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CARBOHYDRATE STORAGE AND LIGHT REQUIREMENTS OF TROPICAL MOIST AND DRY FOREST TREE SPECIES

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Abstract. In many plant communities, there is a negative interspecific correlation between relative growth rates and survival of juveniles. This negative correlation is most likely caused by a trade-off between carbon allocation to growth vs. allocation to defense and storage. Nonstructural carbohydrates (NSC) stored in stems allow plants to overcome periods of stress and should enhance survival. In order to assess how species differ in carbohydrate storage in relation to juvenile light requirements, growth, and survival, we quantified NSC concentrations and pool sizes in sapling stems of 85 woody species in moist semi-evergreen and dry deciduous tropical forests in the rainy season in Bolivia.

Moist forest species averaged higher NSC concentrations than dry forest species. Carbohydrate concentrations and pool sizes decreased with the light requirements of juveniles of the species in the moist forest but not in the dry forest. Combined, these results suggest that storage is especially important for species that regenerate in persistently shady habitats, as in the understory of moist evergreen forests.

For moist forest species, sapling survival rates increased with NSC concentrations and pool sizes while growth rates declined with the NSC concentrations and pool sizes. No relationships were found for dry forest species. Carbon allocation to storage contributes to the growth–survival trade-off through its positive effect on survival. And, a continuum in carbon storage strategies contributes to a continuum in light requirements among species. The link between storage and light requirements is especially strong in moist evergreen forest where species sort out along a light gradient, but disappears in dry deciduous forest where light is a less limiting resource and species sort out along drought and fire gradients.

Key words: Bolivia; growth–survival trade-off; shade tolerance; starch; sugar; total nonstructural carbohydrates (NSC); tropical forest.

INTRODUCTION

Forest succession, composition, and dynamics are often explained on the basis of the light requirements of tree species (Pacala et al. 1996). Tree species vary continuously in their light requirements, ranging from shade-tolerant species that maintain juveniles in the shaded understory to light-demanding species that regenerate only in the high-light conditions of gaps. Species position along this continuum is determined to a large extent by a trade-off between growth and survival (Kitajima 1994, Wright et al. 2003, Poorter and Bongers 2006). A fast growth rate is important for successful regeneration in gaps, as it allows species to attain a position in the top of the regrowing gap vegetation and complete their life cycle before the canopy gap is closed. A high survival rate is important for successful regeneration in the understory, as it allows species to persist under low-light conditions until eventually a gap is formed (Brienen and Zuidema 2006). Thus, when growth rates are plotted against survival rates for seedlings and saplings, there is a strong negative cross-species correlation. Data from species-rich tropical forests demonstrate that individual species fall along this continuum from the "fast-growth, low-survival" end represented by light-demanding species to the "slow-growth, high-survival" end represented by shade-tolerant species (Wright et al. 2003, Gilbert et al. 2006, Poorter and Bongers 2006).

The trade-off between growth and survival is most likely caused by a trade-off between carbon allocation to growth on the one hand and allocation to storage and defense on the other (Kitajima 1996). A large body of literature has focused on the role of plant defenses. Allocation to defense has a clear survival advantage, as it protects plants against biomass loss due to herbivores (Coley 1988), pathogens (Augspurger 1984), and physical disturbance (Putz et al. 1983). At the same time it comes at the expense of a reduced growth rate, as tough, well-protected leaves and stems are costly to produce (Coley et al. 1985, Muller-Landau 2004, Sterck et al. 2006).

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Relatively little is known about the role of storage in the growth–survival trade-off. Energy storage is largely accounted for by photosynthetic income deposited as nonstructural carbohydrates (starch and sugars) in the plant that can be mobilized later to support growth or other plant functions (Chapin et al. 1990) (see Plate 1). Allocation to storage enhances plant survival, as it allows plants to overcome periods of stress and disturbance. Starch and sugar are used to endure periods of negative net carbon balance when plants become suddenly shaded (Veneklaas and den Ouden 2005; Myers and Kitajima, *in press*), droughted (Janzen and Wilson 1974), defoliated (Myers and Kitajima, *in press*), or have lost their stems (Latt et al. 2000). Economic theory predicts that investment in storage leads to reduced growth, but this growth reduction is smaller under low- than under high-resource conditions (Chapin et al. 1990). If a plant in high light invests in storage instead of leaf area expansion, it would miss an opportunity for a compound return in terms of carbon gain and growth. However, these opportunity costs of storage are low in shade because potential carbon gain is constrained by low light availability and because stored carbohydrates do not require any maintenance respiration (Kobe 1997).

Theoretical models suggest that carbon investment in storage is an advantageous strategy in habitats with frequent stress and disturbance (Iwasa 1997). Pathogens, shading, and stem damage are especially frequent in the forest understory (Augspurger 1984, Gartner 1989), and it is therefore likely that allocation to storage would enhance shade tolerance. The evidence for this hypothesis is, however, scarce. Kobe (1997) found that saplings of two temperate shade-tolerant species had higher nonstructural carbohydrate (NSC) concentrations per unit mass than saplings of two light-demanding species. Carbohydrate concentration per unit mass is indicative of relative allocation of new biomass to storage vs. structural mass, as well as amount of carbohydrate available for maintenance respiration per unit mass. However, total carbohydrate pool size per plant may be the critical determinant of plant survival. Myers and Kitajima (*in press*) found for seedlings of seven tropical tree species that the NSC pool size in the plant, rather than NSC concentrations of the tissue, was positively related to their shade survival. They also found that seedlings depended even more strongly on NSC pools for survival after they were subjected to disturbance and stress of experimental defoliation and additional shading. If storage is an important component of shade tolerance, then we predict that more shade-tolerant species should have higher NSC concentrations and pool sizes. Furthermore, during the wet season when the canopy is fully foliated, we predict that species from dark, wet, evergreen forests should have higher NSC concentrations than species from dry, deciduous forests that have a lower and more open canopy. Conversely, if seasonal leaf flush following the dry-season deciduousness is the main driver of species differences in NSC storage among tropical tree species, then species from dry, deciduous forests should have higher NSC concentrations than species from wet forests, especially during the dry season. To our knowledge, no published data compare juvenile NSC storage for a large number of tree species within and across tropical forests with contrasting precipitation regimes.

Here we compare NSC concentrations and pool sizes for saplings of 85 woody species from a dry forest and a moist tropical forest in Bolivia. Nonstructural carbohydrate concentrations were determined in the rainy season after the seasonal leaf flush, because our prime objective was to evaluate the relationship of carbohydrate storage with shade tolerance, but not with drought survival and deciduousness. We relate the carbohydrate concentrations to a quantitative measure of the juvenile light requirements (cf. Poorter et al. 2005) as well as to regeneration guilds of the tree species. We hypothesize that NSC concentrations and pool sizes (1) are larger for moist forest than for dry forest species, (2) increase with the shade tolerance of the species, and (3) are positively correlated with survival probability and negatively correlated with growth rates of the species.

MATERIAL AND METHODS

Research sites

Fieldwork was carried out in the lowland tropical moist semi-evergreen forest of La Chonta (15°47′ S, 62°55′ W) and the dry deciduous forest of INPA (a private company, 16°1′ S, 61°4′ W) in Bolivia. Both are long-term research sites of the Instituto Boliviano de Investigación Forestal (IBIF) and at an altitude between 300 and 500 m. Annual precipitation in La Chonta is 1520 mm, with a dry season (<100 mm/mo) from April until October. The forest has a mean canopy height of 25 m, stem density of 368 stems/ha, basal area of 19.7 m^2/ha, and species richness of 59 species/ha (all data for trees >10 cm diameter at breast height [dbh]; IBIF, *unpublished data*). About one-third of the canopy trees are deciduous in the dry season. Annual precipitation in INPA is 1160 mm, with an 8-mo dry season. The forest has a mean canopy height of 20 m, stem density of 437 stems/ha, basal area of 19.7 m^2/ha and species richness of 34 species/ha. Nearly all canopy trees are deciduous in the dry season.

Species selection

We selected 49 tree species in La Chonta and 38 tree and shrub species in INPA, with seven species in common to both sites (Table 1). The most common species were selected so as to include a wide range of shade tolerance and adult stature. Species were classified into four shade-tolerance groups, based on field observations of distribution patterns (Justiniano et al. 2004, Poorter et al. 2006; J. Justiniano and L. Poorter, *personal observation*): total shade-tolerant species (TST) that can establish and survive in the shade; partial shade-tolerant species (PST) that can establish in the shade but depend on gaps to grow to larger sizes; long-lived pioneers (LLP) that have high light requirements for regeneration and live longer than 30 years; and short-lived pioneers (SLP) that have high light requirements for successful regeneration and live no more than 30 years (Finegan 1992).

The juvenile light requirement was also expressed by a continuous and objective variable from analysis of the crown exposure of each species in relation to individual heights in a separate study (L. Poorter, J. C. Licona, A. Alarcon, C. Leaño, and M. Peña-Claros, *unpublished manuscript*). To this end on average 523 individuals (range 16–9064) per species were measured for their height and crown exposure (CE), using a method adopted from Dawkins and Field (1978). The CE is assigned a value of 1 if the tree does not receive any direct light; 2 if it receives lateral light; 3 if it receives overhead light on part of the crown; 4 when it receives full overhead light on the whole crown; and 5 when it has an emergent crown that receives light from all directions. The CE measurements were repeatable (difference between two independent observers is 0.1 ± 0.01 [mean ± SE]) and well-correlated with independent measures of canopy openness (Davies et al. 1998). For each species, the CE was related to individual height using a multinomial logistic regression (cf. Poorter et al. 2005, Sheil et al. 2006). Using the regression equation, the mean population-level juvenile crown exposure (CE_{juv}) at a standardized height of 2 m was calculated. A low CE_{juv} indicates that a species mainly regenerates in the shaded understory (i.e., a shade-tolerant species), whereas a high CE_{juv} indicates that it mainly regenerates in the high-light conditions of gaps.

Because the dry forest has a lower and more open canopy than the moist forest, the dry forest species have, on average, a higher CE_{juv} (L. Poorter, J. C. Licona, A. Alarcon, C. Leaño, and M. Peña-Claros, *unpublished manuscript*). A direct quantitative comparison of the CE_{juv} amongst dry and moist forest species is difficult, because the researcher tends to rescale the crown exposure values to the range of canopy conditions observed in the forest (Zagt 1997). It allows, however, comparisons of species within the same forest.

Field measurements

For each species ~10 saplings (mean 9.6, range 2–20) between 0.5 and 2 m tall were selected in undisturbed forest and logged forest. Individuals were in principle searched for under closed-canopy conditions, but light-demanding species were also sampled in gaps and along skidtrails or roads to assure a sufficient number of individuals. Sapling height, leaf number, diameter at 5 and 50 cm height, and crown exposure were measured. The height was measured vertically, from the forest floor to the apex of the plants.

In La Chonta plants were clipped in early December, at one-third of the way through the rainy season, when the species had flushed and depleted their carbohydrate reserves. In INPA, the plants were clipped in late January halfway through the rainy season. For each plant a 20-cm stem section was sampled below the crown, between 50 and 70 cm height. A smaller section was sampled from plants that did not attain 70 cm height. The volume of this stem section including bark was calculated as $0.25 \times \pi \times \text{diameter}^2 \times \text{length}$. The samples were oven-dried for at least 48 h at 70°C and weighed. Stem density was calculated as sample mass divided by sample volume.

For each species ~16 additional saplings were selected that occurred under similar conditions and had a height between 0.5 and 2 m. The height growth and survival were monitored several times per year for two years in La Chonta (Poorter and Bongers 2006) and for one year in INPA (L. Poorter, *unpublished data*). See Poorter and Bongers (2006) for a description of the measurement protocol and the calculation of annual growth and survival rates.

Nonstructural carbohydrates

The middle 5 cm length of each sampled stem section (including wood and bark) was ground by a Wiley Mill to pass through a mesh size of 0.425 mm. A pooled sample per species was made by combining 0.3 g ground sample for each of the 10 stem sections. Tissue concentration (in milligrams per gram dry mass) of simple sugars and starch were analyzed following Marquis et al. (1997). Simple sugars were extracted with 80% ethanol in a shaking water bath at 27°C: one overnight extraction followed by a 2-h extraction with fresh 80% ethanol. Supernatants from both extraction sessions were combined and diluted to a set volume. Starch and more complex sugars in solids were hydrolyzed to glucose overnight, using a sodium acetate buffer and amyloglucosidase at 56°C. The glucose concentration in these extracts was determined with a phenol-sulfuric acid reaction, followed by colorimetry at 487 nm. For pooled samples, replicates were run when the values were extreme (two samples with lowest values or sugar and starch concentrations >20%), and if the two replicates differed greatly, we did the third replicate and took the average of the close two values. We also analyzed replicates of random samples of various range to confirm that replicated values were similar enough (<10% difference).

We expressed the carbohydrate concentration per unit dry mass. The total carbohydrate pool size was calculated for a standardized size of 1 m tall plants to facilitate cross-species comparisons. In this way plants are compared when they have attained the same position in the vertical light gradient in the forest canopy. The stem volume for 1 m tall plants was estimated from a regression of ln(stem volume) against ln(plant height) (average $r^2 = 0.80$, range = 0.35–0.99) for individual species. Stem volume was calculated for individual stems for which stem diameter at 5 and 50 cm height and total plant height was known ($n = 9.3$ per species, range 2–12).

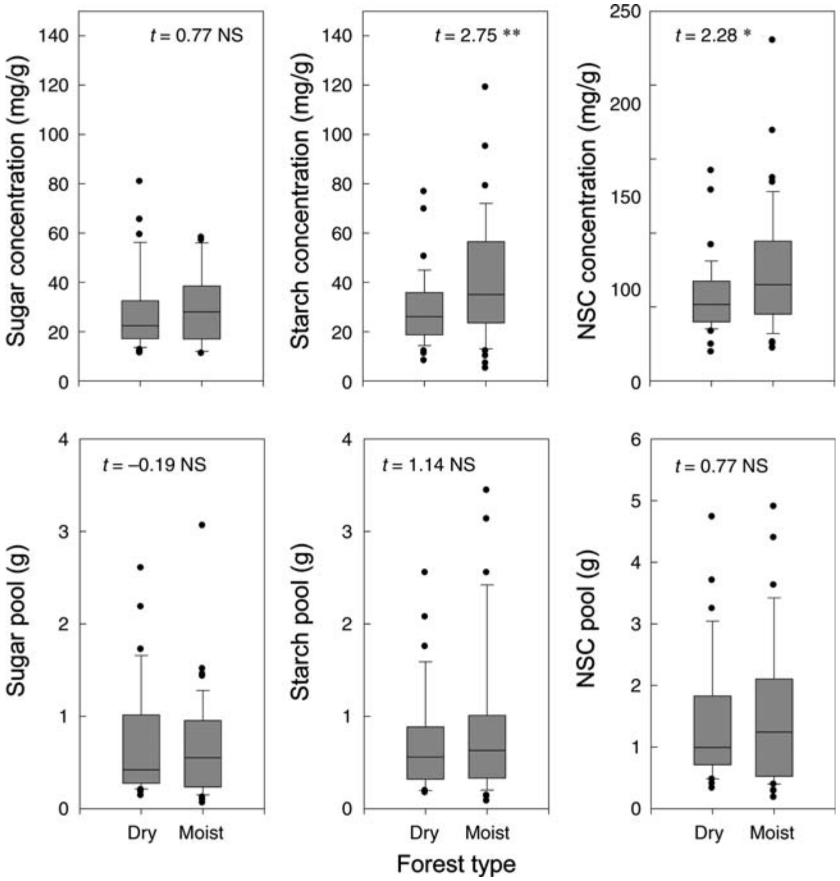

FIG. 1. Box plots of carbohydrate concentrations and pool size of dry ($n = 38$) and moist ($n = 49$) forest tree species. The total carbohydrate pool sizes (sugar, starch, and nonstructural carbohydrates [NSC]) are estimated for stems of 1 m tall saplings. Lower and upper ends of the boxes indicate the 25th and 75th percentile, lower and upper ends of the whiskers indicate the 10th and 90th percentile, and the horizontal lines within the boxes indicate the 50th percentile. Fieldwork was carried out in a lowland tropical moist semi-evergreen forest and a dry deciduous forest in Bolivia.

We assumed a cylinder ($0.25 \times \pi \times$ basal diameter$^2 \times$ plant height) rather than a tapered stem, because the volume of the branches approximates the difference in volume between a cylindrical and a tapered stem (Holbrook and Putz 1989). Total carbohydrate pool size (in grams) was then calculated as stem volume (in cubic centimeters) × stem density (in grams per cubic centimeter) × carbohydrate concentration (in grams per gram). We also calculated structural mass (total mass minus NSC) and NSC per unit volume. Because statistical results using NSC per unit volume was identical to those using NSC per unit mass, we report only the results using the latter as the measure of carbohydrate concentration.

Statistical analyses

For all statistical analyses, species means were used as data points. Carbohydrates were compared between moist and dry forest species, using a *t* test, and between moist and dry forest saplings using a paired *t* test for the seven species in common to both sites. For each site carbohydrates were related to juvenile crown exposure and species-specific growth and survival using a Pearson correlation. Carbohydrate variation among functional groups was analyzed with a one-way ANOVA with a Student-Newman-Keuls post-hoc test. The carbohydrate pool size was $\log_{10}$-transformed prior to analysis, to increase homoscedasticity. Finally, carbohydrate pool size was regressed against its underlying components (stem volume, stem density, and carbohydrate concentrations) to evaluate the relative importance of each component as a contributor to interspecific variation in pool size. In this analysis all variables were $\log_{10}$-transformed. All statistical analyses were carried out using SPSS 12 (SPSS 2003).

RESULTS

Dry vs. moist forest species

Moist forest species had higher starch (*t* test, $t = 2.75$, $P < 0.01$) and NSC concentrations (*t* test, $t = 2.28$, $P < 0.05$) per unit dry mass compared to dry forest species, but there was no difference between the forest types for mean sugar concentrations (Fig. 1). On average, sugar contributed 46% to the NSC pool (range 20–88%) and

TABLE 1. Overview of the tree species studied and guilds (TST, total shade tolerant; PST, partial shade tolerant; LLP, long-lived pioneer; SLP, short-lived pioneer), juvenile crown exposure ($\mathrm{CE}_{\mathrm{juv}}$), and sugar, starch, and nonstructural carbohydrate (NSC) concentrations (in mg/g).

Species	Family	Guild	$\mathrm{CE}_{\mathrm{juv}}$	Sugar	Starch	NSC
Moist forest						
Acacia bonariensis	Mimosoideae	LLP	1.59	35	59	94
Alibertia verrucosa	Rubiaceae	TST	1.35	20	26	46
Ampelocera ruizii†	Ulmaceae	TST	1.35	25	37	62
Aspidosperma cylindrocarpon	Apocynaceae	PST	1.75	38	24	62
Aspidosperma rigidum	Apocynaceae	PST	1.56	34	32	65
Batocarpus amazonicus	Moraceae	PST	1.35	56	59	115
Cariniana ianeirensis†	Lecythidaceae	PST	1.74	15	34	49
Casearia sp.	Flacourtiaceae	TST	1.39	36	34	69
Cecropia concolor	Cecropiaceae	SLP	2.44	21	35	56
Centrolobium microchaete†	Papilionoideae	LLP	1.94	12	13	26
Cordia alliodora	Boraginaceae	LLP	1.95	18	32	50
Cupania cinerea	Sapindaceae	PST	1.79	33	5	38
Dendropanax arboreus	Araliaceae	PST	1.46	25	31	56
Erythrochiton fallax	Rutaceae	TST	1.27	27	64	91
Eugenia florida	Myrtaceae	TST	1.52	24	22	46
Ficus boliviana	Moraceae	LLP	1.93	12	34	46
Gallesia integrifolia	Phytolaccaceae	LLP	1.84	11	38	49
Guarea guidonia	Meliaceae	TST	1.33	26	71	98
Heliocarpus americanus	Tiliaceae	SLP	2.36	30	40	70
Hirtella triandra	Chrysobalanaceae	TST	1.28	16	16	32
Hura crepitans	Euphorbiaceae	PST	1.62	52	39	92
Inga edulis	Mimosoideae	LLP	1.72	18	7	25
Jacaratia spinosa	Caricaceae	LLP	2.02	14	57	72
Licaria triandra	Lauraceae	TST	1.35	57	50	106
Maclura tinctoria	Moraceae	LLP	1.83	23	35	58
Margaritaria nobilis	Euphorbiaceae	LLP	1.84	24	23	47
Neea hermaphrodita	Nyctaginaceae	TST	1.45	14	13	22
Ocotea guianensis	Lauraceae	LLP	1.54	40	56	95
Ocotea sp. 1	Lauraceae	PST	1.37	52	179	230
Ocotea sp. 2	Lauraceae	PST	1.34	58	79	137
Picramnia sellowii	Simaroubaceae	TST	1.34	38	67	105
Pourouma cecropiifolia	Cecropiaceae	PST	1.38	38	95	134
Pouteria macrophylla	Sapotaceae	PST	1.55	57	46	103
Pouteria nemorosa	Sapotaceae	PST	1.57	56	72	128
Pseudolmedia laevis	Moraceae	TST	1.32	48	21	69
Sapindus saponaria	Sapindaceae	PST	1.63	21	19	40
Sapium glandulosum	Euphorbiaceae	LLP	2.23	16	25	41
Schizolobium parahyba	Caesalpinioideae	LLP	2.39	39	43	82
Simira rubescens†	Rubiaceae	PST	1.63	28	39	67
Spondias mombin†	Anacardiaceae	LLP	1.95	13	10	22
Stylogyne ambigua	Myrsinaceae	TST	1.46	31	51	82
Sweetia fruticosa†	Papilionoideae	LLP	1.91	32	12	44
Swietenia macrophylla	Meliaceae	PST	1.62	50	119	169
Tabernaemontana australis	Apocynaceae	TST	1.38	33	44	77
Terminalia oblonga	Combretaceae	PST	1.88	32	52	84
Trema micrantha	Ulmaceae	SLP	2.52	12	20	33
Triplaris americana	Polygonaceae	LLP	1.90	51	61	113
Urera caracasana	Urticaceae	SLP	1.99	11	25	36
Zanthoxylum sprucei	Rutaceae	LLP	2.25	12	28	40
Dry forest						
Acosmium cardenasii	Papilionoideae	TST	1.44	14	20	33
Actinostemon concepcionis	Euphorbiaceae	TST	1.40	22	38	60
Ampelocera ruizii†	Ulmaceae	PST	1.59	16	22	38
Anadenanthera colubrina	Mimosoideae	PST	1.75	38	18	56
Aspidosperma tomentosum	Apocynaceae	PST	1.31	22	27	49
Bougainvillea modesta	Nyctaginaceae	LLP	2.19	12	12	24
Caesalpinia pluviosa	Caesalpinioideae	PST	1.81	30	18	49
Capparis prisca	Capparaceae	TST	1.59	33	42	75
Cariniana ianeirensis†	Lecythidaceae	PST	1.90	32	39	72
Casearia gossypiosperma	Flacourtiaceae	PST	1.71	27	31	58
Centrolobium microchaete†	Papilionoideae	LLP	1.93	21	15	36
Chorisia speciosa	Bombacaceae	LLP	1.64	19	41	60
Chrysophyllum gonocarpon	Sapotaceae	TST	1.42	59	70	129
Cordia sp.	Boraginaceae	LLP	1.69	27	35	62
Erythroxylum daphnites	Erythroxylaceae	TST	1.64	36	26	62
Esenbeckia almawillia	Rutaceae	TST	1.51	16	28	44
Galipea ciliata	Rutaceae	TST	1.49	20	33	53

TABLE 1. Continued.

Species	Family	Guild	CE_{juv}	Sugar	Starch	NSC
Gallesia integrifolia	Phytolaccaceae	PST	1.81	17	33	50
Guibourtia chodatiana	Caesalpinioideae	PST	1.87	56	24	80
Jacaratia sp.	Caricaceae	TST	2.12	21	50	71
Machaerium acutifolium	Papilionoideae	PST	1.39	21	31	52
Manihot guaranatica	Euphorbiaceae	SLP	2.67	14	24	38
Maytenus cardenasii	Celastraceae	TST	1.78	51	18	69
Myrciaria cauliflora	Myrtaceae	TST	1.70	26	25	52
Neea cf. *steimbachii*	Nyctaginaceae	TST	1.63	11	8	19
Phyllanthus sp. nov.	Euphorbiaceae	TST	1.60	14	21	36
Phyllostylon rhamnoides	Ulmaceae	PST	1.49	18	21	39
Platymiscium ulei	Papilionoideae	LLP	2.52	26	44	70
Pogonopus tubulosus	Rubiaceae	TST	1.67	34	15	48
Pouteria gardneriana	Sapotaceae	TST	1.44	65	77	142
Simira rubescens†	Rubiaceae	PST	1.62	30	37	67
Solanum riparium	Solanaceae	SLP	3.00	12	34	46
Spondias mombin†	Anacardiaceae	LLP	2.40	17	19	35
Sweetia fruticosa†	Papilionoideae	PST	1.70	28	26	54
Talisia esculenta	Sapindaceae	TST	1.58	25	25	50
Trichilia elegans	Meliaceae	TST	1.64	23	18	40
Urera baccifera	Urticaceae	SLP	1.81	19	30	49
Zeyheria tuberculosa	Bignoniaceae	LLP	2.09	81	11	92

Notes: Carbohydrate concentrations were based on an average of 9.6 saplings per species (range 2–20). Three species had sample sizes smaller than five: *Maytenus cardenasii* ($n = 2$), *Erythroxylum daphnites* ($n = 4$), and *Phyllostylon rhamnoides* ($n = 4$). Fieldwork was carried out in a lowland tropical moist semi-evergreen forest and a dry deciduous forest in Bolivia.

† Species that occurs at both sites.

starch contributed the remaining 54%. The relative contribution of sugar to the NSC pool was similar for moist and dry forest species ($t = 1.3$, $P = 0.196$). Dry and moist forest species did not differ in their carbohydrate pool sizes (grams of carbohydrates per 1 m tall plant; Fig. 1). Seven species were in common to both forest types; dry and moist forest saplings of these species showed no consistent difference in sugar, starch, and NSC concentrations and pool sizes (paired *t* test, $t < 1.2$, $P > 0.28$ in all cases).

Interspecific variation in reserves

Across species, on average 2.9% of the stem dry mass consisted of sugar, 3.7% of starch, and 6.6% of NSC. Carbohydrate concentrations varied substantially amongst species. The sugar concentration varied from 1.1% to 8.1%, the starch concentration from 0.5% to 17.9%, and the NSC concentration from 1.9% to 23.0% (Table 1).

Interspecific variation in carbohydrate concentration per unit mass is not simply the result of a dilution effect in which species with a high amount of structural tissue have a low carbohydrate concentration. Across species, NSC per unit stem volume was strongly and positively correlated with NSC concentration, structural mass per unit volume, and total mass per volume (all $P < 0.001$). Because results of analyses involving NSC per unit volume are very similar to those involving NSC concentration, we report only the latter in the rest of the results.

In the moist forest, the sugar, starch, and NSC concentrations were negatively correlated with the juvenile crown exposure (i.e., light requirements) of the species (Table 2, Fig. 2). The four shade tolerance groups differed in their sugar (one-way ANOVA, $F_{3,45} =$

TABLE 2. Pearson correlation between stem volume, stem density, and carbohydrates vs. juvenile crown exposure (CE_{juv}), annual survival rate, and $\log_{10}$(annual growth rate) of saplings of tropical tree species.

Variable	Moist forest			Dry forest		
	CE_{juv}	Survival	Growth	CE_{juv}	Survival	Growth
Stem volume	−0.29*	0.18 NS	−0.26 NS	0.60***	−0.34*	0.31 NS
Stem density	−0.68***	0.56***	−0.50***	−0.58***	0.45**	−0.42*
Sugar concentration	−0.43**	0.43**	−0.31*	−0.13 NS	−0.02 NS	−0.39*
Starch concentration	−0.31*	0.19 NS	−0.02 NS	−0.12 NS	−0.13 NS	−0.10 NS
NSC concentration	−0.39**	0.30*	−0.13 NS	−0.15 NS	−0.09 NS	−0.31 NS
Sugar/NSC	−0.10 NS	0.24 NS	−0.36*	−0.10 NS	0.12 NS	−0.31 NS
Sugar pool	−0.58***	0.47***	−0.38**	−0.06 NS	−0.02 NS	−0.39*
Starch pool	−0.36*	0.24 NS	−0.13 NS	−0.05 NS	−0.09 NS	−0.12 NS
NSC pool	−0.43**	0.31*	−0.20 NS	−0.06 NS	−0.06 NS	−0.28 NS

Notes: Correlations are given separately for moist ($n = 45$–49) and dry ($n = 35$–38) forest species. NSC stands for nonstructural carbohydrates.

$^*P \leq 0.05$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$; NS, $P > 0.05$.

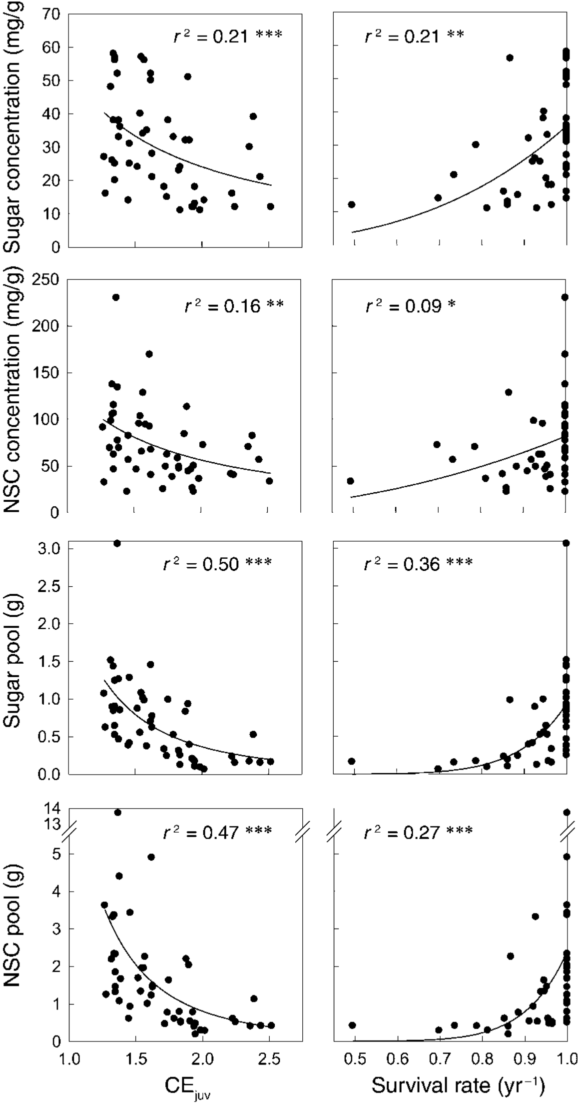

FIG. 2. Relationship of carbohydrate concentrations and pool sizes (sugar and nonstructural carbohydrates [NSC]) to juvenile crown exposure (CE_{juv}) and annual sapling survival rate of 49 moist forest tree species. Regression lines, coefficients of determination, and significance levels are shown.

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS, $P > 0.05$.

6.1, $P = 0.001$) and NSC concentrations ($F_{3,45} = 4.1$, $P = 0.012$), but had statistically similar starch concentrations ($F_{3,45} = 2.2$, $P = 0.099$). Mean concentrations increased in the order of SLP < LLP < TST < PST (Fig. 3), with PST having significantly higher concentrations than SLP and LLP (Student-Newman-Keuls-test, $P < 0.05$; Fig. 3). In contrast, in the dry forest, the sugar, starch, and NSC concentrations were not significantly correlated with the juvenile crown exposure of the species (Table 2), nor did they differ among shade tolerance groups (Fig. 3).

The total pool size of carbohydrates in the stem does not only depend on the carbohydrate concentrations, but also on stem volume and stem density. The standardized regression coefficients indicate that in the moist forest interspecific variation in pool sizes were determined most strongly by interspecific variation in carbohydrate concentration, whereas in the dry forest it is mostly determined by stem volume (Table 3). In the moist forest not only the carbohydrate concentrations but also the stem volume of 1 m tall plants and the stem density were negatively correlated with the juvenile crown exposure of the species (stem volume, $r = -0.29$, $P < 0.05$; stem density, $r = -0.68$, $P < 0.001$; Table 2). In other words, more light-demanding species had slender stems with a low tissue density. Consequently, also the sugar, starch, and NSC pool sizes were negatively related to the juvenile crown exposure (Fig. 2). Likewise, sugar, starch, and carbohydrate pool sizes ($F_{3,45} > 8.6$, $P < 0.001$ in all three cases) differed among the four shade tolerance groups, with TST and PST having larger pool sizes than the LLP and SLP (Student-Newman-Keuls-test, $P < 0.05$; Fig. 3). In the dry forest, stem density was negatively related to juvenile crown exposure (Table 2). However, unlike in the wet forest, stem volume in the dry forest was positively correlated with the juvenile crown exposure, and pool sizes of carbohydrates were not significantly related to the juvenile crown exposure (Table 2) or shade tolerance groups ($F_{3,32} < 0.8$, $P > 0.49$ in all three cases).

Reserves vs. growth and survival

Sapling survival rate in the moist forest was positively correlated with concentration of sugar ($r = 0.43$, $P < 0.01$) and NSC ($r = 0.30$, $P < 0.05$; Table 2, Fig. 2), but not with the concentration of starch ($r = 0.19$, $P > 0.05$). Sapling growth rate in the moist forest was negatively correlated with sugar concentrations, but not with starch and NSC concentrations. The same results were obtained for growth and survival if carbohydrate pool size rather than concentrations were used (Table 2). In the dry forest growth and survival were generally not related to carbohydrate concentrations and pool sizes, with the exception of sugar concentration and pool size, which were negatively related to the growth of the species.

DISCUSSION

Dry vs. moist forest species

We hypothesized that saplings of moist forest species should have higher NSC concentrations and pool sizes than dry forest species, because more reserves are necessary in shadier habitats where they are more likely to encounter periods of limited carbon gain. This hypothesis was partly confirmed by the data, as moist forest species had indeed higher starch and NSC concentrations (Fig. 1). However, these higher concentrations did not translate into larger carbohydrate pool sizes, probably because moist forest species tend to have on average slightly lower stem densities than dry forest species (t test, $t = 1.97$, df = 84, $P = 0.053$), whereas they

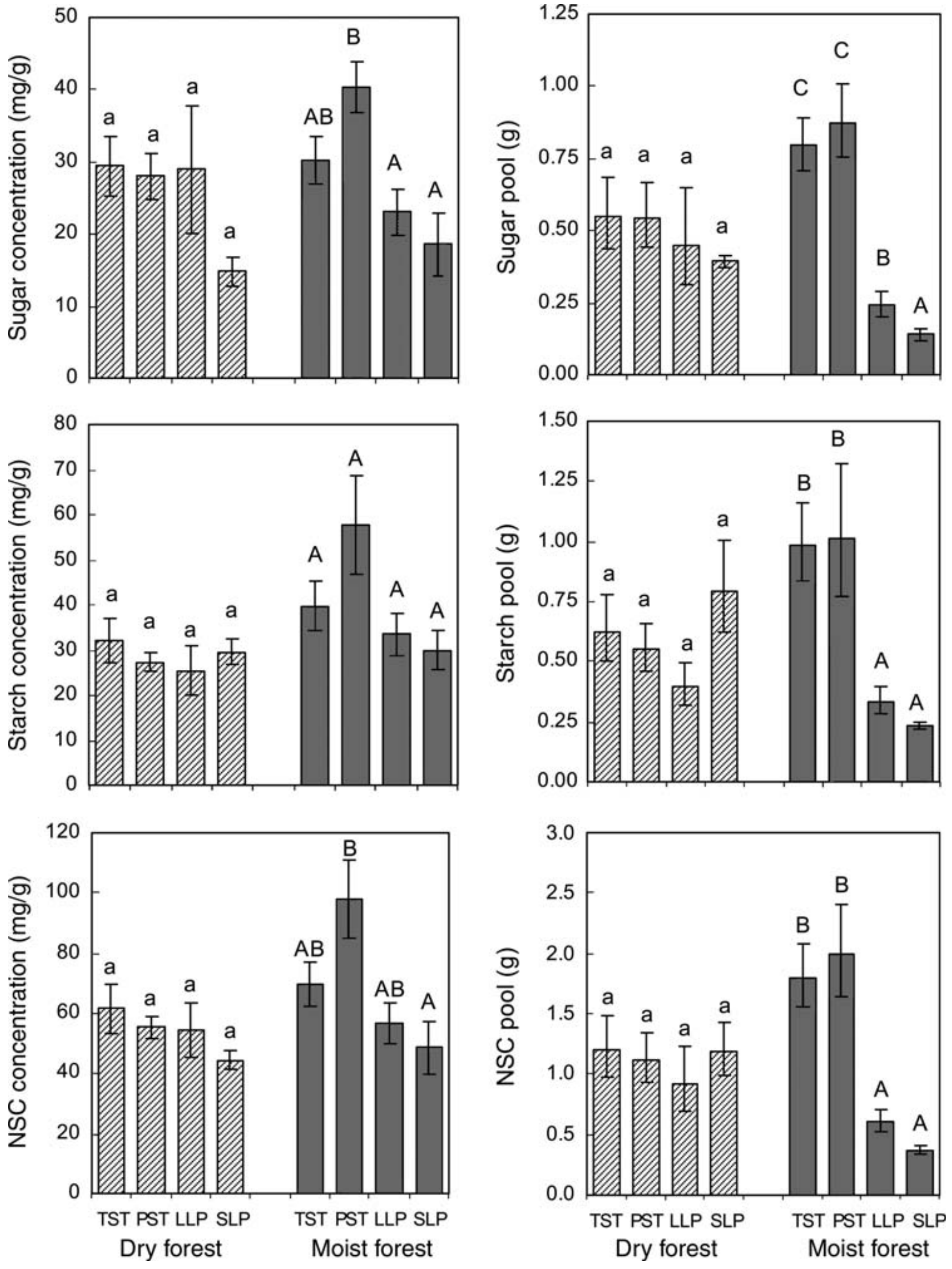

FIG. 3. Carbohydrate concentrations and pool sizes (mean ± SE) of dry (hatched bars) and moist (gray bars) tree species belonging to functional groups differing in shade tolerance (TST, total shade tolerants; PST, partial shade tolerants; LLP, long-lived pioneers; SLP, short-lived pioneers). Bars within forest type accompanied by a different letter are significantly different (Student-Newman-Keuls test, $P < 0.05$). The total carbohydrate pool sizes are estimated for stems of 1 m tall saplings.

have statistically similar stem volumes when 1 m tall (*t* test, $t = 0.92$, $\mathrm{df} = 85$, $P = 0.362$).

The observed differences between dry and moist forest species could be due to long-term adaptive responses of species to dry and moist forest habitats or due to short-term acclimation responses to current environmental conditions. Species common to both forest types did not show any consistent differences in carbohydrate concentrations between the dry and moist forest populations, suggesting that the observed differences are the result of adaptation.

We did not find any comparative studies on carbohydrate storage in dry vs. moist forest trees. Three lines of evidence suggest that in the dry season the carbohydrate reserves might be higher in dry forest trees. First, evergreen species in seasonally dry environments accumulate carbohydrates during the dry season, because photosynthesis continues while growth ceases (Würth

TABLE 3. Multiple regression of carbohydrate pool size on stem volume, stem density, and carbohydrate concentration of moist ($n = 49$) and dry ($n = 36$) forest species.

	Moist forest			Dry forest		
Variable	Volume	Stem density	Carbohydrate concentration	Volume	Stem density	Carbohydrate concentration
Sugar pool	0.43***	0.50***	0.59***	0.75***	0.57***	0.63***
Starch pool	0.39***	0.45***	0.71***	0.81***	0.62***	0.68***
NSC pool	0.43***	0.50***	0.61***	0.84***	0.64***	0.57***

Notes: All variables were $\log_{10}$-transformed prior to analysis. Standardized regression coefficients and significance levels are given.

*** $P \leq 0.001$.

et al. 2005). Second, dry-season deciduous species may accumulate storage carbohydrates by the onset of the dry season to support respiration costs when they are leafless. The dry forest tree *Jacquinia pungens*, for example, loses as much as half of its stored carbohydrate during the deciduous period (Janzen and Wilson 1974). Third, deciduous species have high carbohydrate reserves to be able to flush again at the onset of the wet season (Newell et al. 2002). Dry forest species do not only experience periodic drought stress, but also a higher chance of fire (Cordero et al. 2002). Fire-adapted species have typically higher belowground carbohydrate concentrations (Bond and Midgley 2003) and/or pool sizes (Hoffmann et al. 2004) to facilitate resprouting after fire. The greater representation of deciduous and fire-adapted species in the dry forest than in the wet forest, in combination with more prolonged dry season, may select for higher dry-season carbohydrate reserves. Newell et al. (2002) found that starch exhibits large seasonal flux, while sugar concentration tends to be more stable throughout the season. Many species sampled in early–mid wet season in our study might be exhibiting the lowest seasonal starch level or in the process of replenishing starch reserves.

Carbohydrate reserves in relation to light requirements

We hypothesized that carbohydrate concentrations and pool sizes would increase with the shade tolerance of the species, because carbon gain is low in the forest understory and carbohydrate reserves are needed to endure periods of low light or to recuperate from disturbance. This hypothesis was indeed supported for the moist forest, where carbohydrate concentrations and pool sizes decreased with the juvenile crown exposure of the species (Table 2, Fig. 2). Interestingly, no significant relationships were found between carbohydrates and juvenile crown exposure in the dry deciduous forest. This underscores the fact that storage is especially important for species that regenerate in persistently and deeply shaded habitats, as found in the understory of moist and evergreen forests.

Other studies also found that shade-tolerant species tend to have greater carbohydrate reserves, albeit from comparisons of just a few species. For example, in comparison of saplings of two evergreen and two deciduous species, the more shade-tolerant species in each pair had higher carbohydrate concentrations than the less shade-tolerant one (Kobe 1997). Likewise, saplings of the shade-tolerant *Acer saccharum* had higher NSC concentrations than the intermediate light-demanding *Betula alleghaniensis* (Gaucher et al. 2005), and the shade-tolerant palm *Chamaedora elegans* had higher NSC concentrations than the shade-intolerant *Chrysalidocarpus lutescens* (Reyes et al. 1996*a*, *b*). In contrast, Würth et al. (2005) found that adult trees of five mid-successional species had comparable stem carbohydrate concentrations to those of four early-successional species. It might be that the contrast in shade tolerance between early and mid-successional species is not strong enough to detect differences in carbohydrate reserves or that effects in relation to juvenile shade tolerance disappear when trees reach the bright-light conditions of the canopy, where they have ample carbon gain and storage. Future studies may examine how NSC concentration may change in relation to plant size and environments.

In this study we searched for saplings under closed canopy conditions, but pioneers were sometimes also sampled in gaps, to assure a sufficient sample size. Small interspecific differences in light conditions might potentially have biased the results, as gap plants have higher rates of carbon gain and thus have surplus carbon to allocate to storage. Field studies have shown that NSC concentrations of gap saplings are only slightly higher (Canham et al. 1999) or similar (van Nieuwstadt 2002) compared to understory saplings. The negative relationship between carbohydrate reserves and light requirements of the species would therefore even be stronger if species had been sampled under exactly the same light conditions. Another factor that may have affected our results is that the NSC pool size has been estimated for stems only. However, in seedlings with relatively small root systems, the majority of the NSC pool is present in the stem rather than in roots (Myers and Kitajima, *in press*). Shade-tolerant species have a larger proportion of their biomass in roots compared to light-demanding species (Poorter 2005). If any, we would expect a stronger relationship between NSC pool size and juvenile crown exposure, if NSC reserves in roots had been taken into account.

Plate 1. Stored carbohydrates are important for the ability of dry and moist forest saplings to resprout after damage. Photo credit: L. Poorter.

Analyses that compared the four shade tolerance groups confirmed the overall trend as found with crown exposure. In the moist forest, the carbohydrate reserves and pool sizes were higher in the two shade-tolerant groups than in the two shade-intolerant groups (Fig. 3). Partial shade tolerants (PST) tended to have higher carbohydrate concentrations than the total shade-tolerant (TST) species (Fig. 3), which is surprising, as TST species are more shade tolerant because they can complete their life cycle in the shade. In contrast, PST species can establish in the shade, but need a gap to successfully grow to larger sizes. The PST species may follow a sit-and-wait strategy (cf. Messier et al. 1999) and only grow to larger sizes if there is sufficient light and carbon gain to compensate for the higher total respiration loads that come along with an increase in size and an increase in the ratio of respiring to photosynthesizing tissue (Givnish 1988). The high carbohydrate concentrations of the PSTs may be a reflection of such a sit-and-wait strategy, as carbohydrates continue to accumulate, until biomass growth is resumed.

Reserves vs. growth and survival

The survival rate of moist forest species increased with the concentration and pool size of sugar and NSC, in line with the hypothesis that carbohydrate reserves are important to sustain respiration, facilitate repair, and replace lost tissue. They allow plants to endure periodic stresses such as shading (Veneklaas and den Ouden 2005) or drought (Janzen and Wilson 1974), to withstand pathogen and insect attack (Wargo 1972, Dunn et al. 1990), or to recover after disturbances such as leaf removal (Canham et al. 1999) and stem breakage

(Latt et al. 2000). Few studies have evaluated interspecific relationships between storage and survival. Myers and Kitajima (*in press*) experimentally evaluated the survival advantage of carbohydrate storage for seedling growth and survival using seven tropical tree species in the understory. They found a strong correlation between the carbohydrate pool size and survival rate of the species, and this correlation became even stronger when plants were subjected to deep shade (0.1% irradiance) or defoliation. A large NSC pool size enabled the recovery of leaf area after defoliation and hence survival. Carbohydrate reserves are therefore especially important under adverse environmental conditions where recovery would be too slow if plants depend only upon new photosynthetic income (cf. Chapin et al. 1990).

It was hypothesized that growth rates would decline with increases in species' carbohydrate concentrations and pool sizes. Such a relationship was indeed found for sugar in moist and dry forest trees, but not for starch and NSC. It is possible that starch and sugar contribute differently to the growth–survival trade-off. Starch concentration drops, but sugar concentration is maintained, when plants experience negative carbon balance due to sudden shading (Veneklaas and de Ouden 2005). Poorter and Bergkotte (1992) found a negative relationship between relative growth rate (RGR) and whole-plant insoluble sugar concentration of 24 herbaceous grassland species, while Myers and Kitajima (*in press*) found for seven tropical tree species that seedling RGR was negatively correlated with NSC pool size but not with tissue sugar or starch concentration. Thus, no general conclusion is possible as to how species differences in growth rates may be related to storage of sugar and starch. Even if there is a negative relationship between growth and carbohydrate storage levels, it is unlikely to be a direct proximate result of a trade-off between carbon allocation to storage vs. growth. Instead, it is likely that growth and carbohydrate storage are correlated because they are part of the same shade tolerance syndrome.

Conclusions

Carbohydrate storage strategies were closely related to the juvenile crown exposure of the species; more shade-tolerant species exhibit high carbohydrate concentrations and pool sizes, which can explain their higher survival (Fig. 2). High investment in carbohydrate storage incurs low opportunity costs for shade-tolerant species because of the low potential growth rates in the shade. The benefits of storage for survival are high for shade-tolerant species, because without storage the time to recover from disturbance and tissue loss would be extremely long in the understory. Species that are more light-demanding invest little in carbohydrate storage to enhance growth (Table 2). The trade-off between carbon allocation to storage vs. growth therefore partly underlies the survival–growth trade-off that is frequently observed among tropical tree species (cf. Kitajima 1996), and a continuum in carbon storage strategies gives rise to a continuum in the light requirements of the tree species. However, in our data set the link of carbohydrate storage to growth was weaker than its link to survival. The link between carbohydrates and light requirements is especially strong in moist evergreen forests where species sort out along a light gradient, but disappears in dry deciduous forests where light is a less limiting resource and species may sort out along a drought or fire gradient.

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