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SHORT COMMUNICATION

A new case of neotropical monodominant forest: *Spirotropis longifolia* (Leguminosae-Papilionoideae) in French Guiana

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The main interest in studying monodominant forests in the tropics (i.e. single-dominant forest *sensu* Richards 1996 and Connell & Lowman 1989) is that processes leading to monodominance may highlight mechanisms controlling species diversity (Hart *et al.* 1989). Among the various cases of monodominant forest (Hart 1990), the most intriguing are the rare ones that stand in contact with a considerably more diverse forest, without apparent environmental boundaries, and for many generations (i.e. type I *sensu* Connell & Lowman 1989). Rather than a single mechanism, it is likely that this type of monodominance results from a suite of interacting traits (Torti *et al.* 2001). This has been well illustrated for the neotropical tree *Dicymbe corymbosa* whose monodominance relies on: (1) ectomycorrhizal symbiosis (Henkel *et al.* 2002) linked to (2) mast fruiting (Henkel *et al.* 2005), (3) high seedling survival rate (Henkel *et al.* 2005, McGuire 2007a, 2007b) and, potentially, (4) slow litter decomposition (Mayor & Henkel 2006, McGuire *et al.* 2010), moreover, (5) the reiterative habit of *D. corymbosa* slows the gap dynamics, and reduces species richness (Woolley *et al.* 2008). Thus, a comprehensive understanding of monodominance may only emerge from the comparison of many case studies to point out shared mechanisms. Here, we report a new case of a monodominant species: *Spirotropis longifolia* (DC.) Baill.

Spirotropis longifolia is endemic to the Guiana Shield, ranging from Bolivár (Venezuela) to French Guiana (Stirton & Aymard 1999). We recorded only 30 collections in major herbaria (NY, U, CAY, P), most of them from French Guiana. The western Guiana Shield is known to hold several monodominant forests (Davis & Richards 1934, Henkel 2003, Richards 1996). However, the dominance of *S. longifolia* has never been investigated nor reported.

Only 16 French Guianan sites are known to host *S. longifolia*. We prospected eight of them and selected the two most accessible to evaluate *S. longifolia* dominance: a 20-ha population at Piste de Saint-Élie (PSE: 5°16′36″N, 53°3′0.5″W), and a 7-ha one at Montagne des Chevaux (MDC: 4°42′47″N, 52°23′41″W).

We set three 1-ha plots on upland areas at each site, two in forest dominated by *S. longifolia* (Ps1, Ps2 at PSE ; Cs1, Cs2 at MDC) and one on adjacent mixed forest (Pm1 at PSE; Cm1 at MDC). We censused all living trees with trunk $\geq$10 cm in diameter at 130 cm above the ground (dbh). As most *S. longifolia* individuals produce basal sprouts, we pooled all stems $\geq$ 10 cm in dbh to calculate the basal area of each individual. We also counted the number of shoots with 5 cm $\leq$ dbh $\leq$ 10 cm, and evaluated the number of thinner sprouts. Soils characterization followed Lescure & Boulet (1983). In order to evaluate the dominance of *S. longifolia* in the recruitment pool, we censused all individuals $\geq$ 2 cm in dbh on eight 20 × 20-m plots, five of them within Ps1 (Ps1-subplot). Individuals were most often identified to species or at least assigned to genus or family. Finally, we evaluated the mycorrhizal status of six *S. longifolia* sampled at PSE. Fine roots and mycorrhizas were cleared and stained according to the method described by Kormanik & McGraw (1982).

In all sites, *S. longifolia* was present from hilltops to marshy bottomlands, and always aggregated.

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Table 1. Species richness, diversity and forest structure, for trees ≥ 10 cm in dbh, on 1-ha plots of *Spirotropis longifolia*-dominated forest (Ps1, Ps2, Cs1, Cs2) and mixed forest (Pm1, Cm1) at Piste de Saint-Élie (PSE) and Montagne des Chevaux (MDC) sites. R: species richness; α: Fisher's alpha diversity index; D: plot density (ind. ha^{-1}); G: basal area (m^2 ha^{-1}); DSl: plot density of *S. longifolia* (ind. ha^{-1}); relative abundance (%) of *S. longifolia*, as % ind: among all individuals, % stems: among all stems and % G: of basal area; % sprouting: proportion of sprouting *S. longifolia* for three sprout diameter limits (%); % persistent: proportion of *S. longifolia* with at least one dead stem.

										% sprouting			
Site	Plot	R	α	D	G	DSl	% ind	% stems	% G	all	≥ 5 cm	≥ 10 cm	% persistent
PSE	Ps1	84	28.6	511	33.0	322	63	65	60	40	18	5	4
	Ps2	83	28.4	500	28.9	280	56	58	56	61	23	10	5
	Pm1	180	101	506	25.2	–	–	–	–	–	–	–	–
MDC	Cs1	63	18.9	508	20.8	376	74	76	67	68	31	12	14
	Cs2	90	30.4	557	26.6	360	65	68	53	80	38	12	9
	Cm1	123	42.7	714	32.0	–	–	–	–	–	–	–	–

Populations covered areas ranging from 0.5 ha to hundreds of hectares, in which dominance varied from 20% to 70% of stems ≥ 10 cm in dbh (data not shown).

At PSE, topography and soil-cover of the whole *S. longifolia* stand matched the last stage of transformation of a ferralitic cover on schist, as described by Sabatier *et al.* (1997). At MDC, erosion of the sandstone bedrock (quartzite) produced steep slopes, on which top soil (30 cm depth) was sandy. In spite of their differences in bedrock, topography and soil thickness, the two sites shared thin, superficially drained, hydromorphic soils. Soils of the mixed-forest plots did not differ from those of their neighbouring dominated plots.

In our plots, *S. longifolia* exceeded 50% of stems and/or basal area for trees ≥ 10 cm in dbh (Table 1), the standard threshold of monodominance proposed by Connell & Lowman (1989). In Ps1-subplot, *S. longifolia* accounted for 35% of the recruitment pool. Furthermore, we found a significant positive relationship between the relative abundances of *S. longifolia* trees (dbh ≥ 10 cm) and its own recruitment pool in our 20 × 20-m plots (Pearson $r = 0.79$, $P < 0.01$). Tree species richness and diversity were high in mixed-forest plots and considerably lower in dominated plots (Table 1).

In the eight prospected sites, *S. longifolia* was always found as a low-stature tree, 20–25(–30) m high with a maximum observed dbh of 75 cm. Within our plots, 40–80% of *S. longifolia* trees produced collar sprouts (Table 1), and 18–38% had at least one reiterated trunk ≥5 cm in dbh (Table 1, Figure 1a). On Cs1 and Cs2 we estimated that for 10% and 30% of *S. longifolia* individuals, respectively, the dead main stem has been replaced by one or more reiterated trunks (Table 1). Sprout production was concomitant to the proliferation of basal adventitious roots of two kinds: (1) dense mound of roots, often disconnected from the ground, able to accumulate organic matter and (2) strong arching stilt roots that stabilized the clumps (Figure 1a).

At all stages of development, uprooted *S. longifolia* were able to layer, i.e. to produce sprouts, able to become autonomous, along prostrate or fallen stems (Koop 1987) (Figure 1b, c). Layers grew all along the fallen stems and often remained connected to each other, sharing multiple root systems (Figure 1b). On Cs1 and Cs2, respectively 5% and 11% of *S. longifolia* ≥ 10 cm in dbh were identified as layers. These figures are conservative estimates, since signs of layering disappear with time (Figure 1c). Roots of *S. longifolia* hosted arbuscular mycorrhizas but we did not find evidence of ectomycorrhizas.

Together with *Pterocarpus officinalis*, which dominates the rear mangrove swamp (Migeot & Imbert 2011), *S. longifolia* is one of the rare Papilionoideae forming monodominant stands in tropical forests. Although absent from deep, freely draining soils, it showed a wide environmental amplitude. Surrounding species-rich forests (Table 1) were similar in diversity to those observed elsewhere in the Guiana Shield (ter Steege *et al.* 2000) and on the same soils at PSE (D. Sabatier, unpubl. data). Yet, *S. longifolia*-dominated forests were relatively species-rich (Table 1). Thus, its monodominance seems to result neither from peculiar environmental conditions nor from a lack of competitors.

Our results emphasized that *S. longifolia* recruits beneath its own canopy. Indeed, as for some other monodominant species (Hart 1985, Henkel *et al.* 2005), *S. longifolia* seeds are dispersed autochorously, less than 10 m from the parent tree. Moreover, seeds germinate within 2 d (pers. obs.) thus post-dispersal movement is limited. This set of life traits places *S. longifolia* among the Type I monodominant species (Connell & Lowman 1989).

Through layering, *S. longifolia* is also able to reproduce and propagate vegetatively. Layering does not only allow the survival of the genet, but also its spread in the understorey, increasing the relative abundance of the species in the recruitment pool (Gavin & Peart 1999). Moreover, in case of tree uprooting, layering species may pre-empt the recruitment niche, not only at the stump, but also all along the fallen stem (Negrelle 1995). As basal sprouts do, young layers benefit from larger resources than seedlings and saplings (Dietze & Clark 2008), and

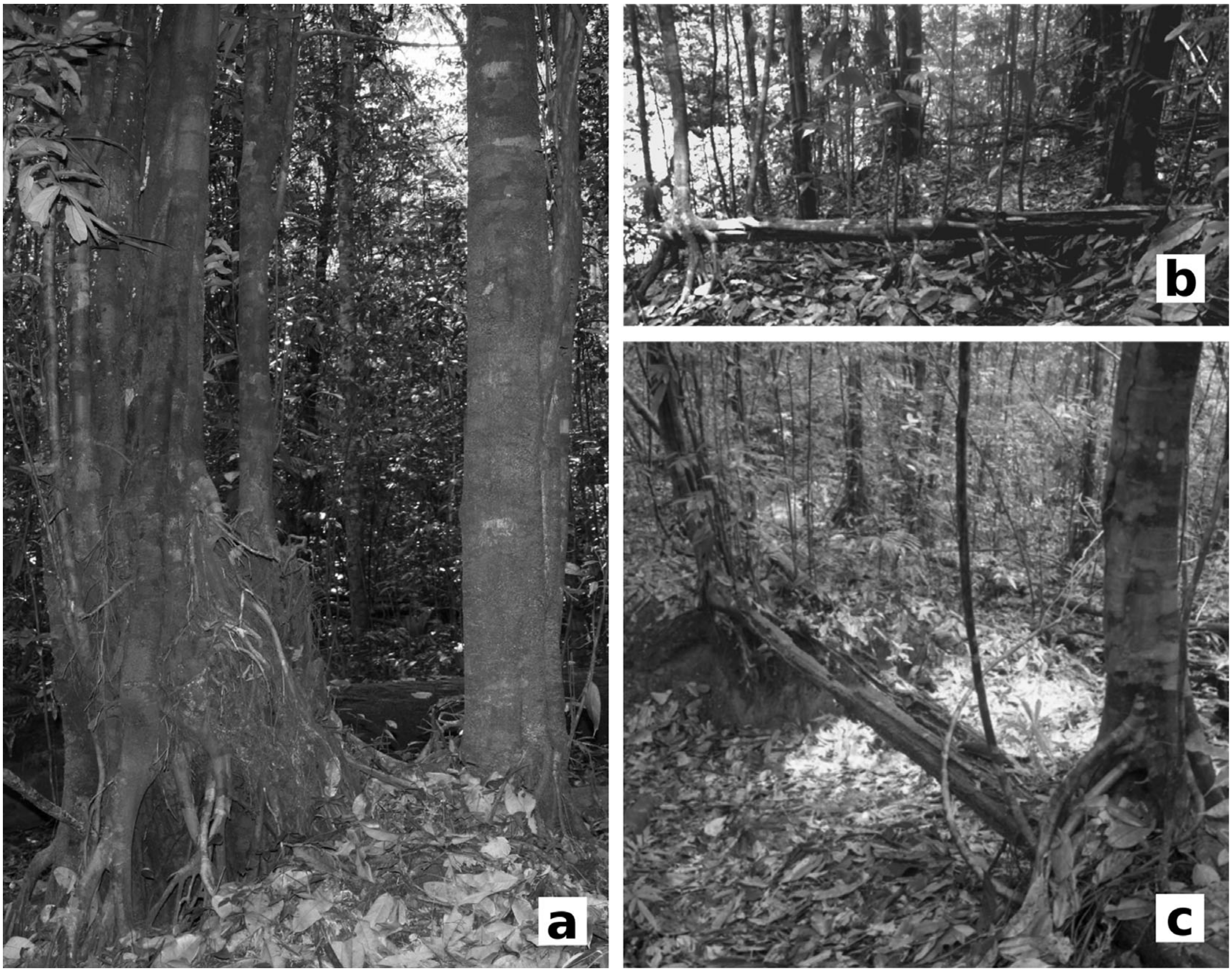

Figure 1. Sprouting abilities of *Spirotropis longifolia*. Two *S. longifolia* showing different habits; the right one was a mono-stemmed tree, the left one was a mature clump made of several reiterated trunks with small arching stilt roots and small mound of roots at its base (a). *S. longifolia* 'walking' in the forest and producing layers (b). Two large layers and their ancient connection now rotted (c). (Photographs: É. Fonty.)

may have access to an already settled root system and even to a still functional photosynthetic system (Sakai *et al.* 1997), allowing them to compete with pioneer species in gap closure (Negrelle 1995).

Bond & Midgley (2001) introduced the concept of the persistence niche (i.e. the capability of an established plant to persist in situ) and pointed out its potential impact on species richness. Indeed, by the constant rejuvenation of their stems and the stabilizing effect of their arching stilt roots, the persistence of the clumps of *Dicymbe altsonii* and *D. corymbosa* reduces the gap dynamic, thus contributing to their monodominance (Woolley *et al.* 2008, Zagt *et al.* 1997). The long-lasting ability of *S. longifolia* to form coppice clumps strongly suggests a similar efficiency to exploit a persistence niche and supports this trait as a realistic mechanism leading to monodominance. On the other hand, we found no evidence that ectomycorrhizal symbiosis could be related to the monodominance of *S. longifolia*.

Thus, *S. longifolia* monodominance seems to rest on the simultaneous use of two strategies: a supporting one (i.e. a competitive advantage for its own recruitment pool by layering) and a suppressive one (i.e. a depletion of the recruitment opportunities of the other species through the persistence niche). However, the relative advantages of these strategies for *S. longifolia* remain to be evaluated. Meanwhile, we suggest that both strategies are not limited to monodominant species and should be better taken into account to explain the variations in alpha diversity observed in tropical rain forests.

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