the *solid line* is for global radiation. Species are grouped into three seasonally distinct leafing types (**a, b, c**)

comparison of means for all organs and conditions, which otherwise would reflect presence or absence of data for a certain species. Tests with all species included did, however, lead to similar results, but slightly different means.

Fig. 4 (Contd.)



Results

Tissue and species specific NSC

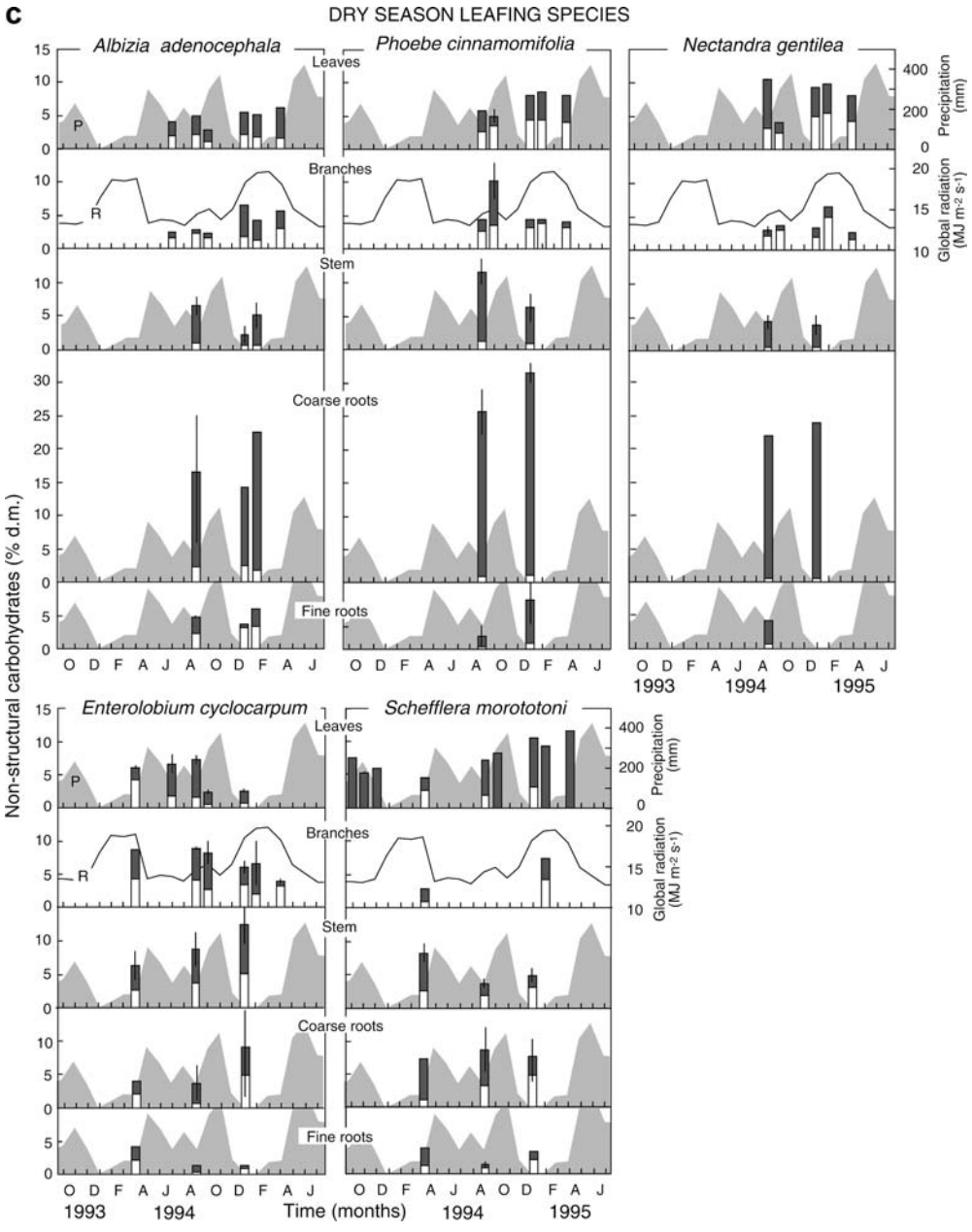
Across seasons and species roughly 4–9% of dry matter of any tissue type sampled was NSC. The lowest mean concentrations were found in fine roots (2–4%), followed by coarse roots (6–8%), leaves (6–7%) and stems or branches (mostly 5–9%). These means are calculated for just the nine species with data for all tissue types and all seasons (Fig. 1). The mean sugar to starch ratio was 2:1 in leaves, ca. 1.5:1 in small branches, 1:2.5 in stems, 1:2 in coarse roots and 1:1 in fine roots (Figs. 2, 3, 4, synthesis in Table 2). Hence, in leaves (the smallest pool) most of the NSC was sugar and in stems (the largest pool) most of NSC was starch with the sugar component playing a minor role.

These cross-species means of NSC mask substantial interspecific variation. The ranges of means for the nine core species across seasons were 2.5–11.6% in leaves, 1.9–15.4% in branches, 2.3–20.4% in stems, 2.6–14.8% in coarse roots, and 1.0–7.3% in fine roots. These 5–10 fold differences would prohibit meaningful projections of community-level patterns from a single species or a small group of species or from a single sample date or season.

We ranked the nine core species plus *Albizia* (which could not be used for Fig. 1, because this species has no shade leaves) by NSC concentration for each tissue type and than averaged these ranks across tissue types and seasons (a species mean at a rank of 1 would represent a species with the highest NSC for all tissue types and seasons, a mean rank of 10 a species with the lowest NSC for all tissue types and seasons). This ranking yielded a high NSC group with *Astronium*, *Castilla* and *Anacardium* (mean rank 2.8, 3.8, 4.6 out of 10), and a low NSC group consisting of *Cordia*, *Albizia* and *Antirrhoea* (mean rank 6.4, 6.6, 8.3). However, these ranks derived from overall means per species mask species specific differences in NSC allocation. For instance, *Albizia* has by far the highest root NSC, but very little NSC in other tissue. In contrast, *Ficus* and *Annona* show highest leaf NSC, but very modest concentrations in axial tissue. *Astronium* has the greatest stem NSC, with moderate concentrations elsewhere. If we include inconsistently sampled species, the three species flushing in the transition season, *Pseudobombax*, *Astronium* and *Spondias*, have the greatest stem NSC (up to 20% with no clear seasonality), and the three species flushing in the dry season, *Albizia*, *Nectandra* and *Phoebe*, have the greatest coarse root NSC (ca. 18–32% again irrespective of season). The thin branches of *Cecropia longipes* seem to burst with NSC with a 27% dry season concentration. Remarkably, *Nectandra* revealed one of the lowest stem NSC concentrations, and vice versa, *Pseudobombax*, exhibited the lowest coarse root NSC. In part these dry matter based concentrations reflect differences in structural tissue density (at the same volume concentration of NSC, soft wood produces a higher percent dry mass), but in any case variation among species is clearly important. Any restriction in species number used in such a survey bears a risk of bias.

There is a slight trend for NSC to be higher in roots, stems, or branches for species that flush leaves in the dry season, the transition season, or the wet season, respectively. In other words, the overall NSC-pool seems to be closer to the leaf canopy the more actively a species grows in the wet season. Full sun exposure compared to shade within the canopy had no significant effect on

Fig. 4 (Contd.)



NSC concentrations in leaves and young branches (Fig. 1). Light conditions within the canopy apparently do not affect local tissue NSC concentrations on a dry matter basis. Given the differences in SLA (Table 1), NSC per unit leaf area would, however, be lower in the shade.

Given these obvious differences among tissue types in the different species, we were surprised that a hierarchical ANOVA for species-effects was significant for leaves and marginally significant for branches only, and not for stems and roots (Table 3). One explanation may be, that leaves show the least seasonal change in ranking among the consistently sampled species, whereas tests for all other tissues conflict with their partially opposing seasonal NSC responses (i.e. season specific variation in ranking). Part of this is captured by a significant species × season interaction in leaves and branches, but again not in stems and roots. Once more this may have to do with inconsistent temporal trends in tissues of different species. But for the bulk of species, the largest NSC pool, which is in the stems (see later), exhibits no significant difference among seasons.

Variability in NSC as described above, in large part reflects differences in the starch fraction, which showed highly significant ($P < 0.001$) effects of tissue type and species. All season means in starch concentration in leaves, for instance, varied between 1.1% in *Spondias* and 3.3% in *Ficus*, with a mean of 2.2%. Mean sugar concentrations in leaves ranged from 1.0% in *Cordia and Enterolobium* to 6.7% in *Annona*, with a mean of 4%. In

Table 2 Mean sugar and starch concentrations (percentage of dry matter) in the nine most consistently sampled species (all data per species and tissue type pooled). The mean minima and maxima given below are calculated from the lowest or highest values ever recorded for each species

Tree species	Leaves		Branches		Stems		Coarse roots		Fine roots	
	Sugar	Starch	Sugar	Starch	Sugar	Starch	Sugar	Starch	Sugar	Starch
Astronium	3.9	1.8	5.2	3.9	1.9	17.0	1.7	11.4	2.4	1.3
Castilla	5.1	1.9	4.5	2.0	3.0	7.2	4.8	7.6	3.1	2.3
Anacardium	4.7	1.5	6.4	2.1	2.4	7.6	2.4	1.0	2.2	3.5
Annona	6.7	3.2	3.1	3.1	2.1	5.0	1.8	5.4	1.4	2.1
Spondias	5.1	1.1	4.6	3.3	4.3	7.4	3.8	1.5	1.3	0.2
Enterolobium	1.0	1.9	3.1	4.3	4.4	6.4	2.7	3.8	0.6	0.7
Ficus	6.4	3.3	3.7	1.7	3.0	4.1	2.0	0.8	1.8	0.5
Cordia	1.0	3.0	3.0	5.4	1.2	2.1	0.9	7.5	0.8	1.1
Antirrhoea	2.1	2.6	1.8	1.5	0.9	2.2	1.3	6.7	0.6	1.4
Mean ± SD	4.0 ± 2.2	2.2 ± 0.8	3.9 ± 1.4	3.0 ± 1.3	2.6 ± 1.2	6.5 ± 4.4	2.3 ± 1.2	5.1 ± 3.6	1.6 ± 0.9	1.5 ± 1.0
Minima ± SD	1.5 ± 1.1	0.8 ± 0.6	1.5 ± 0.7	0.8 ± 0.4	1.9 ± 1.0	5.5 ± 4.0	1.5 ± 0.9	3.7 ± 2.9	1.0 ± 0.7	0.8 ± 0.6
Maxima ± SD	5.9 ± 1.6	4.8 ± 1.3	5.8 ± 1.4	7.7 ± 2.7	3.4 ± 1.1	11.0 ± 5.2	3.4 ± 1.1	6.7 ± 4.5	2.4 ± 0.7	2.6 ± 1.7

stems, starch ranges from 2.1 to 7.6% (one extreme 17 %) with a mean of 6.5%, and sugar from 1.2 to 4.4% with a mean of 2.6 % (Table 2).

Stems deserve special consideration given they contain by far the largest amount of NSC. Once initial tests revealed a large depth of active wood, cores were analyzed to the center of trees. The resultant radial profiles of stem NSC (Fig. 3) illustrate NSC in almost all depth segments, including those close to the center of many trees. Only two species showed a restriction of significant amounts of NSC to the outer 3–4.5 cm, namely *C. peltata* and *Cordia*. In some species NSC peaked at 4.5–6 cm depth (e.g. *Enterolobium*), but others showed only a small decline from the surface to the inner end of our profile (*Luehea*, *Castilla*, *Astronium*, *Anacardium*). The outermost segment commonly shows lower NSC concentrations, because this segment includes part of the cortex. Overall these data illustrate the involvement of almost the entire stem in NSC storage in most of the studied species (at their given age and diameter; see Table 1).

Seasonal differences

Given the dramatic seasonal changes in climate and phenology of this semi-deciduous tropical forest, the rather modest seasonal differences in NSC concentrations came as a surprise (Figs. 2, 4). However, the differences were quite consistent across tissue types, when means for the most consistently sampled species are compared. NSC was always higher in the dry compared to the wet season. Mean dry season increases were smallest in stems (+13%) and leaves (+24%), but were substantial in coarse roots (+ 32%) and branches (+48%; Fig. 1). In relative terms, the effect was even larger in fine roots (+ 76%), but this number is somewhat misleading, given the generally very low NSC concentrations in fine roots. The season effect as well as the season × species interaction are highly significant for leaves, branches and roots (season effect only), but not for stems (Table 3). In some species phenology causes changes in NSC over short periods, but these changes did not overturn the general season effect. At the level of individual species, seasonal differences were significant only in a few cases in leaves and in terminal branchlets (asterisks in Fig. 2).

There was no clear seasonal trend in the starch-sugar ratio in any of the tissues. Surprisingly, sugar concentrations were even slightly higher in the wet season ($P < 0.001$) and were less variable than starch concentrations. Hence, there is no indication of an increasing contribution of sugars (e.g. as osmotics) to the NSC-pool during drought, except perhaps in branches

Table 3 NSC concentrations of the four major tissue types (coarse and fine roots lumped) tested for effects of species and season by hierarchical ANOVA

	Leaves			Branches			Stems			Roots		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Species	15[a]	10.8	< 0.001	13	2.0	0.076	11	1.5	0.190	11	1.4	0.250
Season	2[b]	18.4	< 0.001	2	12.7	< 0.001	2	1.7	0.200	2	6.3	0.008
Species × Season	30	2.2	0.010	26	2.1	0.019	22	0.9	0.571	22	1.0	0.477

[a] *Pseudobombax* has no leaves in the dry seasons, reducing *n* species to 16

[b] Data from the wet/dry or dry/wet transition period were treated as a 'transition season', so there were 3 seasons. Only complete data sets per organ type had been used, hence the variation in *n*

of *Phoebe*. The wet/dry season difference in NSC resulted largely from differences in starch content.

For 17 species, grouped into three leafing phenotypes, Fig. 4 illustrates temporal patterns of NSC for each tissue type together with the rainfall and radiation patterns. There is no obvious association between NSC concentration and climatic variables in most of the species, except perhaps in branch wood. Among the nine species that produce most of their foliage during the wet season, *Antirrhoea*, *Annona*, *Cordia* and *Castillea* (and also *Luehea* and *Ficus*) exhibited lowest branch-NSC during the wet season. For the other species of this group, there were not enough branch data for the core of the dry season. There is no clear seasonal NSC trend in species that flush leaves during the transition period, but in *Astronium*, branches show a dry season peak as well. Among the five species that produce most of their foliage during the dry season, four species show highest NSC concentrations in leaves in the dry season, i.e. concurrently with new leaf production, and the same is true for branches in three of these species, hence they also fit the wet-low, dry-high pattern. In *Phoebe* branches and in *Enterolobium* leaves and branches show a dry season low, while stems and roots do not. Statistical tests for leafing type (not shown) did not yield any significant group specific patterns. The fact that even in dry season leafers NSC can peak during the leafing season underlines that leafing is not necessarily associated with a depletion of mobile C-pools.

Whether flowering and fruit filling (Table 1) draws on the NSC pools (at least in the most sensitive branch pool; Fig. 4) can only be separated from the general wet/dry season trend in species flowering or fruiting in the dry season or wet/dry transition seasons. The dry season fruiting and NSC reduction in *Anacardium* is one positive case, however, in *Luehea* and *Enterolobium* dry season fruiting coincides with the NSC peak. *Enterolobium* produces new leaves, flowers and fruits in the dry season, which somewhat reduced branch NSC in the second dry season studied, but at the same time stem and coarse root NSC exhibited an all-time high during this period. In *Cordia* branch-NSC peaks coincide with the end of dry season flowering. Our data are too widely spaced to interpret effects of reproduction in each individual case with confidence, and phenology data need to be linked directly to the NSC data on a per tree basis, which was beyond the scope of this survey, but overall, such effects, if they exist, appear to be relatively small.

Estimation of total forest NSC pool

According to Houghton et al. (2001), the humid tropical forests of Latin America support an average 271 t of dry above-ground biomass per hectare. This mean for 44 locations covers a range from 95 to 413 t ha^{-1}, with most records (excluding gallery forests) in the 200–300 t ha^{-1} range. Given the semi-deciduous nature and relatively early successional stage of our test forest we assume a 200 t ha^{-1} biomass pool including the below ground fraction. We follow the relatively robust assumption of Houghton et al. (2001) of a mean 21% contribution of below ground biomass to total biomass. Using the common 4% leaf mass ration for evergreen trees (Körner 1994) yields a 75% biomass fraction for stems plus branches (with an approximate 3:1 stem: branch ratio following Hozumi et al. 1969).

Combining the tissue specific NSC concentrations (means across species and seasons from Fig. 1) with these biomass data, yields an NSC pool of 16.1 t ha^{-1} (10.5 t starch and 5.6 t sugars; Table 4). Stems were assumed to store the mean value of NSC found across our coring depth, hence we did not separate active and inactive wood fractions. Inactive wood fractions may be important given that most of the trees we sampled were storing NSC to the stem center. For some of the very large trees this assumption will overestimate the biomass based NSC-pool. On the other hand, using our terminal branch NSC data to represent the complete branch fraction of forest biomass (in large very thick branches) will underestimate NSC stores. Branches and stems together represent ca. 13 t ha^{-1} or 80% of the total pool. Despite the low NSC concentrations found in root tissues, the greater root than leaf mass causes roots to store 5.5 times as much NSC as the leaf canopy, but overall, both root and leaf pools are quite small (20% of total) compared to the stem plus branch pool.

Discussion

The major findings of this broad survey of seasonal mobile carbohydrate concentrations in tropical forest trees are a high species specificity, and (counter to our presumption) a significant increase in NSC concentrations during two extensive drought periods in the majority of species, which was most pronounced in branch tissue close to the leaf canopy. New leaf production and flowering and fruiting do not necessarily

Table 4 Forest NSC-pools as estimated from forest biomass and mean tissue type specific NSC, averaged across all species tested (not accounting for species abundance). All dry mass related data in t ha^{-1}

Organs	Biomass (t ha^{-1})	NSC (d.m.%)	NSC (t ha^{-1})	Starch (t ha^{-1})	Sugar (t ha^{-1})
Leaves	8	6.3	0.50	0.18	0.32
Branches	38	7.0	2.66	1.14	1.48
Stems	112	9.1	10.2	7.28	2.91
Coarse roots	34	7.4	2.52	1.73	0.78
Fine roots	8	3.0	0.24	0.12	0.13
Total	200	8.0	16.1	10.5	5.6

deplete NSC-pools, given that even species flushing and fruiting during the dry season show a dry season NSC-high. Season effects appear to overrun phenology effects, as was concluded by Newell et al. (2002). The wet season reduction of NSC concentration, mainly seen in branches and roots, and less so in leaf and stem tissue, may reflect light limitation due to cloudiness and increased canopy density (Graham et al. 2003). However, more likely this reflects moisture driven sink activity growth and higher nutrient availability. Despite the documented leaf and branch autonomy, leaf and branch tissue from the shade did not significantly differ in NSC dry matter concentration from fully sunlit tissue in any season and leaves and branches from sun and shade positions showed a similar seasonal course.

Given that our sampling strategy was a compromise between sampling five tissue types (two of which were sampled in both shade and sun) in 17 species with as a high a temporal resolution as possible, we may have missed short critical periods in particular species, but this would not change the overall outcome, namely that storage carbohydrates are retained at relatively high levels in this forest throughout the year. In other words, the data do not suggest that any of these 17 tree species was short in C-compounds during the observation period. It rather seems, most of the reserves, particularly the nearly two thirds of the pool stored in stems, were not significantly reduced during any period in most of the species. Small branches seem to represent the major buffer for seasonal and phenological variations in C-demand, as was noted by Newell et al. (2002). The bulk of the NSC-pool may thus simply reflect over-abundance of assimilates during normal forest function, but may become significant in cases of tree damage. The estimated total of ca. 8 t ha^{-1} of leaf biomass corresponds to about 76% of the mean forest starch-pool (assuming similar stoichiometry; Table 3). If the forest leaf canopy were completely lost and only starch reserves were available for rebuilding new leaves, reserves would easily allow for one complete canopy replacement, not accounting for concurrent photosynthetic contribution during regrowth, which is known to be very high. This may not hold for plants in deep shade, whose leaf replacement in such an event would more strongly depend on stored reserves as was shown for the understory shrub *Piper arieianum* (Marquis et al. 1997).

It is widely assumed that plants need reserves to survive stressful periods (e.g. Sampson et al. 2001). However, the only situation where this concept may apply is under 'low light stress' i.e. in shade. It also would apply to disturbances, which however, should not be confused with stress. Under what is commonly considered stress, such as water shortage, it is always meristem activity which is affected first and more significantly and not photosynthesis (Hsiao and Acevedo 1974; Terry et al. 1981; Kriedemann 1986). A similar hierarchy of controls applies to nutrient shortage (Schulze 1982) or low temperature (Hoch and Körner 2003; Körner 2003). Hence, in all these cases sink limitation dominates over source limitation, although, additional resources such as nutrients or higher CO_2 concentrations may mitigate the effects of other limitations. This comparison of carbon reserves in wet versus dry periods in the tropics conforms to this concept.

The amounts of NSC found here match the limited data for mature forest trees from other studies in the tropics. Notably, our numbers for *Anacardium* and *Luehea* stem and branch wood are well within the 8–14% range reported by Newell et al. (2002), but our root NSC concentrations in these two species are lower than in Newell et al.'s analysis, as is the overall concentration in roots, including the other species studied here. Young tropical plantation trees such as those studied by Latt et al. (2001) appear to operate at far lower NSC pools (4–6% in stems of five species). On average, NSC concentrations of terminal branch tissue found here are significantly lower than in temperate zone hardwood species, where seasonal means (with little variation) of 14–18% NSC have been reported (Hoch et al. 2003). However, with 8–10%, the mean NSC storage in stem sapwood in the tropical trees studied here is significantly higher than the 4–7% range for seasonal means reported by Hoch et al. for six dominant European deciduous tree species, and by far exceed the 1.5–3% found in temperate conifers by the same authors and in earlier works. Only *Albizia*, *Nectandra* and *C. peltata* consistently show such low stem NSC concentrations at our study site.

Surprisingly high NSC concentrations were found in wood samples cored from very deep in the trunks, suggesting active ray tissue in what might commonly be termed (dead) heart wood (Fig. 3). The physiologically most active stem fraction (i.e. the fraction containing sugars) in these tropical trees is at least 15 cm thick and also stores considerable amounts of starch (6.7%). Newell et al. (2002), who had cored the outer 5 cm, and in one incidence the outer 10 cm of their study trees, also arrived at the conclusion that trunk stores of NSC are significant. Notably, their two distinctly deciduous pioneer species showed less seasonal variation in the 2–5 cm part of the trunk than did the non-deciduous *Anacardium*. For space reasons, we could not include our seasonal data for all stem core segments, but seasonal variations were very small in the inner trunk, so it may be plausible to assume that these parts of the NSC pool are not very active under the study conditions. Hoch et al. (2003) came to a similar conclusion for temperate forest trees. NSC concentrations also decrease more rapidly with stem depth in temperate zone hard wood trees (though again this depends on species). A particularly sharp radial decline was reported for the pioneer hardwood *Robinia pseudoacacia* (Magel et al. 1994).

In conclusion, this first quantitative 'tip to toe' assessment of mobile carbohydrates in a diverse tropical tree assemblage underlines the need for broad comparative approaches. The coverage of so many species and tissue types adds to the confidence that our findings are representative for the study forest, despite

the tradeoff in the form of restricted temporal resolution. The lack of a significant NSC depletion at any time, for any tissue type or species, leaves us with a picture of a forest with consistently ample carbon supplies. Periods of drought stress even enhanced NSC concentrations in tissues, indicating that investments of carbon (formation of new tissue) were more constrained by the environment than was carbon acquisition (photosynthesis) during these periods. Zotz and Winter (1996) and Kitajiama et al. (1997) found little seasonal change in photosynthetic capacity of canopy trees in this region. Carbon surplus seems to be a widespread phenomenon when environmental conditions become adverse (Körner 2003). It is thus hard to imagine that enhanced carbon fixation (source activity) due to ongoing atmospheric CO_2– enrichment could further stimulate growth, i.e. structural investments in this forest—at least during the drier periods, when growth is limited by sink activity.

Given the small changes and high concentrations in the major NSC pools of this forest, it even seems that carbon is not a particularly limiting resource for most canopy forming trees also during humid periods. Perhaps, this already reflects the elevated atmospheric CO_2 concentration during the study of 365 ppm, which is twice the post-glacial minimum 18,000 years ago and 30% above the pre-industrial value of 280 ppm only two to three tree generations ago. A nearly saturating C-supply would be in line with the observation that recent decades of significant atmospheric CO_2- enrichment have not seen a growth stimulation in dominant tropical forest trees (Clark 2002), but it does not exclude the possibility that light limited subdominant trees, understory regrowth and lianas are still constrained by carbon acquisition and can profit from a higher CO_2 concentration. The stimulation of lianas in particular, could have a significant influence on tropical forest dynamics (Phillips et al. 2002; Wright et al. 2004), with a CO_2 driven stimulation under strong light limitation being the most plausible explanation (Würth et al. 1998b; Granados and Körner 2002). The stimulation of lianas, which are known to be major drivers of tropical forest dynamics, may even cause a reduction of tropical forest biomass carbon storage in the long run (Körner 2004).

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