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SHORT COMMUNICATIONS

Physical Damage in Relation to Carbon Allocation Strategies of Tropical Forest Tree Saplings[1]

ABSTRACT

We show that tropical forest tree saplings with greater belowground carbon allocation have more breakage scars along their stems. We suggest the existence of alternative carbon allocation strategies in relation to physical damage in the forest understorey. "Tolerators" allocate more belowground, have enhanced resprouting ability and slower aboveground growth, whereas "escapers" allocate less belowground, are not well prepared for recovering from damage, but grow fast enough to escape from the damage-susceptible size class.

RESUMEN

Brinzales de árboles tropicales que asignan mayor cantidad de carbono bajo el suelo muestran más cicatrices de fractura en sus tallos. Sugerimos la existencia de estrategias alternativas de asignación de carbono en respuesta a daño físico en el sotobosque: los "tolerantes" asignan mayor cantidad de carbono bajo el suelo, tienen mayor capacidad para rebrotar y su crecimiento aéreo es lento; los "escapistas" asignan menor cantidad de carbono bajo el suelo y no están bien preparados para recuperarse después de ocurrido un daño, pero crecen lo suficientemente rápido para escapar de la clase diamétrica más susceptible a daños.

Key words: *disturbance; forest dynamics; forest regeneration; La Selva; resprouting; root: shoot ratio; sprouting.*

In communities where plants experience high levels of physical damage from fires or large herbivores, plant survival is enhanced by large root systems with belowground carbon storage (Bell 1996, Bell & Ojeda 1999, Bellingham 2000, Bond & Midgley 2001). Plants draw on these belowground carbon stores when they recover from physical damage by resprouting (Chapin *et al.* 1990). However, belowground allocation to large root systems and other storage organs is traded off against aboveground allocation (Mooney 1972). Thus, alternative strategies arise for dealing with high levels of physical damage. At one extreme plants allocate resources to belowground organs, enabling them to tolerate repeated damage by resprouting, *e.g.* lignotubers, bulbs and large root systems. At the other extreme plants allocate resources to aboveground structures, enabling them to escape physical damage, *e.g.* tall and sturdy stems, protective bark or reproductive output (Keeley & Zedler 1978, Bond & Van Wilgen 1996, Gignoux *et al.* 1997, Bellingham 2000, Bond & Midgley 2001).

In tropical rainforests, where disturbance is a less obvious ecological factor, the relationship between belowground allocation and physical damage has received little attention. Nevertheless, the stems of tree saplings in the understorey of tropical forests sustain frequent physical damage via branches falling from the canopy or via the activity of large vertebrates (Aide 1987; Clark & Clark 1989, 1991; Paciorek *et al.* 2000; Scariot 2000; Drake & Pratt 2001). This damage is more frequent within the smaller size classes of saplings (Clark & Clark 1991). Physical damage is an important source of mortality among saplings, but many survive by resprouting a new stem from immediately below the point of breakage and continue growth as a single stem. An enduring scar remains as evidence of past damage (Clark & Clark 1991).

Here, we applied well established ideas in the ecological literature on disturbance-prone systems to the understanding of tropical rainforest ecology. We hypothesized that greater belowground allocation among forest saplings will (1) enhance resprouting ability and thus survivorship after physical damage; and (2) decrease growth rate, such that sapling species with greater belowground allocation will spend a longer period of time in the damage susceptible size class. On the basis of these two hypothesized mechanisms we predicted that saplings with larger root:shoot ratios will have more evidence of physical damage in the form of stem scars.

To test this prediction, we selected eight common tree species (Table 1) in old-growth, selectively

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TABLE 1. *Number of individuals used for calculating the average number of breakage scars and for calculating root:shoot ratio.*

Species[b]	*N* (scar assessment)	*N* (root:shoot ratio)	Code[a]
Brosimum sp.	54	8	BRO
Guarea bullata	12	3	GAU
Naucleopsis sp.	25	4	NAU
Pentaclethra macroloba	25	6	PEN
Pourouma minor	13	6	POU
Symphonia globulifera	16	4	SYM
Trophis sp.	39	5	TRO
Virola sebifera	16	4	VIR

[a] Codes refer to Fig. 1.
[b] Voucher specimens are deposited in the La Selva herbarium.

logged, lowland tropical wet forest at the La Selva Biological Station, Costa Rica (McDade *et al.* 1994). An area of approximately 2 ha was systematically searched for all individuals of the study species between 0.9 and 2.5 m in height. Trees in this size class suffer high levels of physical damage to their stems, and also show the greatest interspecific differences in damage frequency (Clark & Clark 1991). We only used individuals under a closed canopy, because we expected that fewer branches fall in canopy gaps.

We counted the number of breakage scars only along the main stem of each sapling. Evidence of a snapped and re-grown stem included either: (1) a change in the angle of the stem of greater than 10°; or (2) a swelling and an abrupt discontinuity (*sensu* Clark & Clark 1991) of at least 10 percent in stem diameter. Stem scars of this nature have been clearly demonstrated to result primarily from damage caused by falling woody debris (Clark & Clark 1991), but the possibility that some scars may have been caused by dieback following drought could not be ruled out.

Root:shoot ratios were determined for each species using only those individuals that had no breakage scars. In cases where too few undamaged individuals of a species were found in the 2 ha sampling area, additional undamaged saplings were located nearby where the forest structure, light environment, topology, and edaphic factors were similar. Sample sizes are listed in Table 1. Root biomass was determined by excavating and washing all belowground plant parts with a diameter > 3 mm. Roots finer than 3 mm were excluded because they could not be excavated accurately. Both roots and shoots (all aboveground parts excluding leaves and petioles) were oven dried for 48 hours at 70°C before being weighed.

The mean number of breakage scars for a species increased with average root:shoot ratio (Fig. 1). We interpret this finding as preliminary evidence for the existence of alternative strategies among forest saplings in their response to physical damage. "Tolerators" allocate a larger proportion of resources belowground; they have enhanced resprouting ability and/or slower aboveground growth. "Escapers" allocate a smaller proportion of resources belowground; they are less well prepared for recovering from damage, but grow fast enough to escape from the damage susceptible size class. "Escapers" might further improve their chances of escape by investing in sturdy stems (Guariguata 1998, Kennard 1998).

The observed difference in the number of breakage scars between "tolerators" and "escapers" is not an artifact of a difference in the height of samplings sampled in each group. In fact, the slightly greater mean height of samplings in the "escaper" sample ($\bar{x}$ = 166.8 cm; range = 100–250 cm) compared with the "tolerator" sample ($\bar{x}$ = 154.9 cm; range = 90–260 cm) will bias the results in the direction opposite to that predicted by the hypothesis tested here, because, all else being equal, longer stems will accumulate more breaks.

We were not able to assess the relative importance of growth rate and resprouting differences in explaining the observed results. This question could be addressed by monitoring resprouting after experimentally induced physical damage and by directly measuring growth rates. At least one study has shown that root:shoot ratio is negatively correlated with growth rate (Kitajima 1994). This study also showed that root:shoot ratio is positively correlated with shade tolerance. It would be interesting to know whether large root:shoot ratios enhance the shade tolerance of forest saplings by enhancing survival after physical damage.

In a related study Peters *et al.* (2004) found that species-specific differences in branch (or frond)

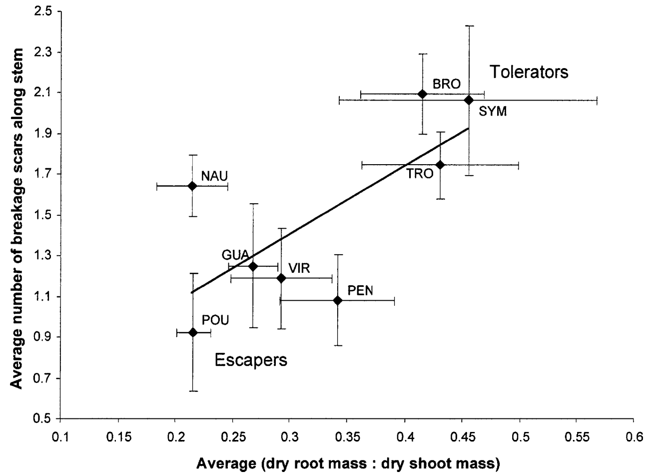

FIGURE 1. Relationship across species between relative belowground biomass allocation and the number of breakage scars along the length of the stem. Bars indicate SE; sample sizes and species codes are given in Table 1. Pearson's product-moment correlation coefficient (r) = 0.72, $P < 0.05$, $N = 8$.

dropping rates among canopy tree species resulted in a patchwork of recruiting environments across a forest. The observations reported here suggest the intriguing possibility that differences in the carbon allocation strategies of saplings to above vs. belowground parts may allow tree species co-existence in this patchy environment, because escapers will be favoured in areas with infrequent branch-fall, while tolerators will be favoured where the branch-fall rate is high.

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