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Resprouting as a persistence strategy of tropical forest trees: relations with carbohydrate storage and shade tolerance

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Abstract. Resprouting is an important persistence strategy for woody species and represents a dominant pathway of regeneration in many plant communities, with potentially large consequences for vegetation dynamics, community composition, and species coexistence. Most of our knowledge of resprouting strategies comes from fire-prone systems, but this cannot be readily applied to other systems where disturbances are less intense. In this study we evaluated sapling responses to stem snapping for 49 moist-forest species and 36 dry-forest species from two Bolivian tropical forests. To this end we compared in a field experiment the survival and height growth of clipped and control saplings for a two-year period, and related this to the shade tolerance, carbohydrate reserves, and the morphological traits (wood density, leaf size) of the species.

Nearly all saplings resprouted readily after stem damage, although dry-forest species realized, on average, a better survival and growth after stem damage compared to moist-forest species. Shade-tolerant species were better at resprouting than light-demanding species in moist forest. This resprouting ability is an important prerequisite for successful regeneration in the shaded understory, where saplings frequently suffer damage from falling debris. Survival after stem damage was, surprisingly, only modestly related to stem reserves, and much more strongly related to wood density, possibly because a high wood density enables plants to resist fungi and pathogens and to reduce stem decay. Correlations between sapling performance and functional traits were similar for the two forest types, and for phylogenetically independent contrasts and for cross-species analyses. The consistency of these results suggests that tropical forest species face similar trade-offs in different sites and converge on similar sets of solutions. A high resprouting ability, as well as investments in stem defense and storage reserves, form part of a suite of co-evolved traits that underlies the growth–survival trade-off, and contributes to light gradient partitioning and species coexistence. These links with shade tolerance are important in the moist evergreen forest, which casts a deep, more persistent shade, but tend to diminish in dry deciduous forest where light is a less limiting resource.

Key words: Bolivia; disturbance; dry forest; growth–survival trade-off; leaf size; resprouting; shade tolerance; total nonstructural carbohydrates (NSC); tropical rain forest; wood density.

Introduction

All terrestrial ecosystems experience some kind of disturbance, such as fire, storms, treefall, branchfall, and herbivory, that result in partial or complete removal of aboveground plant biomass. Resprouting allows plants to persist and recover leaf area and height after such disturbance impacts, and it presents a dominant pathway of regeneration in many plant communities with potentially large consequences for vegetation dynamics and community composition (Putz and Brokaw 1989, Bellingham and Sparrow 2000, Loehle 2000). The ability to resprout is considered to be an important component of plant life history in many plant biomes (Bond and Midgley 2001, Vesk and Westoby 2004), but surprisingly, it is not routinely included in plant strategy schemes (e.g., Westoby 1998, Grime 2001, but see Loehle 2000 for temperate forests, and Pausas et al. 2004 for mediterranean woodland). Most of our knowledge on resprouting strategies for woody species comes from fire-prone systems, in which species are classified as resprouters vs. re-seeders, each with a different suite of co-evolved traits (Pate et al. 1990, Pausas et al. 2004). However, such a dichotomous

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approach does not apply to other systems where disturbances are less intense (Vesk and Westoby 2004). Dietze and Clark (2008) found that the resprouting behavior of North American tree species was only weakly correlated with other life history trade-offs, suggesting that it presents an additional axis of strategy variation and that it contributes to species diversity and coexistence. Clearly, more insight is needed into how resprouting behavior varies across vegetation types and across species, and into the underlying mechanisms.

Although almost all angiosperm woody plants have the ability to resprout (Del Tredici 2001), meta-analyses show that predominance of resprouting behavior varies with vegetation and disturbance types. The proportion of trees that resprout after windthrow tends to increase with site productivity, and resprouting is a more important pathway of forest recovery after disturbance in tropical forests (85% of the cases) than in temperate forests (40% of the cases [Everham and Brokaw 1996]). In contrast, the ability to resprout after clipping at the base has been suggested to decrease with site productivity, being highest in drier vegetation types (Vesk and Westoby 2004). Potentially, resprouting occurs because these plants are adapted to biomass removal or dieback caused by the frequent fires and severe droughts that are typical for those systems. Overall, links between resprouting ability and site productivity remain disputed (e.g., Bellingham and Sparrow 2000, Pausas and Bradstock 2007), and whether species from drier vegetation types are indeed better resprouters clearly merits further experimental investigation.

The ability to resprout is also likely to be linked to species shade tolerance for three different reasons. First, shade-tolerant species that regenerate in the forest understory are more likely to suffer from physical damage by falling debris than light-demanding species that regenerate in gaps. Indeed, in Neotropical rain forests, damage frequencies are higher in closed forest than in open areas (Gartner 1989), and shade-tolerant species tend to experience higher damage rates than light-demanding species (Gartner 1989, Putz and Brokaw 1989, Paciorek et al. 2000). Second, life history theory predicts that species adapted to low resource conditions should have a high inherent survival rate, whereas species adapted to high resource conditions should have a high inherent growth rate (Pianka 1970). The low irradiance in the forest understory allows only for limited carbon gain and growth, and shade-tolerant species should realize high survival rates if they are to make it to the canopy and attain reproductive size. In contrast, light-demanding species regenerating in gaps should realize fast growth rates to outcompete their neighbors (Van Breugel 2007), and to rapidly complete their life cycle before the gap is closed. Traits that enhance the survival of shade-tolerant species under low-light conditions, such as dense wood (Augspurger 1984) and large carbohydrate reserves (Kobe 1997), are also likely to enhance plant survival after damage (Myers and Kitajima 2007). Third, plants are only able to resprout if they have carbohydrate and nutrient reserves stored in well-protected belowground (Bond and Midgley 2001) and aboveground (Sakai et al. 1997) storage organs as well as dormant buds. Investment in reserves and storage organs comes at the expense of a reduced growth, and the opportunity cost of this reduced growth is much smaller for slow-growing species than for fast-growing species (Coley 1987, Kobe 1997). Combined, these observations suggest that shade-tolerant species should be better resprouters than light-demanding species, but there is little empirical evidence for this hypothesis.

Juveniles of shade-tolerant species tend to have more carbohydrate reserves than light-demanding species in wet forests (Myers and Kitajima 2007, Poorter and Kitajima 2007, but see Lusk and Piper 2007), but not in dry forest (Poorter and Kitajima 2007). Theoretical models predict that carbohydrate storage should enhance plant survival (Iwasa and Kubo 1997, Kobe 1997), but surprisingly few comparative studies have been carried out across species on the role of carbohydrate reserves for survival. A field experiment with tree seedlings by Myers and Kitajima (2007) suggests that species with more carbohydrate reserves are better able to survive defoliation, but it is not clear whether this holds for later ontogenetic stages (saplings) and different disturbance types (stem damage) as well.

The way in which species resprout is likely to be influenced by their leaf size, because of a trade-off between the size and number of leaves (Kleiman and Aarssen 2007). Species that make small leaves tend to produce smaller internodes (Poorter and Rozendaal 2008), and as a consequence they have more axillary buds that can be released after loss of apical control, leading to a larger number of sprouts. Ickes et al. (2003) provide some preliminary evidence for this idea, by showing that species with (small) simple leaves produced a larger number of sprouts than species with (large) compound leaves.

This study builds on Poorter and Kitajima (2007), who related sapling performance of 49 moist-forest species and 38 dry-forest species to their carbohydrate reserves. They found for moist-forest species only that survival rates increased, while growth rates decreased with carbohydrate concentrations and pool sizes. Here we evaluate responses to stem damage for nearly the same set of species. To this end we compared, using a field experiment, the survival and height growth rate of clipped and control plants for a two-year period, and related this not only to the carbohydrate reserves, but also to the regeneration light requirements and functional traits (wood density, leaf size) of the species. We expected that clipping would lead to reduced survival but increased height growth of saplings to compensate for lost height and leaf area. We examined the following questions and a priori predictions with regard to

differences between communities and species within each community.

1) How do resprouting responses vary with forest type? We expected that dry-forest saplings, which are exposed to frequent disturbance and dieback events, would show a better survival and resprouting response to stem damage as compared to moist-forest saplings.

2) How is the performance of control and clipped plants related to regeneration light requirements? Based on life history trade-offs, we expected that for both clipped and control plants, survival would decrease and growth would increase with the regeneration light requirements of the species. Shade-tolerant species should show a better relative survival and resprouting response to clipping compared to light-demanding species.

3) Is the response to clipping related to carbohydrate reserves (i.e., concentrations and pool size)? We predicted that survival and growth of clipped plants should be positively related to the carbohydrate reserves of the species, and that responses are better related to the carbohydrate pool size than to the carbohydrate concentrations (cf. Myers and Kitajima 2007).

4) Does species morphology determine resprouting behavior? Leaf mass is thought to be a strong determinant of resprouting behavior, and based on the size–number trade-off we expected that species with small leaves would make many sprouts and leaves.

Materials and Methods

Research sites

Fieldwork was carried out in the tropical moist semievergreen forest of La Chonta (15°47′ S, 62°55′ W), and the dry deciduous forest of Inpa (16°1′S, 61°4′ W), in lowland Bolivia. Both are long-term research sites of the Instituto Boliviano de Investigación Forestal (IBIF), and henceforth they will be referred to as moist and dry forest, respectively. Annual precipitation in La Chonta is 1580 mm, with a dry season (potential evapotranspiration >rainfall) of one month. The forest has an average canopy height of 27 m, tree density of 367 trees/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] Peña-Claros et al. [2008]). About one-third of the trees in the canopy are deciduous in the dry season. Annual precipitation in Inpa is 1160 mm, with a three-month dry season. The forest has an average canopy height of 20 m, tree density of 420 trees/ha, basal area of 19.3 m^2/ha, species richness of 34 species/ha (M. Peña-Claros, *unpublished data*). Nearly all trees in the canopy are deciduous in the dry season, although many saplings in the understory are evergreen.

Species selection

Forty-nine tree species were selected in the moist forest and 36 tree and shrub species in the dry forest, with seven species in common to both sites (Appendix A). Two dry-forest species included in Poorter and Kitajima (2007) were not included here, because for these species no plants were clipped. The most abundant species were selected, and they varied in shade tolerance and/or adult stature. The species represented >70% of the stems >10 cm dbh in each community. Poorter and Kitajima (2007) provided a continuous and objective measure of the regeneration light requirements by calculating for each species the average population-level crown exposure at a standardized height of 2 m (juvenile crown exposure, CE_{juv} [see Poorter and Kitajima 2007 for more details]). A low CE_{juv} indicates that a species regenerates mainly in the shaded understory (i.e., a shade-tolerant species) whereas a high CE_{juv} indicates that it mainly regenerates in the bright light conditions of gaps (i.e., a light-demanding species). A direct comparison of the CE_{juv} between 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 each forest, but it allows a comparison of species within the same forest.

Clipping experiment

A clipping experiment was carried out to determine how species overcome damage. For each species, ~30 saplings between 55 and 200 cm tall were selected in undisturbed forest and logged forest. For all species, individuals were selected over the same size range, so that differences in plant size did not confound the interspecific comparisons. In total ~2500 individuals were included: 1469 saplings in the moist forest, and 1062 saplings in the dry forest. Individuals were searched for in closed-canopy conditions, but light-demanding species were also sampled in gaps and along skid trails and roads to assure a sufficient number of individuals. Saplings were tagged, and their 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.

For each species, half of the saplings were clipped and the other half were left as control (with the exception of the dry-forest species *Phyllostylon rhamnoides*, for which insufficient individuals were available for the control treatment, and all individuals were clipped). The plants were assigned to the clipping treatment in such a way that they did not differ significantly from control plants in their average height before clipping (t test, $P > 0.05$ in all cases). Plants were clipped below the crown, always at 50 cm height above the ground. Plants were left without leaves (only in some cases plants had a few remaining leaves on a lateral branch below the crown), so that for their resprouting response they depended totally on stored carbohydrate reserves for energy demands. In the moist forest, plants were clipped in early December, one-third of the way through the rainy season, when the species had flushed leaves and used part of their carbohydrate reserves. In the dry forest, plants were clipped in late January, halfway through the rainy season. For 10 plants per species, a 20-cm stem

section was sampled just above the cut. The volume of this section was calculated as $0.25 \times \pi \times \text{diameter}^2 \times$ length, and included the bark. Stem samples were oven-dried for at least 48 hours at 70°C and weighed. Stem density (in grams per cubic centimeter) was calculated as stem dry mass divided by stem volume. Because stem density can be confused with number of stems per hectare, we henceforth refer to this measure as wood density, although strictly speaking it also includes bark.

In the moist forest, plants were monitored for their height and survival at ~2, 4, 9, 13, and 25 months after the start of the experiment. In the dry forest the corresponding intervals were 2, 4, 7, 13, and 25.5 months. Please note that in Poorter and Kitajima (2007), dry-forest saplings were monitored up to 13 months only. Henceforth the 13-month census will be referred to as the "one year" census. For the clipped plants the total number of sprouts and buds, their position, total leaf number, and length of the longest sprout were additionally measured. Plants were evaluated as dead when total stem dieback occurred or when stems lost their rigidity. Each plant was monitored until the end of the study to determine whether plants classified as dead indeed remained dead during the study. If a supposedly dead plant resprouted again, then for all the foregoing censuses the plant was recoded as being alive. Height growth was calculated as the cumulative change in height of the leader shoot (for clipped plants) or growing point (for control plants) after the start of the experiment.

Leaf plus petiole samples were taken during the rainy season for five additional, sunlit saplings per species (0.5–3.5 m height), one leaf per sapling. The leaf was scanned with a flatbed scanner and the area measured with pixel-counting software (Van Berloo 1998). Leaves were oven-dried for at least 48 hours at 70°C and weighed.

Nonstructural carbohydrates

Nonstructural starch and sugar concentrations were measured for a pooled sample of each of the 10 stems (including wood and bark), as described in Poorter and Kitajima (2007). We calculated for each species the carbohydrate concentration per unit dry mass, and the carbohydrate stem pool size. The latter was done by multiplying stem volume × wood density × carbohydrate concentration. The stem volume was calculated for 50 cm tall stems (i.e., for the stem section that was left after clipping), assuming a cylinder. No measurements of root nonstructural carbohydrates (NSC) were made because they are logistically quite difficult and would have necessitated destructive sampling of the plants that had to be monitored.

Statistical analysis

Resprouting responses were analyzed at the community level (dry vs. moist forest) and at the species level. For the analysis at the community level, the individuals of all studied species were pooled. Within a community, survival differences between clipped and control plants were evaluated at each census using a χ^2 test. Individuals that were not found during subsequent censuses were considered to be dead. At each census cumulative growth of the leader sprout of clipped individuals was compared to the cumulative growth of the leader shoot of control individuals using a t test. Plants that experienced >10 cm height loss during the monitoring period were excluded from the height growth analysis for that period. Nearly all of these excluded plants suffered from dieback, or were damaged, or bent over by animals or falling debris.

At the species level, the two-year survival response of clipped and control plants was analyzed with a Kaplan-Meier survival analysis and log-rank test. Cumulative survival and growth were also evaluated at each census (survival with a χ^2 test, growth with a t test) to evaluate *when* species start to show for the first time a significant response to the clipping treatment. Because most species responses to the clipping treatment occurred within the first year, for subsequent analyses all comparisons were made after one year when both light-demanding and shade-tolerant species still had a sufficient number of surviving individuals for comparison. First-year growth and survival of clipped and control plants were related to the CE_{juv} of the species, using Pearson correlation and regression. Because light-demanding and shade-tolerant species have different inherent growth and survival rates, we calculated for each species the responsiveness to clipping as the difference in mean performance (survival, growth) of clipped plants minus the mean performance of control plants. We calculated the leaf area produced one year after clipping as the leaf number multiplied by the average area of individual leaves of the species. The leaf area recovery was calculated as the number of leaves one year after clipping, divided by the number of leaves at the start of the experiment just before clipping. All these statistical analyses were carried out using SPSS 15 (SPSS 2007). The way species resprout (in terms of sprout and leaf number and total leaf area) may be affected by the leaf mass of the species. To this end, the average sprout number, leaf number, and leaf area after one year were related to average leaf dry mass of individual leaves of species, using standardized major axis (SMA) regression. Whether dry- and moist-forest species differed for these bivariate relationships in their allometric slopes and intercepts was evaluated using the (S)MATR package (Warton et al. 2006). Individual leaf mass data (including petioles) were available for 31 dry-forest species and 47 moist-forest species. To evaluate whether present-day relationships are caused by repeated evolutionary divergences, evolutionary correlations were calculated for most of the abovementioned analyses as well, using phylogenetically independent contrasts. In this analysis, each branching divergence in the phylogenetic tree contributes one data point. A

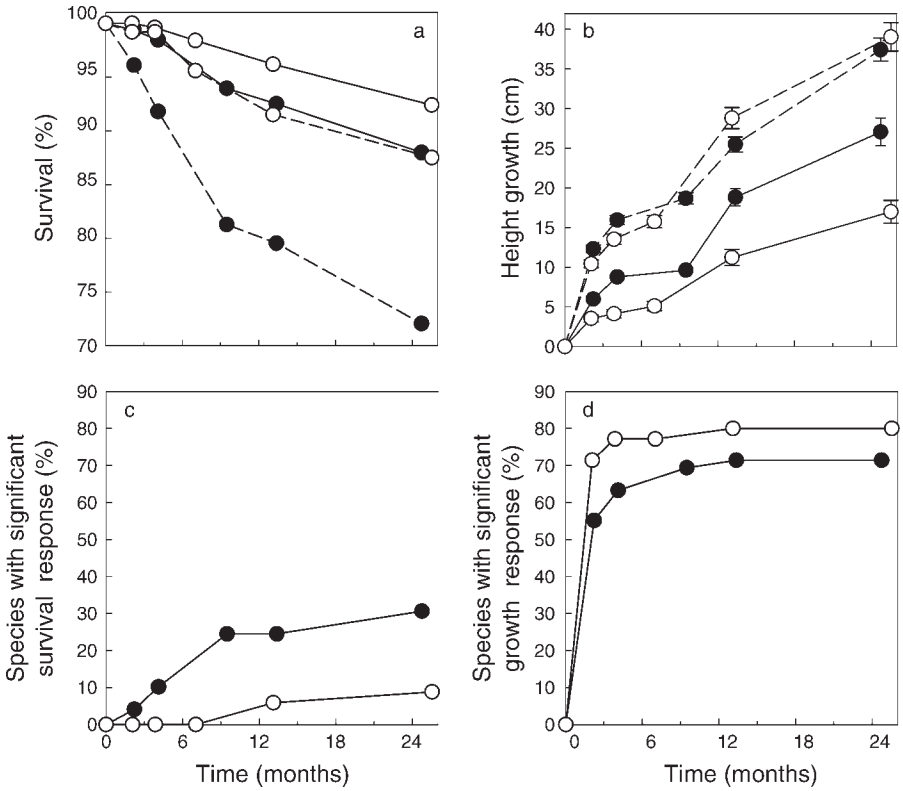

FIG. 1. Sapling response to clipping for 49 moist-forest species and 36 dry-forest species from two Bolivian tropical forests over a two-year period. (a) Survival and (b) cumulative height growth (mean ± SE) of clipped and control plants over time. Separate curves are shown for plants from moist (solid symbols) and dry forest (open symbols), and for clipped (dashed lines) and control (solid lines) plants. (c, d) Cumulative number of species (as a percentage of the total number) that have shown at one or more census times significant (c) survival and (d) growth responses to the clipping treatment. Separate curves are shown for dry (open symbols) and moist (solid symbols) forest species. For panels (c) and (d), statistical tests (t test for cumulative growth, χ^2 test for cumulative survival) were performed for each census period, and the cumulative percentage of species that showed a significant response is plotted. The reason for this cumulative percentage is that some significant responses of species disappear over time because of the small sample size. (For cumulative growth the number of saplings included in the test become progressively smaller because they die due to clipping or to natural causes, and for cumulative survival the clipped plants initially die fast, but the control plants start to die later as well.) $P \leq 0.05$ for all significant values.

phylogenetic tree was made using the program Phylomatic (Webb and Donoghue 2005) based on the maximum resolved angiosperm phylogeny. If one genus was missing from the megatree, then for that family the genera were included as polytomies, and species were always included as polytomies within a genus. Phylogenetic correlations were calculated using the "Analysis of Traits" module of Phylocom 4.0.1b (Webb et al. 2008). Phylogenetic independent contrasts were calculated as the difference in mean trait values for the two nodes (or two species) descending from a node. Phylogenetic branch lengths were set to 1 and polytomies were resolved to provide one contrast. See Webb et al. (2008) for further details.

RESULTS

Community-level responses

Clipping led to a decreased survival of both dry- and moist-forest plants, as early as two months after clipping ($\chi^2 = 4.76$, $P = 0.03$ for the dry forest; $\chi^2 = 18.1$, $P <$ 0.001 for the moist forest; Fig. 1a), and this significant effect persisted over time. The survival rate of control plants was much lower, and the clipping impact was much stronger in moist-forest compared to dry-forest plants (Fig. 1a). After two years clipped plants in the moist forest had 72% survival, compared to 88% for control plants, whereas in the dry forest this was 88% vs. 92%. Clipped plants responded quickly to the damage; ~90% of the individuals had already formed buds or sprouts within one month after clipping. Clipping led to an increase in height growth rate, more strongly so for the dry-forest species than for the moist-forest species, and this effect persisted over time (Fig. 1b). After two years, clipping led to a 2.3-fold increase in growth (height) for the dry-forest plants, compared to a 1.4-fold increase for the moist-forest plants.

Species level

After two years, clipping led to a significant decrease in survival for 31% (15 out of 49 species) of the moist-

forest species, compared to 6% (2 out of 35 species) of the dry-forest species (Kaplan-Meier survival test, Fig. 1c; full species names are listed in Appendix A, but in the text are referred to by genus). For those species whose survival was affected by clipping, significant differences in survival between clipped and control plants appeared early, between 4 and 12 months (Fig. 1c). In the moist forest, species with the lowest first-year survival rates after clipping were short-lived pioneers such as *Heliocarpus* (0%), *Trema* (13%), and *Jacaratia* (14%). The dry-forest species that showed the lowest first-year survival after clipping were long-lived pioneers such as *Platymiscium* (20%) and *Chorisia* (80%), and the shade-tolerant species *Neea* (86%; Appendix A).

Most species that showed a significant growth response to clipping did so within the first four months (Fig. 1d). In the dry forest, after one year, clipping led to a significant increase in height growth for 63% of the species, whereas in the moist forest clipping led to a significant increase in height growth for 37% of the species, and a significant decrease in height growth for 4% of the species (*Zanthoxylum*, *Picramnia*) (*t* test; Appendix A).

Species-specific growth and survival rates of clipped plants were strongly correlated with those of control plants (Appendix B; for survival of moist-forest species, $r = 0.74$, $P < 0.001$, $N = 49$; for growth of moist-forest species, $r = 0.48$, $P < 0.001$, $N = 49$; for survival of dry-forest species $r = 0.80$, $P < 0.001$, $N = 35$; for growth of dry-forest species, $r = 0.91$, $P < 0.001$, $N = 35$), indicating that there is little crossover in species rank performance due to damage.

Species performance vs. juvenile crown exposure

In both forest types the annual survival and growth rates of clipped and control plants were closely related to the regeneration light requirements of the species (Fig. 2). The greater the CE_{juv} of a species, the lower were its survival rates in both forests. Clipping reduced the survival rates much more for species with high CE_{juv} than those with low CE_{juv} (Fig. 2a, b). This trend was much more pronounced in moist forest than in dry forest. The difference between the survival rates of clipped and control plants indicates how sensitive species are to clipping. In the moist forest this sensitivity was also negatively related to the CE_{juv} ($r = -0.45$, $P = 0.001$, $N = 49$), indicating that light-demanding species suffered more from damage than shade-tolerant species, although for the dry forest this was only marginally significant ($r = -0.33$, $P = 0.052$, $N = 35$). In both forests the growth rates of clipped and control plants increased strongly with CE_{juv} of the species (Fig. 2c, d). The difference between growth rate of the clipped and control plants indicates how responsive species are to clipping. In the moist forest, shade-tolerant species (with low CE_{juv}) showed a positive growth response to clipping, whereas light-demanding species (with high CE_{juv}) showed a negative response to clipping (Fig. 2e). In the dry forest, clipped plants nearly always grew faster than control plants, but the strength of the response was not related to CE_{juv} (Fig. 2f).

Clipped plants had their whole crown and all their leaves removed, and they rapidly formed new leaves to continue photosynthetic carbon gain. After one year, the total leaf area per plant varied 74-fold among species, ranging from 300 to 22 000 cm^2. Total leaf area was positively related to CE_{juv} for the dry-forest species only (Fig. 3a, b). The leaf area recovery in both forests was positively related to CE_{juv}, with shade-tolerant species with low CE_{juv} showing on average a recovery of <1 (i.e., after one year they still had less than the pre-treatment leaf area), and light-demanding species showing on average a recovery >1 (Fig. 3c, d).

Species performance vs. carbohydrate reserves

It was expected that the average annual survival and growth rate of species would be related to carbohydrate concentrations and pool sizes in the plant. Plant performance was generally better related to sugar concentration than to starch or NSC concentrations, and plant performance was generally slightly better related to carbohydrate pool sizes than to carbohydrate concentrations (Appendix C). Survival of clipped plants in both forest types, and of control plants in the moist forest, increased significantly with sugar pool size in the stem, in line with the expectations (Fig. 4a, b). In the dry forest, the relationship between sugar pool size and survival was stronger for clipped plants (that need those reserves to resprout) compared to control plants, in line with the expectations. However, in the moist forest, this relation was similar for control and clipped plants, in contrast to the expectations. In both forests, the growth of control plants was negatively correlated with the sugar pool size, whereas growth of clipped plants was not significantly related to sugar pool size (Fig. 4c, d).

Time course of survival-trait correlations

The relationship between species traits (carbohydrate concentrations and pool sizes, wood density, and CE_{juv}) and plant performance (survival of clipped plants) changed over time (Fig. 5). Just after clipping, the correlations were weak, because little mortality had taken place. Within six months, the correlations rapidly increased in strength, after which they remained constant. In both forests, CE_{juv} was the best predictor of species survival after clipping, followed by wood density (with species with high wood density showing greater survival), sugar reserves, and NSC reserves (Fig. 5).

Morphological traits determine resprouting behavior

Species varied tremendously in the way they resprouted after one year. Across species, the sprout number varied 8-fold (from 1 to 8), the leaf number 30-fold

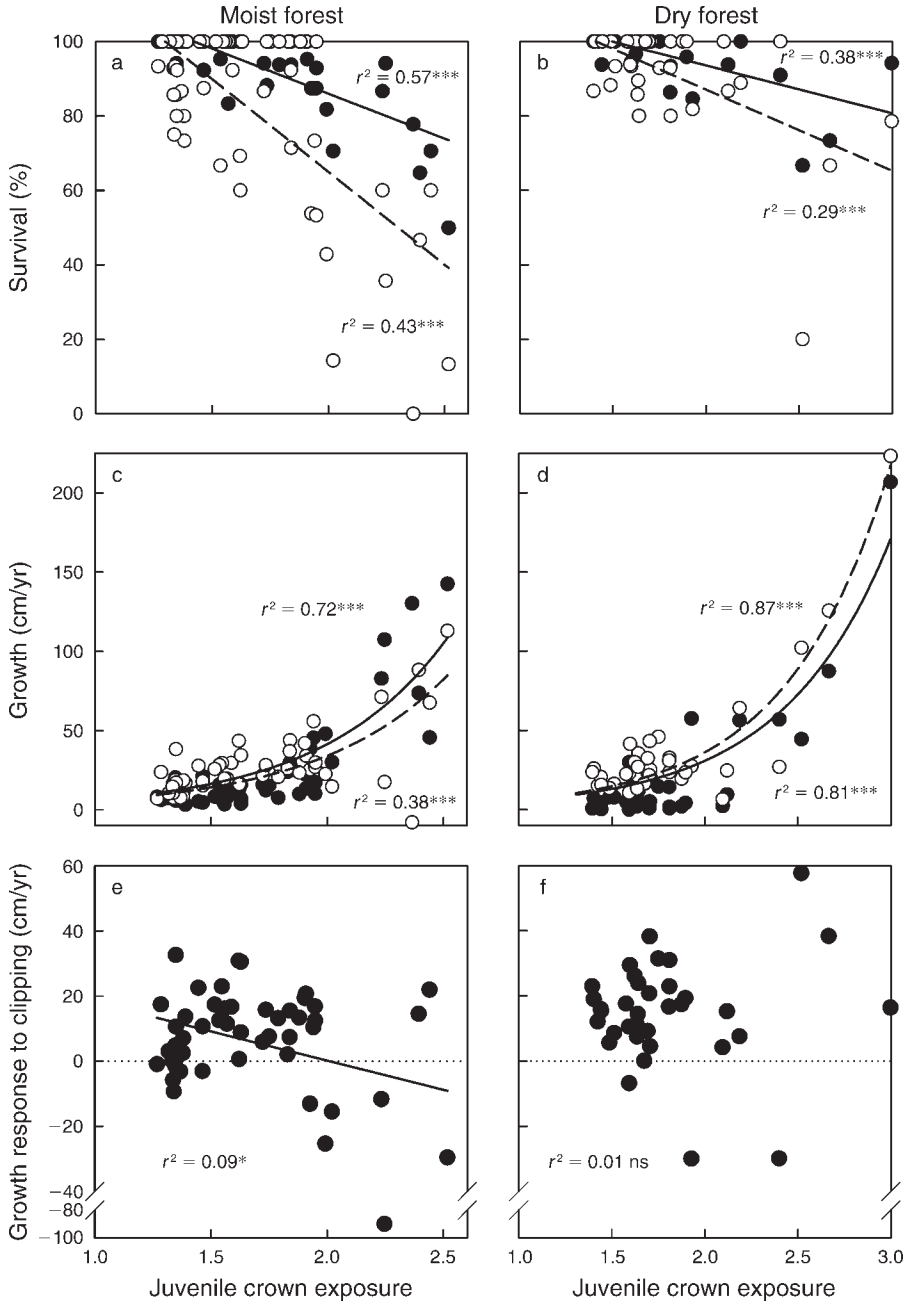

FIG. 2. (a, b) Survival and (c, d) growth of clipped (open symbols, dashed lines) and control (solid symbols, solid lines) plants in relation to the juvenile crown exposure (CE_{juv}) for moist-forest (left panels, $N = 48–49$) and dry-forest (right panels, $N = 36$) species. (e, f) The growth response to clipping is also shown, defined as the growth of clipped plants minus the growth of control plants. Regression lines, coefficients of determination (r^2), and significance levels are shown. Note that the scaling of the x-axis differs between the two forest types.

* $P < 0.05$; *** $P < 0.001$; ns, $P > 0.05$.

(from 4 to 115), and total plant leaf area 74-fold (from 305 cm^2 to 22 434 cm^2) (Fig. 6). Species varied strongly in their leaf size as well; the mass of individual leaves varied 345-fold (from 0.022 to 7.597 g) among species. Leaf mass determined the resprouting behavior of the species; the sprout number and total leaf number decreased, and the total plant leaf area increased with individual leaf mass (Fig. 6). The strength of this relationship is underscored by the fact that dry- and moist-forest species exhibited exactly the same relationship with leaf mass; they did not differ in their slopes, and they differed only for total leaf area in their

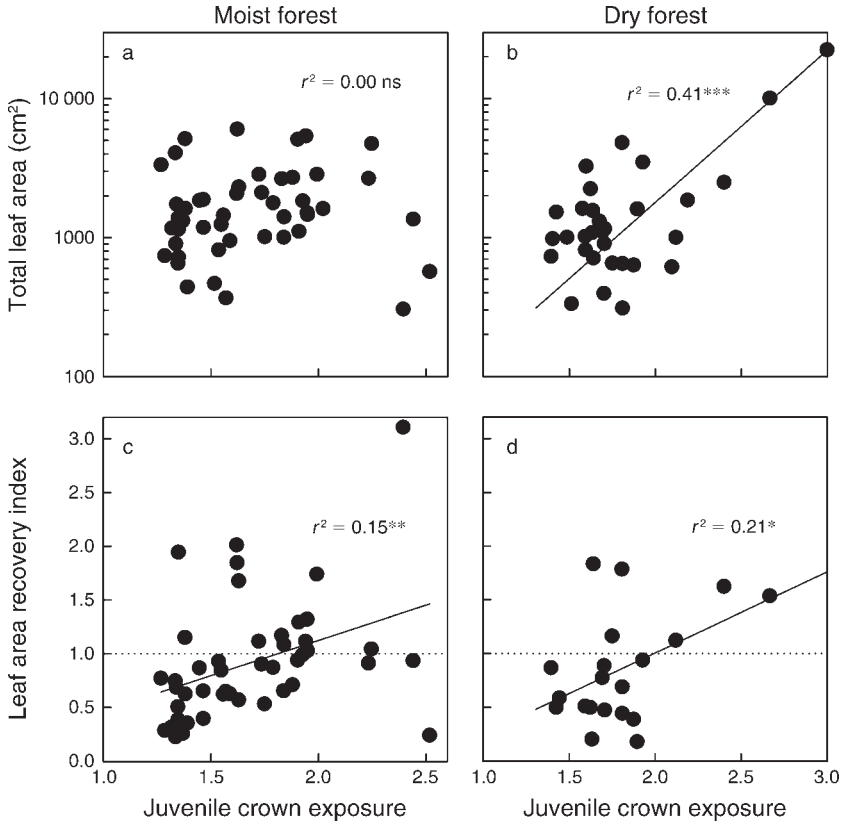

FIG. 3. (a, b) Total leaf area (note the log scale) and (c, d) leaf area recovery of clipped plants of moist-forest species (left panels, $N = 47$) and dry-forest species (right panels, $N = 31$), one year after the application of the clipping treatment in relation to juvenile crown exposure (CE_{juv}). Leaf area recovery is calculated as the leaf number, one year after clipping, divided by the leaf number of the same individual just before clipping. Regression lines, coefficients of determination (r^2), and significance levels are shown. Note that the scaling of the *x*-axis differs between the two forest types.

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

intercepts. (For the results of the SMATR analysis, see Fig. 6 legend.)

Cross-species vs. phylogenetic correlations

For the moist-forest species the phylogenetic correlations were very similar compared to the cross-species correlations, or even slightly stronger, as is the case for the correlation between growth response to clipping and CE_{juv} (Appendix D). This indicates that the observed present-day trait associations in this plant community have also been the result of repeated evolutionary divergences in the past. For the dry-forest species the phylogenetic and cross-species correlations were still similar, but a bit more variable than for the moist-forest species. The most striking difference concerned the growth rate of clipped plants, which was significantly positively related to CE_{juv} in the cross-species correlation, and tended to be negatively associated to CE_{juv} in the phylogenetic correlation (Appendix D). Consequently, there was also a lack of relationship between the growth rate of control and clipped plants for the phylogenetic correlation.

DISCUSSION

Community-level responses

In the two tropical forests, virtually all individuals (88%–95%) resprouted in the first few months after clipping. Similar fast-resprouting responses have been found for other tropical forest trees (Kennard 1998, Van Nieuwstadt 2002, Ickes et al. 2003). Dry-forest species were better resprouters than moist-forest species, in line with the first hypothesis: after clipping they showed a higher survival and realized a faster height growth compared to moist-forest plants (Fig. 1). One might argue that dry-forest species are better sprouters than moist-forest species, because many of them are drought deciduous and should possess additional storage reserves in the dry season to be able to flush again in the wet season. However, this is not a likely explanation, because the experiment started in the rainy season after flushing, and at this moment moist-forest species had higher NSC concentrations than dry-forest species (Poorter and Kitajima 2007). Dry-forest species sprout well, both as juveniles and adults (cf. Mostacedo et al. 2009), probably because they are better adapted to disturbances that frequently occur in dry-forest envi-

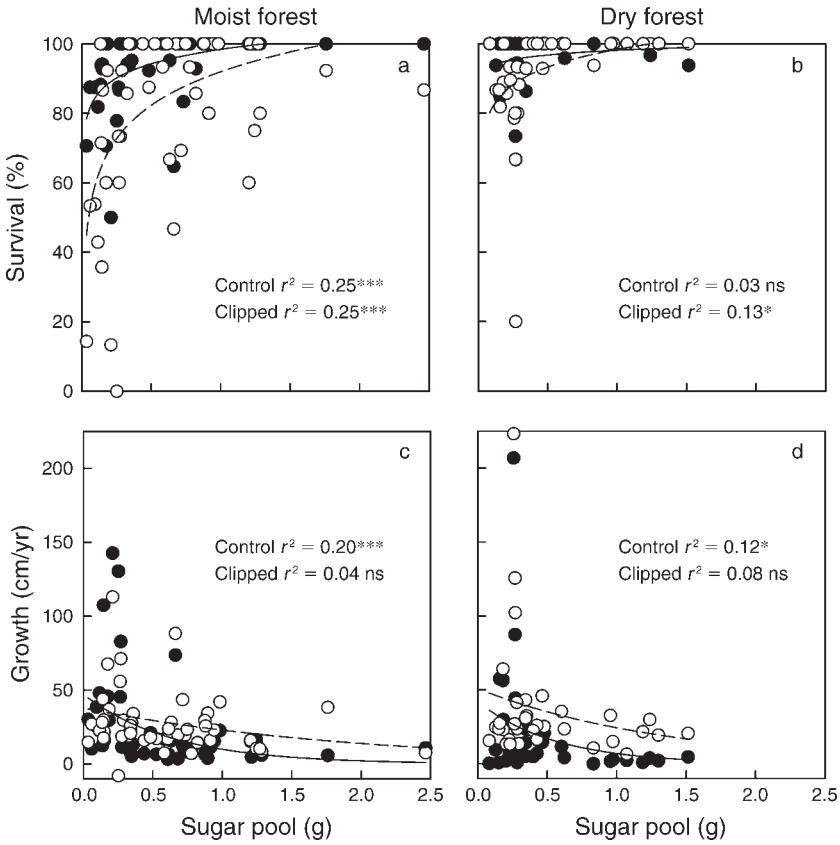

FIG. 4. (a, b) Survival and (c, d) growth of clipped (open symbols, dashed lines) and control (solid symbols, solid lines) plants in relation to the stem sugar pool for moist-forest (left panels, $N = 48–49$) and dry-forest (right panels, $N = 35$) species. The stem sugar pool is for clipped and control plants is calculated for 50 cm tall stems (i.e., the stem section that remained for clipped plants after clipping). Regression lines, coefficients of determination (r^2), and significance levels are shown.

* $P < 0.05$; *** $P < 0.001$; ns, $P > 0.05$.

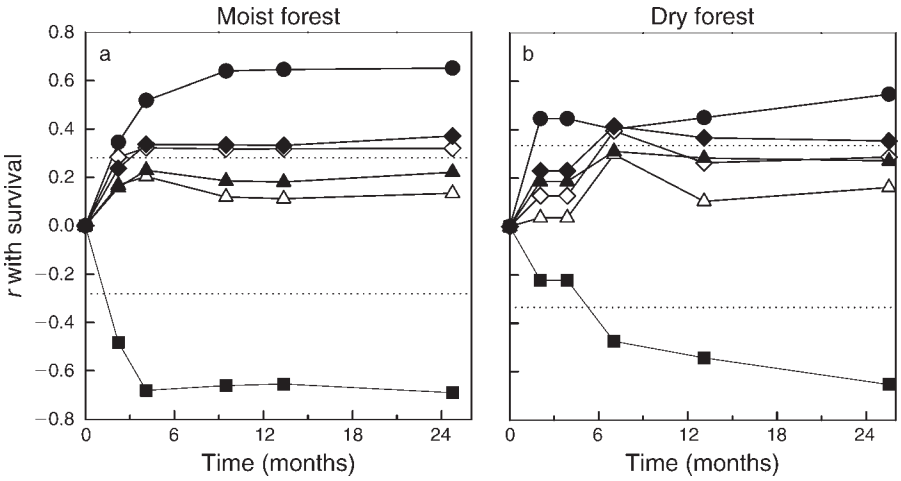

FIG. 5. Time-dependent course of the Pearson correlation between species survival after clipping and species traits for (a) moist-forest ($N = 48–49$), and (b) dry-forest ($N = 35–36$) species. Traits included are juvenile crown exposure (solid square), wood density (solid circle), sugar concentration (open diamond), sugar pool (solid diamond), nonstructural carbohydrate (NSC) concentration (open triangle), and NSC pool (solid triangle). Concentrations and pools are calculated for stems only; for the pool this is based on 50 cm tall stems (the stem section remaining after clipping). Absolute correlations (a) $r > 0.28$ or (b) $r > 0.33$ (indicated by the dotted reference lines) are significant at $P < 0.05$.

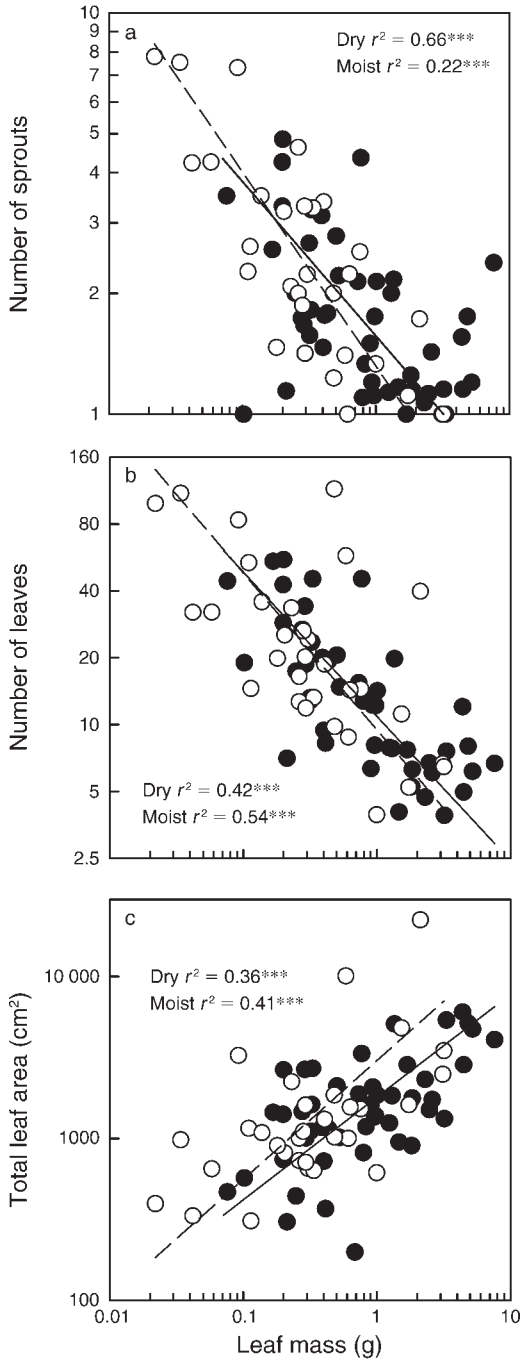

FIG. 6. Sprouting responses in relation to leaf mass (leaf plus petiole): (a) number of sprouts, (b) number of leaves, and (c) total leaf area in relation to individual leaf mass of dry-forest (open symbols, dashed lines, $N = 31$) and moist-forest (solid symbols, solid lines, $N = 47$) species. Standard major axis regression lines, coefficients of determination (r^2), and significance levels are shown for each forest separately. Values were plotted on a logarithmic axis. Tests were done for common slopes and elevation differences for the dry and moist forest: (a) slopes were nonheterogeneous ($P = 0.186$), did not differ in elevation ($P = 0.284$), and there was a shift along the slope ($P = 0.005$); (b) slopes were nonheterogeneous ($P = 0.632$) and did not differ in elevation ($P = 0.586$), and there was a shift along the slope ($P = 0.002$); (c) slopes were nonheterogeneous ($P = 0.434$) and differed in elevation ($P = 0.016$), with a larger leaf area for a given leaf mass for the dry-forest species.

ronments, such as biomass removal by fires and shoot dieback by droughts (Segura et al. 2003), and because in harsh, dry environments regeneration from sprouts is more successful than regeneration from seeds (Bellingham and Sparrow 2000, Mostacedo et al. 2009, but see Pausas and Bradstock 2007). This is also reflected in the morphology of dry-forest saplings; they are frequently shrubby, crooked, and stunted, reflecting the frequent occurrence of past disturbance and stress events. A larger part of the dry-forest community consists of shrubs, which also tend to be better resprouters than large-sized tree species (Bellingham and Sparrow 2000).

Clipped plants realized faster growth than control plants for 40 out of the 84 taxa, thus compensating for the lost height and leaf area (Appendix A). According to the functional equilibrium hypothesis of Brouwer (1963), plants invest in those organs that capture the resource that is in limiting supply. Light is clearly a limiting resource for clipped plants that lack a crown, and clipped plants vigorously resprout and make new leaves to restore the balance between resource capture potential of the shoot–root system (Zeng 2003). This leads to the paradoxical situation that clipped plants with initially no photosynthesizing tissue grow faster than control plants, even after two years (Fig. 1b). This "compensatory growth" is possible through the mobilization of carbohydrate reserves stored in the root and stem. Van Nieuwstadt (2002) distinguished two different phases in the development of new shoots. In the first phase, lasting 3–5 months, sprout height growth is fast and totally dependent on carbohydrate reserves, because photosynthesizing tissue is minimal and new leaves are still being formed and expanding. In the second phase, sprout height growth is much slower because green leaves provide most of the photosynthates and few reserves are mobilized. In the second phase, the growth of clipped plants might remain faster than that of control plants because the old crown with old, shade-grown leaves is replaced with young light-grown leaves that are physiologically more active (Anten and Ackerly 2001) and supported by a relatively large root system. The growth rate advantage of clipped saplings is therefore largest shortly after clipping, but is likely to decline in the course of time. This is reflected in our data on cumulative height growth, with the largest changes in growth differences realized in the first few months after clipping (Fig. 1b).

Species performance vs. juvenile crown exposure, and its consequences for the growth–survival trade-off

In both forests the performance of control plants was closely related to the regeneration light requirements of

the species, in which survival was highest for shade-tolerant species with a low CE_{juv} (Fig. 2a, b), and growth was highest for light-demanding species with a high CE_{juv} (Fig. 2e, f). This growth–survival trade-off may therefore underlie species partitioning of the light gradient, thus contributing to species coexistence (Kitajima 1994, Kobe et al. 1995, Walters and Reich 1996, Baraloto et al. 2005). Interestingly, the trade-off between growth and survival was much stronger in the moist forest ($r = -0.72$, $P < 0.001$, $N = 49$) than in the dry forest ($r = -0.52$, $P = 0.001$, $N = 35$). Similarly, the association between survival and regeneration light requirements was much stronger in the moist than in the dry forest (Fig. 2a, b). In combination, this suggests that light gradient partitioning is much more important in wetter forests that cast a deeper shade, compared to drier forests with a (seasonally) more open canopy (cf. Poorter 2009, Lebrija-Trejos et al. 2010). In contrast, other factors may be more important for species coexistence in drier forests, such as the ability to tolerate drought, fire, or heat load (Valladares and Niinemets 2008).

Species-specific growth and survival rates of clipped and control plants were strongly correlated (Appendix B). This indicates that there is little crossover in species rank performance due to damage, and that good survivors tend to be always good survivors, and fast growers tend to be always fast growers (cf. Myers and Kitajima 2007). Stem clipping led to larger interspecific variation in survival rates, and therefore to steeper relationships with regeneration light requirements compared to those of control plants (Fig. 2a, b). However, stem clipping in the moist forest tended to diminish interspecific variation in growth rate, resulting in less tight relationships with regeneration light requirements. As a consequence of these opposite trends, the growth–survival trade-off of clipped plants was similar ($r_{dry} = -0.54$, $P = 0.001$, $N = 36$) or weaker ($r_{moist} = -0.34$, $P = 0.020$, $N = 48$) compared to control plants.

The difference between the performance of clipped and control plants indicates how sensitive species are to clipping. Light-demanding species suffered more from damage then shade-tolerant species, more strongly so in the moist than in the dry forest, and more strongly so in terms of survival than in terms of growth (Fig. 2a, b, e, f). Similarly, in a Panamanian moist forest, Myers and Kitajima (2007) found that light-demanding tree species were also much more sensitive to disturbance (defoliation) and stress (temporal light deprivation) than shade-tolerant tree species, and Lasso et al. (2009) found that within the genus *Piper*, light-demanding shrub species were less able to resprout from shoot fragments than shade-tolerant shrub species. Ickes et al. (2003) found in a Malaysian rain forest that canopy species had the highest mortality after stem snapping, and understory species the lowest mortality. It is likely that the canopy species are more light-demanding than the understory species (Poorter et al. 2003), which supports the results of the current study that light-demanding species suffer most from stem damage. Low carbohydrate reserves may constrain light-demanding species from meeting their energy demands during periods of net negative carbon balance (Myers and Kitajima 2007, Poorter and Kitajima 2007), and from producing new shoots and leaves (see *Species performance vs. carbohydrate reserves*). Damaged plants may also die from fungal and pathogen attack because of their exposed unprotected tissues and reduced vigor (Romero and Bolker 2008), and it is especially the light-demanding species that are sensitive to these disease agents (McCarthy-Neumann and Kobe 2008). Light-demanding species might also be more sensitive to a setback in height. Putz and Brokaw (1989) noted that many pioneer species coppice readily in clearings made by farmers, but rarely do so in a forest environment. The height loss places them at a disadvantage in the highly competitive environment of treefall gaps. This might explain the paradoxical situation that light-demanding species not only die faster, but also grow faster after clipping compared to shade-tolerant species (Fig. 2c, d). Light-demanding species should grow faster in their race for the canopy, because otherwise they will lag behind their neighbors and eventually die. This is also reflected in the leaf area recovery; after one year light-demanding species have already recovered their initial leaf area, whereas shade-tolerants are still recuperating from the damage (Fig. 3c, d).

Species performance vs. carbohydrate reserves

We hypothesized that survival and growth of plants should be positively related to the carbohydrate reserves of the species, especially so for the clipped, crownless plants that need reserves to meet respirational demands, repair damaged tissue, and make new sprouts. Such a positive relationship was indeed found in both forests for the survival phenomenon (Fig. 4a, b), but not for growth (Fig. 4c, d). Most of our knowledge on carbohydrate reserves comes from within-species responses to disturbance, and surprisingly few comparative experiments have been carried out across species on the role of carbohydrate reserves for survival in the field. Myers and Kitajima (2007) found, in a comparative experiment with seven rain forest tree species in Panama, that carbohydrate reserves enhanced survival of control seedlings, defoliated seedlings, and deeply shaded seedlings growing in the forest understory. For four temperate deciduous forest species, Canham et al. (1999) found a positive relationship between overwinter seedling survival and carbohydrate reserves in the previous fall, without a clear relationship between carbohydrate reserves and shade tolerance per se. However, in their analysis they pooled different species and treatments, so it is not clear whether this relationship was due to within- or cross-species effects.

In our study, sugar was a better predictor of species survival than starch or total NSC's, but the underlying

reason is not clear. Maybe sugar is a more readily available and easily mobilized resource than starch. Alternatively, perhaps not all stored starch is available to the plant, as suggested by repeated defoliation experiments with the same plants, in which carbohydrate reserves never drop below a certain level (e.g., 12% NSC [McPherson and Williams 1998]). In our study, also, carbohydrate pool size was a better predictor than carbohydrate concentrations, in line with the findings of other studies (Canham et al. 1999, Myers and Kitajima 2007). The amount of reserves available for maintenance and repair depends to a larger extent on the size of the storage organs than the carbohydrate concentrations in those organs (Canham et al. 1999), and many species adapted to aboveground disturbance have large, well-protected belowground storage organs such as taproots (Paz 2003) or lignotubers (Del Tredici 2001). This may also explain why in our study the relationship between carbohydrate reserves and survival was weaker than expected, because pool sizes were calculated for the remaining aboveground stem section only. In fire-prone savanna systems, for example, carbohydrate concentrations are higher in the root than in the stem (Hoffmann et al. 2003), although the reverse has been observed for moist-forest seedlings (Myers and Kitajima 2007). A more important confounding factor is the large interspecific variation in root mass. For example, field-grown seedlings of our study species may vary fourfold in their seedling biomass fraction in roots (16–64% [Markesteijn and Poorter 2009]). On the other hand, Myers and Kitajima found for first-year seedlings that across species, the TNC pool size in stems was highly correlated with TNC pool size in roots.

In both forests, height growth rate of control plants was negatively related to carbohydrate reserves (Fig. 4c, d). Likewise, height growth rates of clipped plants, which initially totally depend on stored carbohydrates for resprouting, was also negatively (although not significantly) related to carbohydrate reserves, in contrast to the third hypothesis. It is therefore likely that growth and carbohydrates are correlated because they are part of the same life history syndrome (Poorter and Kitajima 2007): light-demanding species that tend to grow very fast also tend to invest little carbon in reserves. Although in the first phase of resprouting they depend on the few reserves they have for resprouting, in the second phase they can continue to grow very fast because of the inherently high assimilation rates of their leaves (Poorter and Bongers 2006).

Time course of survival-trait correlations

Most species responded within 4–12 months to the clipping treatment (Fig. 1c, d), after which the clipping effect persisted over time. Similarly, the relationships between species traits and plant performance were established in the first half-year, after which they remained constant (Fig. 5). These results suggest that one year is a sufficient time window to evaluate the effects of clipping, and that those effects will persist over time. Other studies also have shown that long-term survival is lower for damaged compared to undamaged plants. In Borneo, 67% of the resprouting saplings survived after 3 years, compared to 91% of the undamaged saplings (Ickes et al. 2003). In Panama, 63% of the resprouting poles survived after five years, compared to 89% for the undamaged poles (Paciorek et al. 2000). The mortality rate of resprouted individuals therefore declines with time, but continues to be elevated, up to 10 years after resprouting (Paciorek et al. 2001).

Of all traits evaluated, CE_{juv} was the best predictor of survival after clipping (Fig. 5), probably because it reflects the life history strategy of the species. Shade-tolerant species (with low CE_{juv}) possess a whole suite of co-evolved traits that all enhance plant survival. Wood density is the second best predictor of survival after clipping. This can be for mechanistic reasons, as species with high wood density tend to have low water content (Poorter 2008) and small vessel diameters that can impede fungal spread and pathogen activity, thus compartmentalizing and reducing xylem decay after stem damage (Romero and Bolker 2008), and enhancing plant survival (Loehle 1988). Alternatively, this can be for life history reasons, as wood density is a good indicator of the shade tolerance of species (Van Gelder et al. 2006). Alvarez-Clare and Kitajima (2007, 2009) found that high wood density of shade-tolerant species is associated with biomechanical strength of their seedling stems, which does not decrease the probability of being damaged by litterfall and browsing animals, but instead, reduces the mortality following damage. Interestingly, wood density is emerging as a core plant functional trait (Curtis and Ackerly 2008), not only because of its apparent role in preventing (Van Gelder et al. 2006) or tolerating (Zimmerman et al. 1994; this study) plant damage and disease, but also because it affects the stability, architecture, drought tolerance, hydraulic conductance, carbon gain, and growth of trees (Curtis and Ackerly 2008).

Morphological traits determine resprouting behavior

Sprout number and leaf number decreased, and the total plant leaf area increased, with leaf mass (Fig. 6), in line with the fourth hypothesis. The strength of this relationship is underscored by the fact that dry- and moist-forest species show exactly the same relationship with leaf mass. For a given amount of leaf biomass, species can only produce a few large leaves or many small ones. Similar patterns were found for resprouting Bornean tree species (Van Nieuwstadt 2002): species with heavy leaves produced few sprouts, and those sprouts were relatively thick, to support the mass of the heavy leaves. Therefore, biomass allocation constraints (Kleiman and Aarssen 2007) and biomechanical and hydraulic constraints (Poorter and Rozendaal 2008) may give rise to the observed trade-off between leaf size

and leaf number. Kleiman and Aarssen (2007) suggested that there is a premium to small leaf size, because it not only implies many leaves (cf. Fig. 6b), but also many lateral buds, and hence, the opportunity to replace shoots lost to browsers or physical damage, which is indeed what we found (Fig. 6a). In contrast, the premium of a large leaf size is a large total sapling leaf area (Fig. 6c).

Conclusions

Resprouting is an important persistence strategy in dry and moist tropical forest trees; virtually all saplings resprouted readily after stem damage, although dry-forest species realized, on average, a better survival and growth after stem damage compared to moist-forest species. Loehle (2000) considered resprouting a dimension that critically affects species persistence in addition to shade tolerance and adult stature. Our results suggest that resprouting capacity, like wood density, is not so much a different dimension, as one that is associated with shade tolerance. Shade-tolerant species were better at resprouting than light-demanding species in the moist forest. This resprouting ability is an important prerequisite for successful regeneration in the shaded understory, where saplings frequently suffer from damage by falling debris (Clark and Clark 1991). Survival after stem damage was only modestly related to stem reserves, and much more strongly related to wood density, possibly because a high wood density enables plants to resist fungi and pathogens, and reduce stem decay. A high resprouting ability, investments in stem defense, and storage reserves appear to be part of a suite of co-evolved traits that underlies the growth–survival trade-off, and contributes to light gradient partitioning and species coexistence. These links with shade tolerance are especially important in the moist evergreen forest, which casts a deep, more persistent shade, but tend to diminish in dry deciduous forest where light is a less limiting resource, and species sort out along drought and fire gradients.

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APPENDIX A

Overview of the dry- and moist-forest species included in this study with their juvenile crown exposure (CE_{juv}) and mean survival (%) and growth (cm) of control and clipped plants approximately one year (13 months) after the start of the experiment (*Ecological Archives* E091-187-A1).

APPENDIX B

First-year performance of clipped vs. control plants for moist-forest and dry-forest species (*Ecological Archives* E091-187-A2).

APPENDIX C

Relation between species survival and log-transformed height growth one year after clipping, and regeneration light requirements (CE_{juv}), carbohydrate reserves (concentrations and pool sizes of sugar, starch, and nonstructural carbohydrates [NSC]), and wood density (*Ecological Archives* E091-187-A3).

APPENDIX D

Bivariate associations between species traits of moist-forest and dry-forest tree species as analyzed with regular cross-species correlations (r_{cross}) and phylogenetic (r_{phylo}) correlations (*Ecological Archives* E091-187-A4).